The Crayfishes of Georgia

HORTON H. HOBBS, JR.

SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY • NUMBER 318

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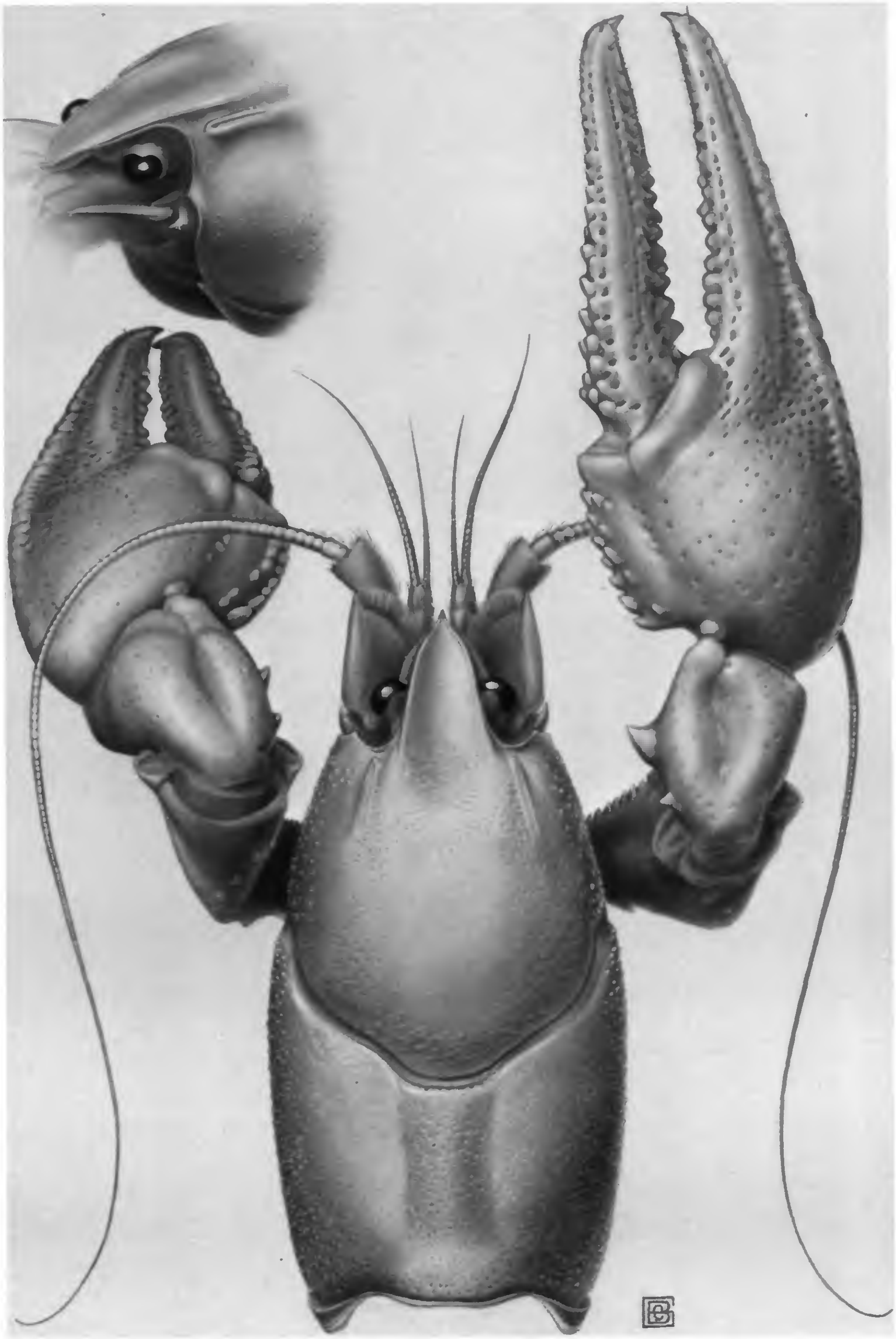

FRONTISPIECE.—*Cambarus (Puncticambarus) hiwasseensis*: Dorsal view of carapace and chelipeds of holotype; left cheliped depicted as mirrored image of right one (regenerated appendage in specimen). Upper left, cephalosinistral view of cephalothoracic region.

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ABSTRACT

Hobbs, Horton H., Jr. The Crayfishes of Georgia. *Smithsonian Contributions to Zoology*, number 318, 549 pages, 262 figures, 3 tables, 1981.—Sixty-six species and subspecies, 18 of which are endemic, comprise the crayfish fauna of Georgia: the genera *Cambarus* represented by 33, *Fallicambarus* and *Faxonella* by 1 each, *Orconectes* by 3, and *Procambarus* by 28. Of these, 19 are described as new: *Cambarus (Depressicambarus) harti*, *C. (D.) reflexus*, *C. (D.) strigosus*, *C. (D.) truncatus*, *C. (Hiaticambarus) coosawattae*, *C. (H.) fasciatus*, *C. (H.) manningi*, *C. (H.) speciosus*, *C. (Lacunicambarus) acanthura*, *C. (Puncticambarus) coosae*, *C. (P.) georgiae*, *C. (P.) hiwasseensis* *C. (P.) parrishi*, *C. (P.) scotti*, *Procambarus (Distocambarus) devexus*, *P. (Hagenides) caritus*, *P. (H.) talpoides*, *P. (Leconticambarus) pubischelae deficiens*, and *P. (Pennides) petersi*. The subgenus *Distocambarus* is the only new supraspecific taxon proposed. Brief accounts of previous work on the Georgia crayfish fauna, physiographic regions, and drainage systems precede a more detailed discussion of habitats and the crayfishes frequenting them. This is followed by postulates of the affinities and distribution of the extant crayfishes and their ancestors in space and geologic time. Keys are provided for identification of the genera, subgenera, and species. The systematic section consists of synonyms for the genera, subgenera, species, and subspecies. The supraspecific categories are diagnosed, their ranges defined, and the numbers of species and a summary statement of the habitats occupied by them are included. A complete synonomy is presented for each species and subspecies, and for most there is also a complete bibliography; this is followed by a summary of previous reports of the species in Georgia, a diagnosis (and descriptions of new and several previously described species), statements concerning location of types, type-locality, range, specimens examined, variations, ecological and life history data, a list of crayfish associates, and, for new taxa, etymological notes. One of the two appendices consists of a summary of the distribution of the crayfishes in the 159 counties in the state, and the other consists of a list of the crayfishes and the symbionts parasitizing or infesting them. Members of the genera *Cambarus* and *Orconectes* are concentrated in upland sections of the state, whereas those of *Procambarus* are more abundant in the coastal plain and lower piedmont. With few exceptions, representatives of the other genera are largely restricted to the latter. The numbers of species and subspecies occurring in the major drainage basins are as follows: Altamaha 22, Aucilla 1, Chattahoochee 14, Chattooga 9, Coosa 15, Flint 14, Hiwassee 7, Little Tennessee 2, Newport 6, Ochlockonee 3, Ogeechee 16, Saint Marys 7, Satilla 10, Savannah 20, Suwannee 8, Tallapoosa 6, and Tennessee 12. Illustrations include generalized morphological features, habitats, dendrograms postulating affinities, sketches depicting color patterns, morphological characters of each species, and maps noting the localities from which each has been collected.

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Contents

The Crayfishes of Georgia

Horton H. Hobbs, Jr.

Introduction

It is a coincidence that the preparation of this contribution toward a knowledge of the crayfishes of Georgia is being completed 100 years after an expression of interest in crayfishes by Joseph Henry (1878), the first Secretary of the Smithsonian Institution. In a circular of inquiry "relative to the Natural History of the American Crawfish and other Fresh Water Crustacea," he wrote as follows:

Smithsonian Institution
Washington, D.C., March 1, 1878

The Smithsonian Institution desires to call attention to the importance of securing for the National Museum full series of the Crawfish and other fresh-water Crustacea of North America.

Recognizing the fact that the agency of man has already exterminated forms which once inhabited the streams and fresh-water basins of the eastern side of the continent, it perceives the necessity for speedy preparation to secure the species belonging to the various faunal areas before they are forever lost to science.

Many facts have recently been added to the recorded history of the Crawfishes which enable a more exact position to be taken with regard to their origin and affinities. Many more observations, however, will be needed to fill out their history; and every fact bearing upon the subject will be of interest and value.

The student can no longer be satisfied with a bare designation of the species, but he must admit that each stage of growth has its meaning, and that so has every step in physical advance or divergence.

It should be remarked that the habits of a form may vary according to environment and attending circumstances. Thus in the crawfish, a species will build chimneys of mud in some localities, while it will not do so in others. At one season of the year it will wander over a wide range of surface, and at another it will remain confined within narrow limits.

Distinct species live in the mountain streams and in the springs at their sources. Some frequent the marshes of the lowlands, (both the fresh and salt marshes) either near the streams, or adjacent to the bays, sounds, or ocean. Some occur beneath stones in rivers, creeks, or branches; in the muddy basins; beneath stones in the rapids; among grass and weeds in more quiet places, and in coves; under shelving grassy banks; in holes at the bottom of ponds, lakes, dams, and mill-races. Others bore holes in the meadows, or even in the hill-tops near water; and in bringing up the mud and clay from their tube-like holes, pile it as a chimney at the entrance. These species at particular times place a plug of clay in the orifice of the chimney and seal themselves in for a certain length of time.

Still others reside in the drains and mud of the rice fields and plantations of the south, and sometimes burrow through the embankments allowing the water to flood the region.

In order to secure a more full and accurate knowledge of these creatures, the Smithsonian Institution respectfully requests replies, as far as possible, to the following queries. A reference to the number will suffice in cases when it is inconvenient to write at greater length.

There are three great groups of Crawfish which may be distinguished by the difference in the shape of the front end of the head.

1. The first has the tip of the head with acute spine, and farther back with another sharp, long spine each side.

2. The second has the tip of the head acutely triangular, and usually with a minute tooth or notch each side just back of it.

3. The third has the tip of the head almost conical, with the sides a little rounded, or with the extreme tip armed with a short tooth.

Other crustacea will be found parasitic upon fishes and other aquatic creatures, some in their mouths, stomachs, or

Horton H. Hobbs, Jr., Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

intestines, or attached to their gills, or gill covers. Other kinds inhabit the shores of bays, creeks, coves, & c., beneath rubbish, or grass, or in the sand, or on the plants submerged in the waters, or even beneath stones and other matter in ponds, sometimes at great depths.

Some attack fishes, wound them, suck their blood, or devour them; while others feed upon their eggs.

Various kinds of fishes swallow crustacea, and they may be found in their stomachs.

Catfishes often cram themselves with them, and with their eggs. Their eggs form a dainty morsel for aquatic insects and other creatures.

All these creatures of whatever form or kind will be acceptable, in all their stages, from the egg to the adult. They can be sent in alcohol, or alive, as may be most convenient.

When placed in fluid, their colors and markings should be noted and sent at the same time as the specimens.

On the last page of the present circular will be found the figure of a crawfish with a separate representation of the tail, taken from the "First Book of Zoology," by Professor E. S. Morse, (D. Appleton & Co., New York.)

Answers to the queries may refer merely to the number of the questions.

Full credit will be given to all who interest themselves to send specimens and observations.

JOSEPH HENRY,
Secretary Smithsonian Institution.

QUESTIONS

1. What kinds of Crawfish live in your vicinity?
2. Have you one kind in your springs, and a different kind in the streams which run from them?
3. Do they live in holes made by themselves at the bottom of the springs?
4. If so, do other creatures live with them in these holes?
5. Are they active there, or elsewhere in winter?
6. Do the different parts of your streams yield different kinds?
7. If so, please report any differences in their habits?
8. Does one species master the other and chase it away, or exterminate it?
9. Does the kind in the springs destroy the floors or other parts of your spring houses?
10. Will you secure a few of the largest specimens you may find?
11. Are these large ones more shy and secretive than the medium sized ones?
12. The males may be known by the forked, hooked, or twisted ends of the first pair of legs on the fore part of the belly proper. Are the males or the females of any one kind more abundant?
13. At what dates do you find eggs on the belly of the female?
14. Does the male, or another female, help to place the eggs on the legs of the belly?
15. What is the size of the smallest female you have ever seen with eggs; and what of the largest?
16. Are the eggs sometimes smaller, or fewer, than at other times?
17. If a specimen loses her eggs does she lay a new set?
18. How soon after laying do the young ones hatch out?
19. How many times do they change their shell before leaving the mother?
20. How many times do they change within the year after leaving the mother?
21. Do they split the shell lengthwise, or how, in making the change?
22. Does the change so exhaust their energies as to cause them to remain inert?
23. If so, for how long a time?
24. Do they unite sexually at all times of the spring, summer, or autumn?
25. Do they ever so unite in winter?
26. Are they affected in any way at the times of changing of the moon?
27. Do the males fight among themselves for the possession of the female?
28. Does any species live in the wells of your region?
29. If so, in what kind of water?
30. Does the cold or darkness of such places deform them in any way?
31. How deep in the well do they live, and in what parts of it?
32. Do you find them in the standing water of limestone quarries?
33. Do they live in the pools of other kinds of quarries?
34. Are they found anywhere in strong limestone, iron, sulphur, or alkaline waters?
35. Does the sand or grit carried down by freshets kill or disable them?
36. Are they more numerous in some places now than they were formerly?
37. Has a new form come in and destroyed a former one?
38. What are its enemies in your vicinity?
39. How far does it distribute itself over your region, and does it leave localities to return to them again?
40. Are they nocturnal or diurnal in feeding, or traveling?
41. Does one sex differ from the other in such habits?
42. Do they destroy vegetables or other garden products in your region?
43. Do they cause dams to burst by burrowing through the embankments?
44. Do they sometimes swarm after rains, either during the day or night?
45. What fish feed on them in your vicinity?
46. Do they live singly, in pairs of the sexes, or in communities?
47. Does either sex choose the young for food?

48. Such as burrow in meadows away from water, how deep do they bore the hole? And in what kind of subsoil?
49. Do they always burrow until moisture or water is reached?
50. How long does it take to finish the burrow; stating the kind of ground?
51. Do they use the tail as a shovel to scoop out the soil?
52. How do they carry it to the surface, and how build the chimney?
53. How do they plug it from beneath?
54. How high do they build the chimney?
55. Does the winter rain wash it away and leave the hole open?
56. At what times, in what seasons, does it build chimneys?
57. In what kind of weather do they plug the chimney?
58. How long at a time does one work, and at what hours?
59. Do they select a tree and burrow beneath its roots, or carry the chamber beneath an underground stone for protection?
60. Does a single species sometimes live in the water, and at another time live in holes on the land?
61. Does it sometimes colonize beneath a stone or log in ditch or meadow on the approach of cold weather?
62. Have you more than one kind living upon the branches, or on the tops of, submerged weeds in your streams or ponds?
63. What is the greatest depth of water at which they are found?
64. Do the kinds which live on the weeds affect other kinds of places?
65. Do they generally rest with heads directed up stream?
66. At what seasons and times of day do these unite sexually?
67. How soon after this do they lay their eggs?
68. Does the male unite sexually with the female when she has eggs under her body?
69. Where does she go after being fecundated?
70. Does she feed during incubation?
71. Is she, or he, soft-shelled at the time of sexual union?
72. Please note peculiarities of spot from which your specimens are taken? And state temperature and depth of water?

Name and address of observer,

Date of statement,

Many of the questions posed are those that I have asked myself as I have assembled the collections on which this report is based. While satisfactory answers are available to some, most remain either unanswered or can be responded to provisionally or with such qualifications as to be hardly satisfactory.

Nevertheless, I am pleased that, even though 100 years have elapsed since Dr. Henry's circular was published, I am able to make this contribution to the natural history of the crayfishes of Georgia.

For a number of years it has been apparent that the richest crayfish fauna in the Americas occurs in the southeastern part of the United States. Hobbs (1972b) noted the numbers of described species and subspecies that had been reported to occur in each state, and from the southeast he listed the following: Alabama (56 + 1 questionable), Florida (49), Georgia (45), Kentucky (33 + 3 questionable), Louisiana (33), Mississippi (40 + 4 questionable), North Carolina (22 + 1 questionable), South Carolina (23 + 1 questionable), and Tennessee (52 + 2 questionable). The only subsequent listing of which I am aware is that of Bouchard (1976c), in which he recorded the presence of 60 species (two of which remain undescribed) in Alabama.

The tabulation (Table 1) of numbers of species and subspecies of crayfishes occurring in the southeastern states, having the largest crayfish faunas, is believed to be current as of 1 October 1978. These figures are provided to give the reader an appreciation of the comparative crayfish faunas in Georgia and nearby areas.

TABLE 1.—Crayfish fauna of southeastern United States: numbers of species and subspecies

States	Crayfish Genera									
	Barbicambarus	*Cambarellus*	*Cambarus*	*Fallicambarus*	*Faxonella*	*Hobbseus*	*Orconectes*	*Procambarus*	*Troglocambarus*	Totals
Alabama	—	3	20	3	1	1	11	25	—	64
Florida	—	1	5	1	1	—	—	41	1	50
Georgia	—	—	33	1	1	—	3	28	—	66
Kentucky	1	—	19	—	—	—	16	2	—	38
Louisiana	—	2	2	4	3	—	8	16	—	35
Mississippi	—	4	4	5	1	6	9	26	—	55
North Carolina	—	—	18	1	—	—	2	6	—	27
South Carolina	—	—	10	1	1	—	—	16	—	28
Tennessee	1	2	31	3	—	—	22	8	—	67

My study of the Georgia crayfishes was initiated some 43 years ago, and since that time I have endeavored to conduct personal field work in all sections of the state. Because of the diversity of habitats occupied by these animals, several collecting techniques (Hobbs, 1972b:4–6) had to be employed in each area; furthermore the apparent ranges of some species are so small (for example, those of *Cambarus (D.) harti* and *Procambarus (D.) devexus*) that in selecting localities to be investigated, consideration had to be given to drainage patterns, potential barriers, and micro- as well as macrohabitats. In choosing the latter, not only was it necessary to include all types of lentic and lotic waters but also bogs, swamps, flatwoods, and wet hillsides where the crayfishes construct burrows that descend to or near the water table. Even within a body of water in a single locality, certain crayfishes are so limited in their distribution that unless all of the microhabitats are examined, one or more species could well have been (and undoubtedly were) often overlooked. As for the burrowers, representatives of as many as four species have been obtained within a 10-square-meter area. Thus it is obvious that a meaningful survey of the fauna in a species-rich region could not have been based solely upon collections obtained through using a single technique.

To emphasize the importance of field work by an experienced collector of crayfishes, I relate the following. As late as the spring of 1977, after having collected in all of the counties of the state and being reasonably certain that I had obtained representatives of virtually all of the species that occur in Georgia, I almost literally stumbled upon specimens of a previously undescribed species. Several juvenile crayfishes were dug from shallow burrows in an area where I had collected on several previous occasions. They appeared to me to be the young of one of the most common species in the state, but for some reason a few were kept alive and returned to the laboratory. Much to my surprise, indeed, they were members of an undescribed species, *P. (D.) devexus*, the relationships of which still perplex me. In October I returned to the same area, and, in searching for additional specimens, I unearthed representatives of another previously unknown species, *C. (D.) strigosus*! In one locality the burrows of the two were less than one meter apart. Thus even a person with almost a half-century's experience in collecting these animals sometimes, if not frequently, fails to obtain samples of all species present in a locality.

This report is based upon some 21,000 specimens obtained from the localities noted on Figure 1. As indicated, concentrations of collecting sites occur in the northern and southeastern parts of the state. Partly responsible for the more intensive work in these areas were the apparently richer faunas, but more important were the taxonomic problems encountered and the efforts expended in attempting to gain an understanding of the interrelationships of the species—their kinship as well as their geographic and ecological distribution. Although some progress has been made in deciphering their affinities (Figures 11–25) and their ranges within the state (Table 2 and distribution maps), little has been learned concerning the microhabitats exploited by many of the species. Particularly puzzling is how two closely related species, that throughout most of their respective ranges give every evidence of vicariating for one another, manage to maintain apparently thriving populations when one becomes established in the midst of the range of the other, even occasionally sharing at least a major habitat in a single locality.

ACKNOWLEDGMENTS.—Numerous persons have assisted me in the acquisition of the specimens on which this report is based; to all of them I extend my sincere thanks. Among those who have accompanied me on forays in the field, handling brail poles, wielding a shovel, and/or personally excavating the animals from burrows are several on whom I have imposed repeatedly: T. A. English, Jr., Eastern Air Lines, Atlanta, Georgia; E. T. Hall, Jr., Georgia Department of Natural Resources; C. W. Hart, Jr., Smithsonian Institution; D. J. Peters, York High School, Virginia; and J. E. Pugh, Christopher Newport College, Virginia.

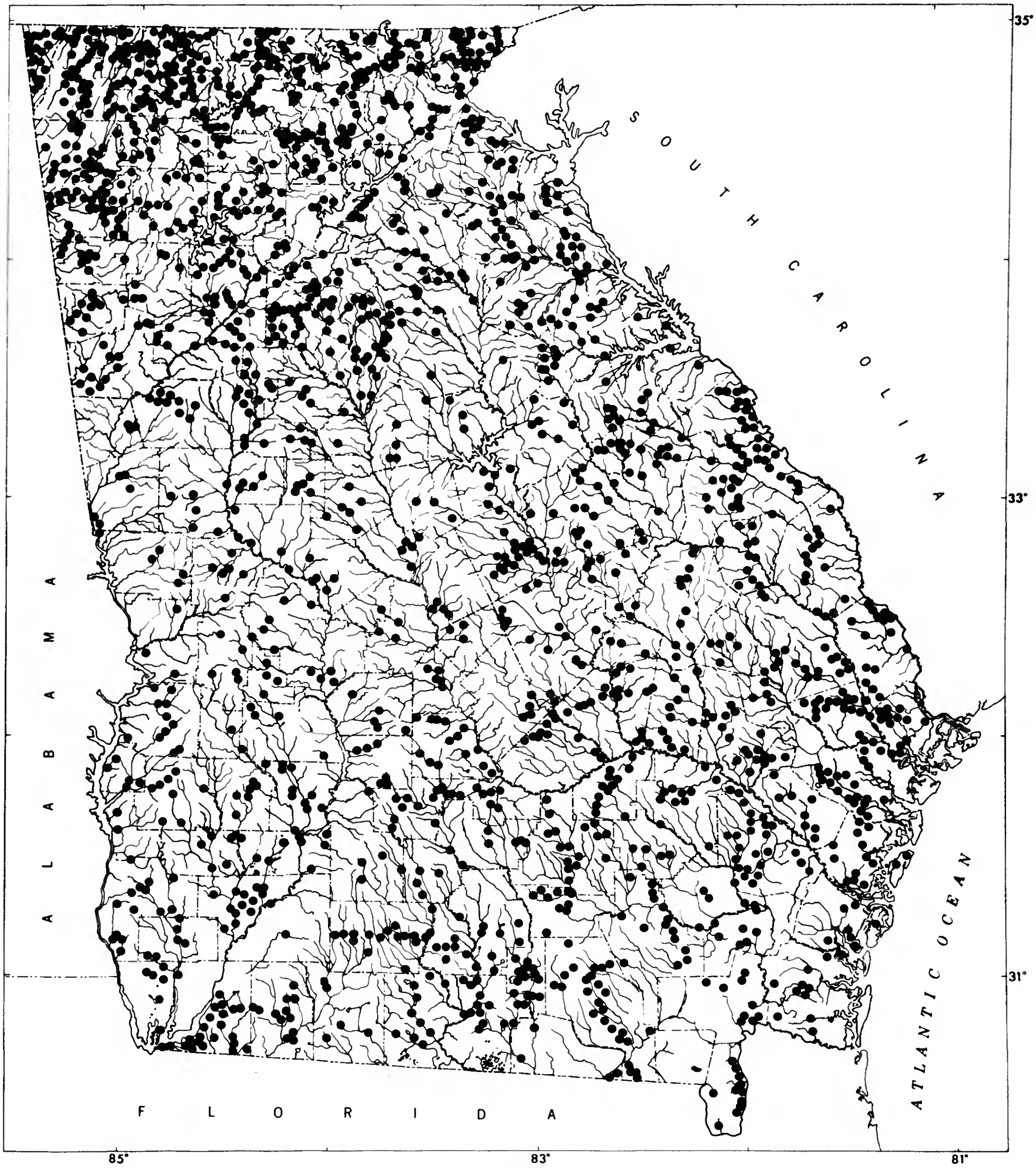


FIGURE 1.—Localities in Georgia where crayfishes have been collected.

Others who have been helpful companions on one or more field trips include: E. H. Blount and E. J. Blount, Savannah, Georgia; N. T. Blount, Falls Church, Virginia; J. L. Boyce, Emory University, Georgia; R. J. Dubois, Verviers, Belgium; J. F. Fitzpatrick, Jr., University of South Alabama; H. E. Hale, Georgia State University; H. H. Hobbs, Sr. (deceased); H. H. Hobbs III, Wittenberg University, Ohio; T. L. Johnson, Mary Washington College, Virginia; W. D. Kennedy, Georgia Department of Natural Resources; K. R. Martin, Georgia State University; J. F. Payne, Memphis State University, Tennessee; K. W. Simonds, Epworth, Georgia; Torgny Unestam, Upsala, Sweden; H. H. Wallace and H. K. Wallace, University of Florida; and F. N. Young, Indiana University.

Those who have devoted special effort to obtain specimens for me include: L. G. Abele, Florida State University; the late H. M. Blount, Waynesboro, Georgia; R. W. Bouchard, Wildwood Crest, New Jersey; B. A. Caldwell, R. M. Gaddis, and Max W. Walker, Georgia Department of Natural Resources; C. E. Carter, Gloucester, Virginia; the late M. E. Carter, Valdosta State College, Georgia; J. H. Chandler, Jr., Southeastern Fish Control Laboratory, Warm Springs, Georgia; C. S. Dunn, Forestry Service, Chatsworth, Georgia; R. W. Heard, Gulf Coast Research Laboratory, Ocean Springs, Mississippi; B. C. Kinney, Athens, Georgia; G. C. Miller, Southeast Fisheries Center, Miami, Florida; F. K. Parrish and G. H. Wharton, Georgia State University; J. S. Ramsey, Auburn University, Alabama; E. C. Raney, formerly of Cornell University, New York; D. C. Scott, University of Georgia; J. W. Sullivan, formerly of the University of Georgia; and G. K. Williamson, Savannah Science Museum. Others who have contributed specimens are cited under "Specimens Examined" in the treatments of the species.

The cooperation of the Environmental Protection Division (formerly the Water Quality Control Board) of the Georgia Department of Natural Resources has been continuous. Not only have the personnel of the division transmitted their crayfish collections to me but also have been helpful in identifying localities and in lending or donating to me numerous maps that were invaluable in this study. In addition to the names of those members of the staff cited above, K. W. Martin, G. L. Petersen, and G. Q. Tuggle should be included. E. T. Hall, Jr., and M. W. Walker deserve special thanks for their generous compliances to repeated calls for assistance.

For lending specimens in the collections of the Museum of Comparative Zoology, I am indebted to H. W. Levi, as I am to P. F. Huddlestun of the Georgia Department of Natural Resources for discussing problems relating to the influence of the geological history of the coastal plain of the state on the distribution of crayfishes, as well as for reading sections of the manuscript.

My thanks are extended to Carolyn B. Gast of the Smithsonian Institution for the splendid illustrations rendered by her and for the assistance given me in my execution of a number of the stippled drawings. I am also grateful to J. A. Bernazani, Vienna, Virginia, who is responsible for Figures 45, 104, 109, 112, 114, 131, and to M. R. Carpenter, of the Smithsonian, who assisted with the preparation of Figures 7–9.

For encouragement, suggestions, and criticisms of the manuscript, I extend my appreciation to my colleagues, Fenner A. Chace, Jr., Raymond B. Manning, and Isabel Pérez Farfante, as well as to Raymond W. Bouchard, Joseph F. Fitzpatrick, Jr., and H. H. Hobbs III.

Both Margaret A. Daniel and my wife, Georgia, assisted me in so many facets of the preparation of the manuscript that no attempt is made here to enumerate their contributions. The former, with unbelievable tolerance for my suggestions, emendations, and modifications, prepared all tables and graphs and arranged and labeled most of the line illustrations. The latter verified all of the bibliographic citations in the text and accompanied me on a number of field trips. Both of them criticized preliminary drafts of the manuscript and assisted in all of the proofreadings. For their continued encouragement and their patient labors, I am deeply grateful. Finally, I

extend my thanks to Mary Frances Bell and Barbara Spann for the interest, patience, tact, and restraint they demonstrated in editing this work.

Remarks on Presentation

In the accounts of the individual species, a synonomy is followed by a summary of the literature, sometimes restricted to that pertaining to Georgia, and a diagnosis. Descriptions, where deemed appropriate, are included for certain taxa, and except for the two troglobitic species, are extended to include notes on color. Statements concerning the types and type-locality precede a synopsis of the range and a summary or detailed list of the specimens examined. These are followed by a discussion of variation, notes on size, life history, and ecology. Whereas discussions of relationships are emphasized in the section of the study devoted to "Phylogenetic Considerations" and in those treating the genera and/or subgenera, a few remarks concerning affinities are included in the accounts of the previously undescribed species. The treatment of each is concluded with a list of crayfishes with which the species has been collected in one or more localities in the state. Appended to the sections dealing with the new species and subspecies are derivations of the proposed names.

A tabulation of the species occurring in each of the counties in the state is presented in Appendix 1 (accompanied by a map of the counties), and another listing of the symbionts of the Georgia crayfishes appears in Appendix 2.

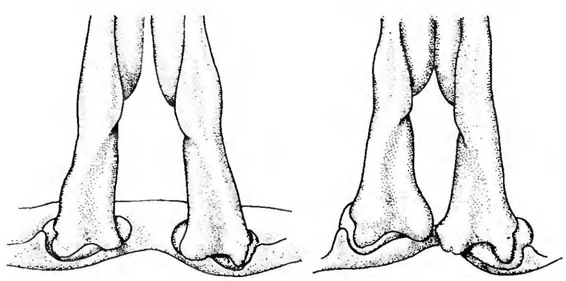
The following explanations of the rationale and of conventions adopted in preparing several aspects of the accounts of the species seem desirable.

SYNONYMIES.—The species bibliographies that introduce each of the taxa treated are variable in their scope. For the majority, they are as nearly complete as I have been able to make them. For some of the wide-ranging species, however, a selected bibliography is provided, largely because of uncertainties of identifications upon which many of the recorded localities were based. Nevertheless, all references to their occurrence in Georgia that I have encountered are included and noted by asterisks.

DIAGNOSES.—In the diagnoses of the species and subspecies, references to secondary sexual characters of the male are based on those in the first form (form I; see "Taxonomic Characters"). Whereas many of the statements are applicable to adult specimens in the second form, at least occasional difficulties will be encountered in reconciling certain descriptive phrases applied to these nonbreeding males. For example, asymmetry of the first pleopods (Figures 2, 146*l*) does not appear until the male molts to the first form. In fact, in small juveniles a broad interval exists between the pleopods when they first appear, and, in succeeding molts, the distance becomes less and less. In those species with asymmetrical pleopods, not until the molt to first form is there a distinct caudal shift in the position of the sinistral member.

The diagnoses of, and keys to, the superspecific taxa are prepared primarily to distinguish species groups occurring in Georgia and cannot always be relied upon in identifying crayfishes from elsewhere.

DESCRIPTIONS.—The original accounts of the species from Georgia described by LeConte (1856), while adequate when they were prepared, are no longer diagnostic. Therefore descriptions are offered for those of his species that are currently recognized except *Cambarus (D.) latimanus*,



a *b*

FIGURE 2.—Basal parts of first pleopod and sternum in *Procambarus (O.) lophotus*: *a*, juvenile male; *b*, second form male.

which was recently redescribed by Bouchard (1978:34). In addition, complete descriptions are included for 18 new specific and subspecific taxa.

COLOR NOTES.—Observations on the color patterns and color are included for all of the pigmented species, and among those in which there appear to be regional variations in the pattern, such are noted and illustrated.

TYPES.—In reporting the location and/or disposition of the types of the species and subspecies, the following abbreviations of institutions or initials of persons have been employed.

- AMS Australian Museum, Sydney, Australia
- ANSP Academy of Natural Sciences of Philadelphia, Pennsylvania
- BSNH Boston Society of Natural History, Boston, Massachusetts
- CM Carnegie Museum, Pittsburgh, Pennsylvania
- IBM Instituto de Biología de la Universidad Nacional Autónoma de México, Mexico City, Mexico
- MCZ Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts
- MHNP Muséum National d'Histoire Naturelle, Paris, France
- RNHL Rijksmuseum van Natuurlijke Historie, Leiden, The Netherlands
- RR Collection of the late Rendell Rhoades, Ashland, Ohio
- RWB Collection of Raymond W. Bouchard, Wildwood Crest, New Jersey
- TU Department of Zoology, Tulane University, New Orleans, Louisiana
- USNM United States National Museum collections (in the National Museum of Natural History), Smithsonian Institution, Washington, D.C.
- UZM Universitetets Zoologiske Museum, København K., Denmark

RANGES.—In reporting the ranges of the species and subspecies, the total range is broadly circumscribed. The area occupied within the state is defined in terms of drainage systems, physiographic regions, and occasionally political boundaries, and spot maps are included.

GEORGIA SPECIMENS EXAMINED.—Unless otherwise indicated, the specimens on which this study was based are deposited in the National Museum of Natural History. For some of the species (particularly those that appear to have a limited range as well as those for which there are comparatively few localities known within a broad range) all localities are cited in the text and are included on the spot maps. For those more wide-ranging species that occur in virtually every stream within their ranges in the state, references to the localities are limited to the spot maps. In citing locality records, the conventions adopted here are as follows: United States highways are consistently referred to as "highways," state roads as "routes," and county roads as "roads."

Although the metric system has been employed in most measurements given in this work, distances cited in the locality data are recorded to the nearest tenth of a mile. This has been done because the majority of the vehicles in the United States are provided with odometers graduated in miles, and the scales on all maps that I have consulted are presented in the same units.

GEORGIA CRAYFISH ASSOCIATES.—In the sections devoted to the associates, the numbers in parentheses following the names of the crayfishes denote the number of times each has been found in the same locality with the species under discussion.

TAXONOMIC CHARACTERS.—The features of the crayfish that are used in the diagnoses and descriptions of the various taxa included herein are illustrated (Figures 3, 4). Not clarified, however, is the repetitively used "first form male" (or male, form I) and "second form male" (or male, form II). Even though the dimorphism that exists in the Cambaridae has been discussed in almost every monographic or regional report on the American crayfishes, because such publications may not be available to one wishing to use this work, the following explanation offered by Hobbs (1972b:7) is quoted here.

> As is true of many invertebrate and at least some vertebrate animals, the identification of juvenile crayfishes is difficult, and frequently, without locality data, cannot be made. Furthermore, in localities in which two or more closely allied species occur together, it is oftentimes almost impossible to distinguish between the younger members of populations. Compounding this difficulty among the male members of the subfamilies Cambarinae and Cambarellinae is the existence of a cyclic dimorphism associated with the reproductive cycle that, in the more northern representatives,

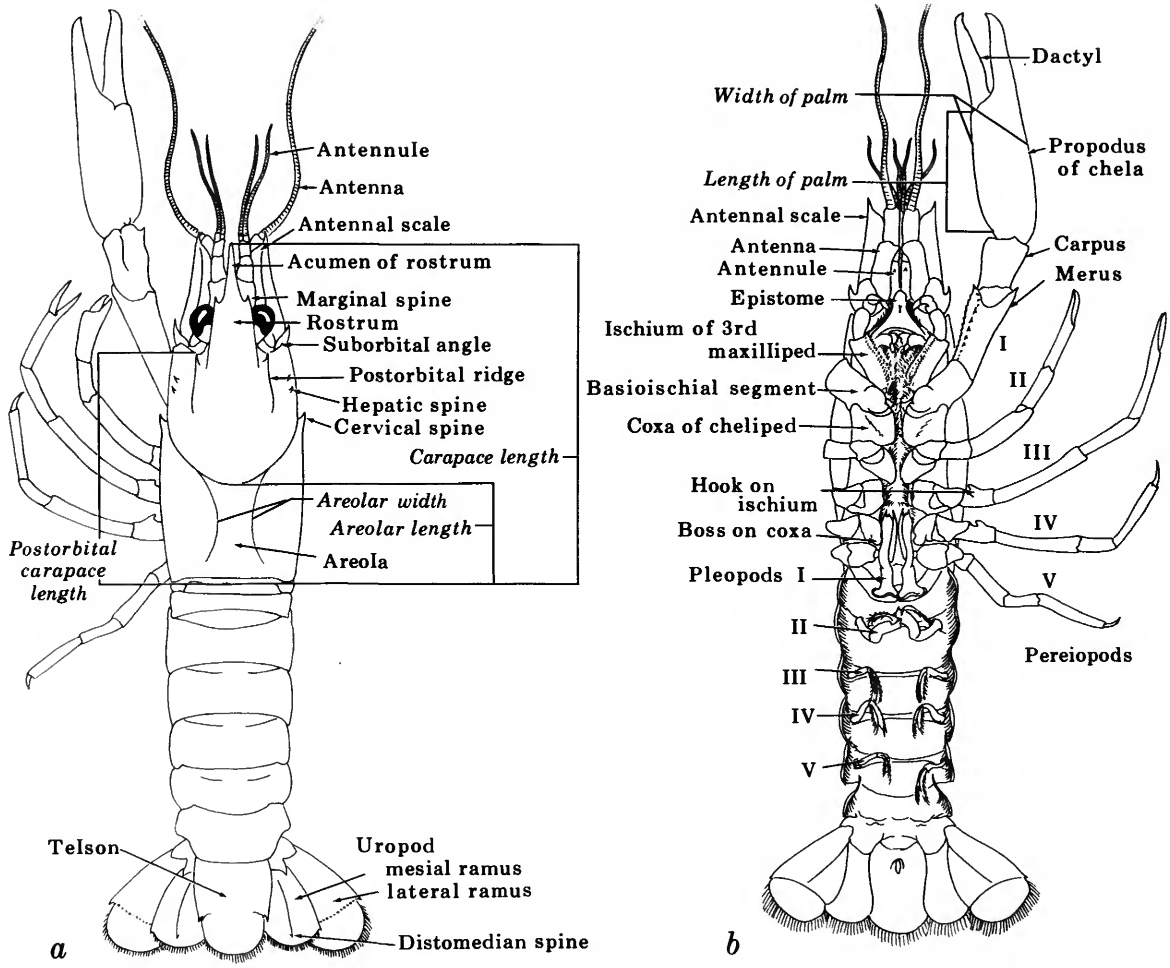


FIGURE 3.—Generalized crayfish: *a*, dorsal view; *b*, ventral view.

occurs typically in a circadian rhythm. Among those species that have an annual reproductive cycle, the breeding ("Form I," or "first form") males of the population, at the end of their first season, molt and are transformed to essentially a juvenile morphology ("Form II," or "second form") that is retained until the advent of the next breeding season when the second semiannual molt returns them to the adult form (Form I). Thus between each breeding season there is a regression to the quasi-juvenile (Form II) stage, which may have a duration of three to perhaps as long as six months. For those species that have a seasonal reproductive cycle, the entire male population may be in the juvenile or quasi-juvenile (Form II) stage throughout most of the summer months. In many of the species occurring in the lower temperate latitudes, there is no well defined breeding season, and, with staggered molting periods, the male members of a population consist of juveniles, quasi-juveniles (Form II), and adults (Form I) throughout the year.

Inasmuch as an individual may have three or more actively reproductive periods during its life span, and, with few exceptions, there is an increase in size of the individual with each molt, it is to be expected that quasi-juveniles (Form II) following their first or second breeding seasons are larger than an adult (Form I) male in its first. Consequently size alone cannot be used in distinguishing between first and second form males. [Characteristic of the juvenile male first pleopod is an oblique suture in the proximal half of the shaft. At least occasionally, second form males exhibit this "juvenile suture" (Figure 201*d*).]

. . . These first form males may be distinguished from

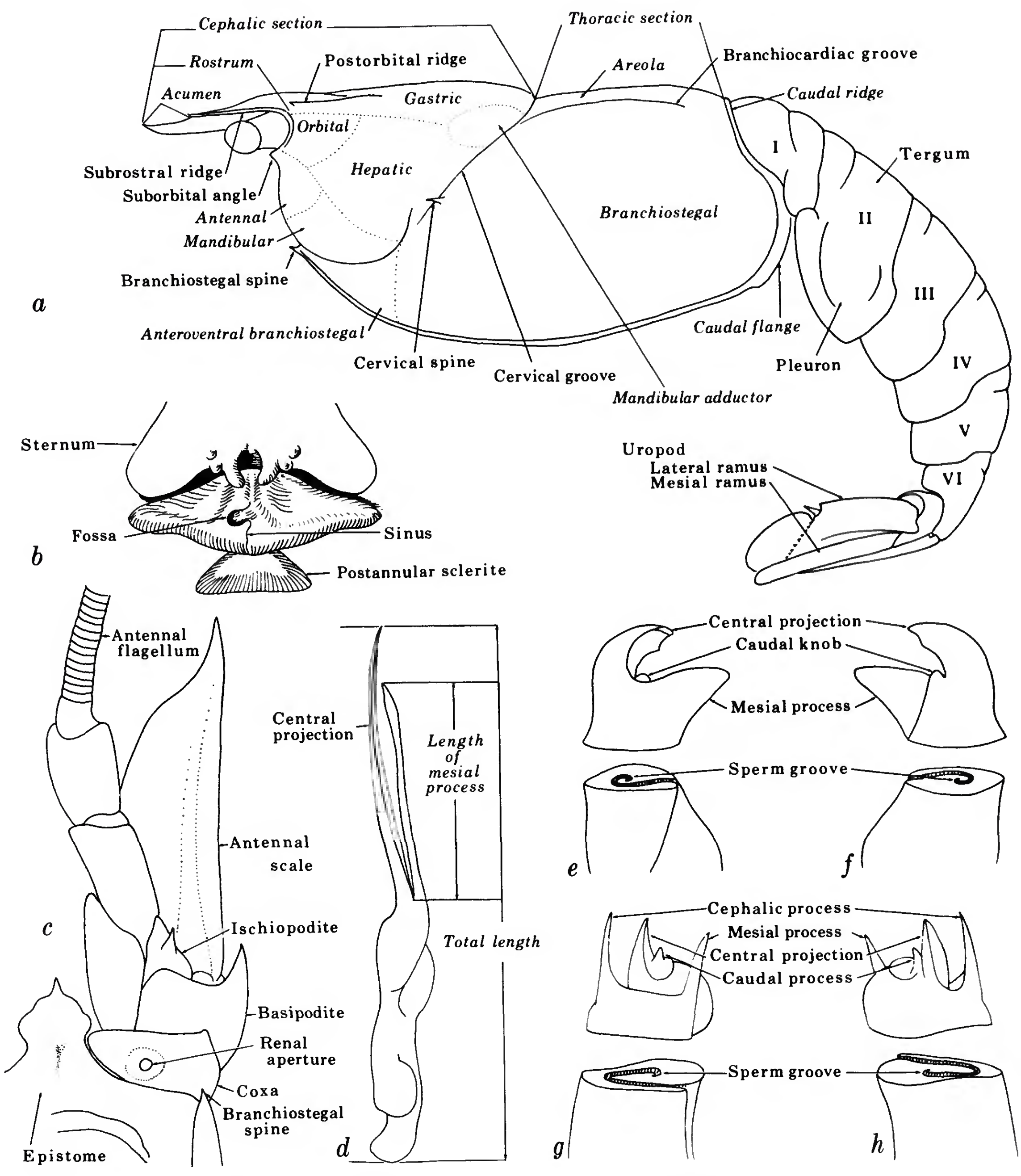


FIGURE 4.—Body regions and structures referred to in keys and descriptions: *a*, carapace and abdomen of generalized crayfish; *b*, annulus ventralis and associated sternal areas; *c*, ventral view of epistome and basal part of antenna; *d*, mesial view of first pleopod of male member of genus *Orconectes*; *e*, mesial view of distal part of first pleopod in generalized member of genus *Cambarus*; *f*, lateral view of same; *g*, mesial view of distal part of first pleopod in generalized member of genus *Procambarus*; *h*, lateral view of same.

juvenile and second form males by the presence of one or more corneous, or horny, terminal elements (projections) on the distal ends of the first pleopods. These rigid pleopods (Figures . . . [3*b*, 4*d–h*]), in their usual position, extend from the base of the abdomen forward between the bases of the pereiopods and lie against the sternum of the cephalothoracic region. The first pleopods of the juvenile and second form males have no corneous terminal elements; the projections are more bulbous and much less clearly defined than in the first form males, and the entire pleopod is of similar texture . . . In females these pleopods are small and flexible or lacking.

[In examining the pleopods, always use the left member of the pair.] For convenience of description, the first pleopod is considered to hang pendant from the abdomen. Toward the attached end is *proximal*; toward the free end, *distal*; the side toward the head, *cephalic*; that toward the telson, *caudal*; that facing the corresponding pleopod of the pair, *mesial*; and that facing away from the midline of the body, *lateral*.

Also in need of a brief explanation are the descriptive terms applied to the annulus ventralis. Among the Georgia crayfishes, the degree of mobility of this structure is markedly different. In the more primitive species (members of the genus *Procambarus*), as well as in one of the more advanced (*Faxonella clypeata*), it is surrounded by a flexible cuticle, rendering it "freely movable." In most advanced forms (members of the genera *Orconectes* and *Cambarus*), the cuticle joining the annulus to the sternum immediately anterior to it is sclerotized so that little if any motion is possible between them. In the Georgia members of *Orconectes*, no motion between the fused elements is possible, and the annulus is described as being "inflexibly fused with the sternum." In those species belonging to the genus *Cambarus*, the annulus itself is not uniformly sclerotized, and, even though it is fused with the sternum, a slight hingelike action occurs between the anterior and the more heavily calcified posterior part. Such annuli are referred to as "capable of a slight hingelike motion." Strongly resembling in its mobility the annulus ventralis of members of the genus *Cambarellus* is that of *Procambarus (D.) devexus*, which can move only slightly laterally but swings through a broad arc in the anterior-posterior axis of the body, and, in its caudalmost position on the arc, can be partly covered posteroventrally by the postannular sclerite (cf., Figure 116*l* and *m*). Other terminology applied to the annulus is illustrated in Figure 4*b*.

LITERATURE CITATIONS.—The manuscript of this study was completed on 30 September 1978; thus, most of the articles appearing since that date are included in neither the text nor list of references. *The Natural Environments of Georgia* (Wharton, 1978) was not available until after this study was in press, and, whereas references to the crayfishes mentioned in it are noted in the synonymies herein, Wharton's contributions are not included in the discussions of the literature.

Composition of the Fauna

The crayfish fauna of the State is outlined in the following taxonomic list. Sixty-six species and subspecies have been found within the political boundaries. Because there is good reason to believe that at least two additional species, *Cambarus (A.) hamulatus* and *Procambarus (O.) leonensis*, are also present, they, too, are included in the list as well as in annotations and discussions.

Family CAMBARIDAE Hobbs, 1942a (elevated to familial rank by Hobbs, 1974a)
- Subfamily CAMBARINAE Hobbs, 1942a
  - Genus *Cambarus* Erichson, 1846
    - Subgenus *Aviticambarus* Hobbs, 1969a
      - *Cambarus (Aviticambarus) hamulatus* (Cope, 1881)
    - Subgenus *Cambarus* Erichson, 1846
      - *Cambarus (Cambarus) bartonii* (Fabricius, 1798)
      - *Cambarus (Cambarus) howardi* Hobbs and Hall, 1969
    - Subgenus *Depressicambarus* Hobbs, 1969a
      - The *halli* Group Bouchard, 1978
        - *Cambarus (Depressicambarus) englishi* Hobbs and Hall, 1972
        - *Cambarus (Depressicambarus) halli* Hobbs, 1968a
      - The *latimanus* Group Bouchard, 1978
        - *Cambarus (Depressicambarus) cymatilis* Hobbs, 1970
        - *Cambarus (Depressicambarus) harti*, new species
        - *Cambarus (Depressicambarus) latimanus* (LeConte, 1856)
        - *Cambarus (Depressicambarus) reflexus*, new species
        - *Cambarus (Depressicambarus) striatus* Hay, 1902a
        - *Cambarus (Depressicambarus) strigosus*, new species
        - *Cambarus (Depressicambarus) truncatus*, new species
    - Subgenus *Hiaticambarus* Hobbs, 1969a
      - *Cambarus (Hiaticambarus) coosawattae*, new species
      - *Cambarus (Hiaticambarus) fasciatus*, new species

Cambarus (Hiaticambarus) girardianus Faxon, 1884
Cambarus (Hiaticambarus) longirostris Faxon, 1885a
Cambarus (Hiaticambarus) manningi, new species
Cambarus (Hiaticambarus) speciosus, new species
Subgenus *Jugicambarus* Hobbs, 1969a
Cambarus (Jugicambarus) asperimanus Faxon, 1914
Cambarus (Jugicambarus) conasaugaensis Hobbs and Hobbs, 1962
Cambarus (Jugicambarus) cryptodytes Hobbs, 1941b
Cambarus (Jugicambarus) distans Rhoades, 1944
Cambarus (Jugicambarus) nodosus Bouchard and Hobbs, 1976
Cambarus (Jugicambarus) parvoculus Hobbs and Shoup, 1947
Cambarus (Jugicambarus) unestami Hobbs and Hall, 1969
Subgenus *Lacunicambarus* Hobbs, 1969a
Cambarus (Lacunicambarus) acanthura, new species
Cambarus (Lacunicambarus) diogenes diogenes Girard, 1852
Subgenus *Puncticambarus* Hobbs, 1969a
The *coosae* Group, designated herein
Cambarus (Puncticambarus) coosae, new species
Cambarus (Puncticambarus) scotti, new species
The *extraneus* Group, designated herein
Cambarus (Puncticambarus) chaugaensis Prins and Hobbs, 1972
Cambarus (Puncticambarus) extraneus Hagen, 1870
Cambarus (Puncticambarus) georgiae, new species
Cambarus (Puncticambarus) hiwasseensis, new species
Cambarus (Puncticambarus) parrishi, new species
Genus *Fallicambarus* Hobbs, 1969a
Subgenus *Creaserinus* Hobbs, 1973b
Fallicambarus (Creaserinus) hedgpethi (Hobbs, 1948)
Genus *Faxonella* Creaser, 1933b
Faxonella clypeata (Hay, 1899a)
Genus *Orconectes* Cope, 1872
Orconectes erichsonianus (Faxon, 1898)
Orconectes forceps (Faxon, 1884)
Orconectes spinosus (Bundy, 1877)
Genus *Procambarus* Ortmann, 1905d
Subgenus *Distocambarus*, designated herein
Procambarus (Distocambarus) devexus, new species
Subgenus *Hagenides* Hobbs, 1972a
The *advena* Group Hobbs, 1942b
Procambarus (Hagenides) advena (LeConte, 1856)
Procambarus (Hagenides) caritus, new species
Procambarus (Hagenides) pygmaeus Hobbs, 1942b
Procambarus (Hagenides) talpoides, new species
The *truculentus* Group Hobbs, 1954
Procambarus (Hagenides) truculentus Hobbs, 1954
Subgenus *Leconticambarus* Hobbs, 1972a
Procambarus (Leconticambarus) barbatus (Faxon, 1890)
Procambarus (Leconticambarus) pubischelae pubischelae Hobbs, 1942b
Procambarus (Leconticambarus) pubischelae deficiens, new subspecies
Subgenus *Ortmannicus* Fowler, 1912
The *blandingii* Group Ortmann, 1905a
Procambarus (Ortmannicus) acutissimus (Girard, 1852)
Procambarus (Ortmannicus) acutus acutus (Girard, 1852)
Procambarus (Ortmannicus) lophotus Hobbs and Walton, 1960b
The *pictus* Group Hobbs, 1942b
Procambarus (Ortmannicus) angustatus (LeConte, 1856)
Procambarus (Ortmannicus) enoplosternum Hobbs, 1947a
Procambarus (Ortmannicus) epicyrtus Hobbs, 1958c
Procambarus (Ortmannicus) litosternum Hobbs, 1947a
Procambarus (Ortmannicus) pubescens (Faxon, 1884)
The *seminolae* Group Hobbs, 1942b
Procambarus (Ortmannicus) fallax (Hagen, 1870)
Procambarus (Ortmannicus) leonensis Hobbs, 1942b
Procambarus (Ortmannicus) lunzi (Hobbs, 1940b)
Procambarus (Ortmannicus) seminolae Hobbs, 1942b
Subgenus *Pennides* Hobbs, 1972a
Procambarus (Pennides) gibbus Hobbs, 1969b
Procambarus (Pennides) petersi, new species
Procambarus (Pennides) raneyi Hobbs, 1953b
Procambarus (Pennides) spiculifer (LeConte, 1856)
Procambarus (Pennides) versutus (Hagen, 1870)
Subgenus *Scapulicambarus* Hobbs, 1972a
Procambarus (Scapulicambarus) howellae Hobbs, 1952b
Procambarus (Scapulicambarus) paeninsulanus (Faxon, 1914)
Procambarus (Scapulicambarus) troglodytes (LeConte, 1856)

Previous Studies of the Georgia Crayfishes

Before the first North American crayfish (presumably from the vicinity of Philadelphia, Pennsylvania) had been described by Fabricius in 1798, William Bartram (1771:43), in an account of his travels in Georgia, recorded the following observations made on a tributary of the Broad River, an affluent of the Savannah River.

> On my return towards camp, I met my philosophic companion, Mr. M'Intosh, who was seated on the bank of a rivulet, and whom I found highly entertained by a very novel and curious natural exhibition, in which I participated with high relish. The waters at this place were still and shoal, and flowed over a bed of gravel just beneath a rocky rapid: in this eddy shoal were a number of little gravelly pyramidal hills, whose summits rose almost to the surface of the water, very artfully constructed by a species of small cray-fish (Cancer macrourus) which inhabited them: here seemed to be their citadel, or place of retreat for their young against the attacks and ravages of their enemy, the gold-fish: these, in numerous bands, continually infested them, except at short intervals, when small detachments of veteran cray-fish sallied out upon them, from their cells within the gravelly pyramids, at which time a brilliant fight presented; the little gold-fish instantly fled from every side, darting through the transparent waters like streams of lightening; some even sprang above the surface, into the air, but all quickly returned to the charge, surrounding the pyramids as before, on the retreat of the cray-fish; in this manner the war seemed to be continual.

There is little doubt in my mind that he must have been watching young individuals of *Cambarus (Depressicambarus) latimanus*, although I hasten to deny having seen "detachments" of crayfishes unite in any consorted effort.

Some eighty-five years elapsed before the second reference to Georgia crayfishes appeared. John LeConte (1856) reported the occurrence of nine species in the state, of which only one, *Astacus Blandingii*, had been previously described: *Astacus advena*, *A. angustatus*, *A. Blandingii*, *A. fossarum*, *A. latimanus*, *A. maniculatus*, *A. penicillatus*, *A. spiculifer*, and *A. troglodytes*. Believing that "... the very slight and not very apparent differences which have been adopted to distinguish between [the genera *Astacus* and *Cambarus*] ... to be of little moment ...," he declined to employ Erichson's (1846) *Cambarus* that had been accorded generic rank by Girard (1852).

In his monograph of the North American crayfishes, Hagen (1870: 100) stated that "Georgia, thanks to the monograph of Mr. John LeConte, is as yet still the best explored State." It was Hagen's opinion that LeConte's *A. fossarum* was a synonym of *C. troglodytes*, and because he had not seen *A. Blandingii*, he did not include it among the species recorded from the state. As a result of an error of transposition (see "Review of the Literature" under "*P. (H.) advena*"), he included *C. Carolinus* in his list of Georgia crayfishes. *Cambarus extraneus* and *C. Lecontei*, both described by him in this study, were recorded from Georgia.

The next contribution to our knowledge of the species occurring in the state was that of Bundy (1877), who described *Cambarus spinosus* from the vicinity of Rome. Seven years later, Faxon (1884) added descriptions of two new species that had been collected in Georgia, *Cambarus pubescens* and *C. Jordani*, and (1885a:167) noted that the crayfish fauna consisted of 13 species, deleting *C. Carolinus* but returning *C. Blandingii* to Hagen's list and adding *C. spinosus*, *C. pubescens*, and *C. Jordani*. He questionably added "*C. Bartonii*," the record based on a specimen with erroneous data, "Savannah."

Faxon (1890:621) proposed the name *Cambarus barbatus* as a substitute for LeConte's *Astacus penicillatus*, which was preoccupied (see "Review of the Literature" under *P. (L.) barbatus*), and (1898:646) cited a new record, Burke County, for his *C. pubescens*.

No new data were added until 1914, when Faxon (p.375) described *Cambarus spinosus gulielmi* from Rossville, Walker County, and cited two new records for *C. latimanus* from Milledgeville and Roswell. He also listed *C. maniculatus* among the "Doubtful Species." Insofar as I am aware, the crayfishes of the state were ignored from 1914 until 1929, when Edwin P. Creaser from the Museum of Zoology, University of Michigan, made a series of collections that were later transferred to the National Museum of Natural History, many lots of which were not identified until this study was in progress.

In his comprehensive work on the crayfishes of the Southern Appalachians and Cumberland Plateau, Ortmann (1931), utilizing a nomenclature proposed by him in 1905(a) and modified by Fowler (1912), made several references to crayfishes occurring in Georgia and cited a number of new state records, several of which were based on misidentifications. These references are as follows: (p. 68) he reported (*C. (Faxonius) erichsonianus* from Walker and Catoosa counties and pointed out that Faxon's *C. spinosus gulielmi* is a synonym of *C. erichsonianus* Faxon (1898), which had been described from specimens collected in Greene County, Tennessee; (p. 88) he considered that because of discrepancies in Bundy's and Faxon's remarks concerning their *Cambarus spinosus* the species "... remains doubtful"; (p. 98) the records for *C. (C.) extraneus* in Floyd and Gilmer counties are based on erroneous determinations of *C. (P.) coosae* and *C. (H.) coosawattae*, respectively, that are described herein; (p. 110) his record of the presence of *C. (C.) montanus acuminatus* in Chattooga County is based on a probable misidentification of *C. (P.) scotti*; (p. 115) the stated occurrence of *C. (C.) montanus montanus* in Fannin County was derived from the confusion of his concept of that species with *C. (P.) hiwasseensis* (also described herein); and (p. 127) the record of *C. (C.) bartoni cavatus* in Walker County is now included among those for *C. (C.) bartonii* in this study.

Few collections were made in the state during the next decade, but in 1936 I obtained specimens from two localities in Early County, and additional lots were secured in 1937 and 1938. By the close of 1938, I had made several collecting trips in various regions of the state and continued to obtain occasional specimens until 1950. In the late 1940s and early 1950s, Donald C. Scott, Edward C. Raney, and students of the latter, studying freshwater fishes, contributed to me a large number of specimens to me that had been collected in Georgia. During the late summer of 1955, C. W. Hart, Jr., and I surveyed the crayfish fauna in the lower Chattahoochee-Flint watershed. Except for the field work of Kenneth W. Simonds in the Hiwassee Basin in the late 1950s comparatively little collecting was conducted in Georgia during the next 10 years. Since 1965, however, through the courtesy of Edward T. Hall, Jr., and his colleagues in the Environmental Protection Division of the Department of Natural Resources of Georgia, through the assistance of many other persons whose names appear in the section devoted to acknowledgments, and through extensive personal field work, a large number of specimens have been obtained from numerous localities.

Eleven years elapsed following the posthumous publication of Ortmann's (1931) study before other data were contributed on the Georgia crayfishes. The first of these was that of Hobbs (1942a), in which the genus *Cambarus* was revised, altering the names of several of the crayfishes that had been reported from the state. In his summary of the crayfishes of Florida, Hobbs (1942b) presented data on the occurrence of the following species in Georgia: *Cambarus d. diogenes*, *C. latimanus*, *Orconectes (Faxonella) clypeata* (= *Faxonella clypeata*), *Procambarus advena* (= *P. (H.) advena*, *P. (H.) caritus*, and *P. (H.) talpoides*), *P. barbatus*, *P. fallax*, *P. paeninsulanus*, *P. pubischelae* (= *P. (L.) p. pubischelae* and *P. (L.) p. deficiens*), *P. pygmaeus*, *P. seminolae*, and *P. spiculifer*.

Penn (1942:645) noted that 18,000 crayfishes belonging to *Cambarellus shufeldtii* (Faxon, 1884: 134) and *Faxonella clypeata* "from Pearl River, La. were planted in a private fish-cultural project, the Peg Factory Lake near Hamilton [Harris County], Georgia on March 15, 1937. The lake is on the Blue Springs Farm owned by Cason Callaway." In none of the collections from the area that are available to me was *C. shufeldtii* present, but it is of interest that the only record of the occurrence of *F. clypeata* outside of the Coastal Plain Province in the state is that from a swamp pool and burrows, 2.7 miles south of Waverly Hall on a secondary road, in Harris County, where a collection was made on 25 April 1966. Whether or not the specimens obtained there were descended from introduced ancestors is not known.

Two additional crayfishes, *Procambarus enoplosternum* and *P. litosternum*, were described by Hobbs (1947a) from the southeastern part of the state, and *P. howellae*, *P. raneyi*, and *P. truculentus* were named by him in 1952(b), 1953(b), and 1954, respectively. The only other new data recorded on these animals in Georgia prior to 1956 were distribution records for *Procambarus spiculifer* presented by Hobbs (1953b). Thus one hundred years after the report of the first specifically named crayfish from the state, the following crayfishes had been recorded from Georgia (in the first column, the original citation to their presence in the state follows the nomenclatural combination; comments or current combinations are listed in the second).

Astacus advena.—LeConte, 1856	*Procambarus (H.) advena* (LeConte)
Astacus angustatus.—LeConte, 1856	*Procambarus (O.) angustatus* (LeConte)
Astacus Blandingii.—LeConte, 1856	*Procambarus (O.) acutus acutus* (Girard)
Astacus fossarum.—LeConte, 1856	*Procambarus (S.) troglodytes* (LeConte)
Astacus latimanus.—LeConte, 1856	*Cambarus (D.) latimanus* (LeConte)
Astacus maniculatus.—LeConte, 1856	Nomen oblitum
Astacus penicillatus.—LeConte, 1856	*Procambarus (L.) barbatus* (Faxon)
Astacus spiculifer.—LeConte, 1856	*Procambarus (Pe.) spiculifer* (LeConte)
Astacus troglodytes.—LeConte, 1856	*Procambarus (S.) troglodytes* (LeConte)
Cambarus Carolinus.—Hagen, 1870	Erroneously reported from Georgia
Cambarus extraneus.—Hagen, 1870	*Cambarus (P.) extraneus* Hagen
Cambarus Lecontei.—Hagen, 1870	Erroneously reported from Georgia*
Cambarus spinosus.—Bundy, 1877	*Orconectes spinosus* (Bundy)
Cambarus Bartonii.—Faxon, 1884	*Cambarus (C.) bartonii* (Fabricius)
Cambarus Jordani.—Faxon, 1884	*Cambarus (D.) latimanus* (LeConte)
Cambarus pubescens.—Faxon, 1884	*Procambarus (O). pubescens* (Faxon)
Cambarus spinosus gulielmi.—Faxon, 1914	*Orconectes erichsonianus* (Faxon)
Cambarus (C.) bartoni cavatus.—Ortmann, 1931	*Cambarus (C.) bartonii* (Fabricius)
Cambarus (C.) extraneus.—Ortmann, 1931	*Cambarus (H.) coosawattae*, new species
	Cambarus (P.) coosae, new species
Cambarus (Faxonius) erichsonianus.—Ortmann, 1931	*Orconectes erichsonianus* (Faxon)
Cambarus (C.) montanus acuminatus.—Ortmann, 1931	*Cambarus (P.) scotti*, new species
Cambarus (C.) m. montanus.—Ortmann, 1931	*Cambarus (P.) hiwasseensis*, new species
Cambarus d. diogenes.—Hobbs, 1942b	*Cambarus (L.) d. diogenes* Girard
Orconectes (Faxonella) clypeata.—Hobbs, 1942b	*Faxonella clypeata* (Hay)
Procambarus fallax.—Hobbs, 1942b	*Procambarus (O.) fallax* (Hagen)
Procambarus paeninsulanus.—Hobbs, 1942b	*Procambarus (S.) paeninsulanus* (Faxon)
Procambarus pubischelae.—Hobbs, 1942b	*Procambarus (L.) p. pubischelae* Hobbs
	Procambarus (L.) p. deficiens, new subspecies
Procambarus pygmaeus.—Hobbs, 1942b	*Procambarus (H.) pygmaeus* Hobbs
Procambarus seminolae.—Hobbs, 1942b	*Procambarus (O). seminolae* Hobbs
Procambarus enoplosternum.—Hobbs, 1947a	*Procambarus (O.) enoplosternum* Hobbs
Procambarus litosternum.—Hobbs, 1947a	*Procambarus (O.) litosternum* Hobbs
Procambarus howellae.—Hobbs, 1952b	*Procambarus (S.) howellae* Hobbs
Procambarus raneyi.—Hobbs, 1953b	*Procambarus (Pe.) raneyi* Hobbs
Procambarus truculentus.—Hobbs, 1954	*Procambarus (H.) truculentus* Hobbs

* This crayfish was reported from two localities in the state, Athens and Milledgeville. Both specimens were in the Museum of Comparative Zoology, but only that from the former could be found in 1978. It is indeed a member of *P. (O.) lecontei* (Hagen, 1870) and almost certainly the specimen that Faxon (1885a:30) "... found in a jar with *C. spiculifer*... from Athens, Ga.," but I am confident that this crayfish is from elsewhere and was inadvertently placed in the container with the specimens from Athens. That from Milledgeville reported by Hagen, according to Faxon (1885a:30) "... ill agrees with the types [of Hagen's *C. lecontei*], on account of the shortness of the acumen of the rostrum (the rostrum being like that of *C. Blandingii*), the short and broad antennal scales, breadth of the hand, etc." Unfortunately the identity of this specimen remains unknown.

Thus of the 34 species that had been reported to be present in the state by 1956, 28 have been confirmed to be present or the identifications corrected.

Hobbs (1958a,b,c) included data on members of the *pictus* Group of the genus *Procambarus*, describing *P. epicyrtus*. In 1959, he and Hart added new records for several species occurring in the southwestern part of the state and reported the presence of *Cambarus floridanus* and *C. fodiens*, two species that had not previously been collected in Georgia. The former has subsequently been shown to be a synonym of *Cambarus striatus*, and the specimens of the latter have been assigned to *Fallicambarus (C.) hedgpethi*. Warren (1961) recorded the presence of *Cambarus cryptodytes* in Climax Cave in Decatur County, the only locality in which it has been found in the state.

The next species to be reported from Georgia was *Cambarus conasaugaensis*, which was described by Hobbs and Hobbs (1962) from the Conasauga River basin in Murray County. In his notes on the members of the "Blandingii Section" of *Procambarus*, Hobbs (1962) added *Procambarus chacei* and *P. versutus* to the crayfishes that occur within the state. Fitzpatrick (1963:62), in his study of variation in *Faxonella clypeata*, presented a spot map showing several localities for the species in Georgia and a list of counties in which the species had been found. *Cambarus halli* was described from the Tallapoosa River basin of Georgia by Hobbs (1968a), and *Cambarus asperimanus, C. carolinus, C. striatus, C. longirostris,* and *Orconectes juvenilis* were reported by Hobbs (1968b) to be present elsewhere. (The records for *C. carolinus* and *O. juvenilis* were based on erroneous determinations of *C. nodosus* and *O. spinosus*, respectively.) He also implied the presence of *O. forceps* in Georgia, and specific localities were cited later by Anonymous (1970c).

In his study of *Cambarus*, Hobbs (1969a) proposed certain revisions, including the assignment of the previously described species of the genus to 10 subgenera. Additions to the state fauna included *Cambarus girardianus*, and ranges of eight undescribed species (listed as *Cambarus* sp. B, C, E, F, G, H, J, and K) were noted to encompass sections of the state. (Of these species, "K" was subsequently described by Hobbs and Hall (1969) as *C. howardi*, "E" by Prins and Hobbs (1972) as *C. chaugaensis*, and "F" proved to be a local variant of *C. latimanus*; the remaining ones are described herein.) *Procambarus gibbus*, which frequents a segment of the Flint watershed, was named by Hobbs (1969b), and he and Hall (1969) described *C. unestami* from a tributary to Lookout Creek on Sand Mountain in Dade County. The following year, Hobbs reported the burrowing *Cambarus cymatilis* from Murray County, and Anonymous (1970c) recorded the presence of *Procambarus lophotus* in Walker County. On the basis of specimens collected from the Tallapoosa River in Haralson County, Hobbs and Hall (1972) described the riffle-inhabiting *Cambarus englishi*.

By far the greatest number of precise locality records for crayfishes occurring in Georgia are recorded in the monograph of the entocytherid ostracods by Hart and Hart (1974). Most of their specimens from the state were gleaned from the crayfishes that were collected in the course of this study and, in citing their locality records for the ostracods, the hosts were also included. A large number of records are noted in the Anonymous reports of biological surveys in the state, conducted by what is now the Environmental Protection Division of the Department of Natural Resources of Georgia. References to all of these records are included in the individual species bibliographies.

Bouchard (1976a,b) added information on the crayfishes occurring in the Appalachian Plateau Province of the state, and he and Hobbs (1976) described *Cambarus (J.) nodosus* from the Blue Ridge Province. The most recent study involving crayfishes occurring in Georgia is Bouchard's (1978) review of the subgenus *Depressicambarus*, in which two members of the state fauna are redescribed, and ecological and distributional data are provided for all of the members of the subgenus. The two infrasubgeneric species groups proposed by him are adopted herein.

Thus by 1978, 47 crayfishes had been reported to occur within the political boundaries of the state. As will become obvious in perusing the accounts of the species, not all of the literature has been reviewed in this summary, for there exist a number of additional references that contain locality records, discussions of relationships, statements of ranges, keys to aid in the identification, and a few ecological data. The major works and earliest records of the occurrence of each of the species, however, have been briefly summarized.

Physiographic Regions, Drainage Systems, and the Crayfish Fauna

FIGURES 5, 6; TABLE 2

The physiographic regions of the state, as employed herein, are those delineated by Clark and Zisa (1976). Inasmuch as the crayfishes of none of the provinces except the Coastal Plain Province are limited to specific "districts," few other than those of this province are employed in the following discussion and only those of the Coastal Plain Province are delineated in Figure 5. Furthermore, from the standpoint of crayfish distribution, there seems to be no reason to recognize the Fort Valley Plateau District of this province. The fauna there does not differ from that of the surrounding Fall Line Hills, and therefore it has not been included. In preparing these brief treatments of the physiographic regions I have relied heavily upon Cooke (1925), Smith and Green (1968), Hoyt and Hails (1974), and Clark and Zisa (1976).

THE APPALACHIAN PLATEAU PROVINCE (Cumberland Plateau Section).—In Georgia this province is represented by the Lookout Mountain District, which includes all of Dade County, the western part of Walker County, and the northwestern corner of Chattooga County. Most of the streams flowing from the sandstone cap find their way to the Tennessee River. The principal stream of the area is Lookout Creek, which courses between Sand and Lookout mountains. This stream, spanning the length of Dade County, flows northeastward over Ordovician limestones and is flanked by escarpments of 334 to 400 meters. The elevation of the plateau is approximately 667 meters and that of Lookout Creek is 266 to 334 meters.

Three crayfishes occurring in the state are limited to small upland streams in this province: *Cambarus (J.) distans*, *C. (J.) parvoculus*, and *C. (J.) unestami*. In addition, *C. (C.) bartonii* and *C. (D.) striatus* are found in both epigean and hypogean streams, and *C. (H.) longirostris*, *C. (H.) girardianus*, and *Orconectes erichsonianus* frequent Lookout Creek.

THE RIDGE AND VALLEY PROVINCE.—As the name implies, this province is marked by a series of ridges and valleys extending for the most part from northeast to southwest and lying between the Appalachian Plateau on the northwest and the Blue Ridge and Piedmont provinces on the east and south. The northwestern sector of the province is drained by South Chickamauga Creek, which discharges directly into the Tennessee River, and the remainder by tributaries of the Coosa River, chiefly the Conasauga and Chattooga rivers. The Conasauga arises in the Blue Ridge and flows southwestward in the eastern part of the province, and the Chattooga lies wholly within the western part of it. The ridges of the province are, for the most part, capped with sandstone, and in the valleys the streams flow over eroded beds of early Paleozoic limestone, dolomite, and shale. Elevation within the area ranges from approximately 200 to 534 meters, with the taller ridges (the Armuchee Ridges District) extending slightly west of the central axis of the province and dividing the watershed of the Conasauga from those of South Chickamauga Creek and the Chattooga River. The divide between the latter two is a low one at best, and north of Lafayette, there is no obvious ridge separating them. As low as the divide is, at the present time it serves as an effective barrier to at least some of the crayfishes occurring in the two streams.

The three principal watersheds and the crayfishes inhabiting them are as follows.

Tennessee: *Cambarus (C.) bartonii*, *C. (D.) striatus*, *C. (H.) girardianus*, *C. (J.) unestami*, *C. (L.) acanthura*, *C. (P.) extraneus*, *Orconectes erichsonianus*,

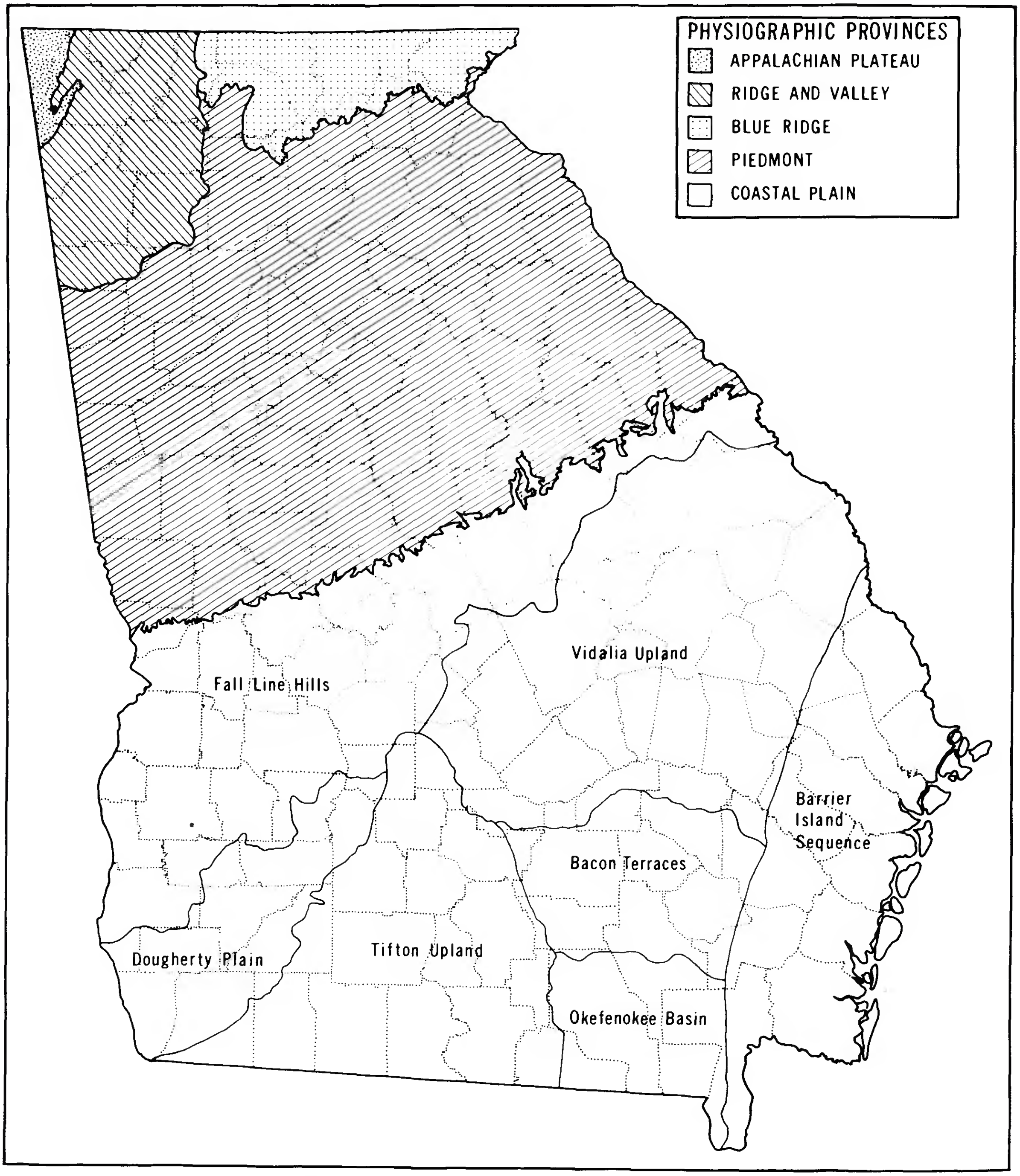


FIGURE 5.—Physiographic provinces, and districts of the coastal plain, of Georgia. (Based on Clark and Zisa, 1976.)

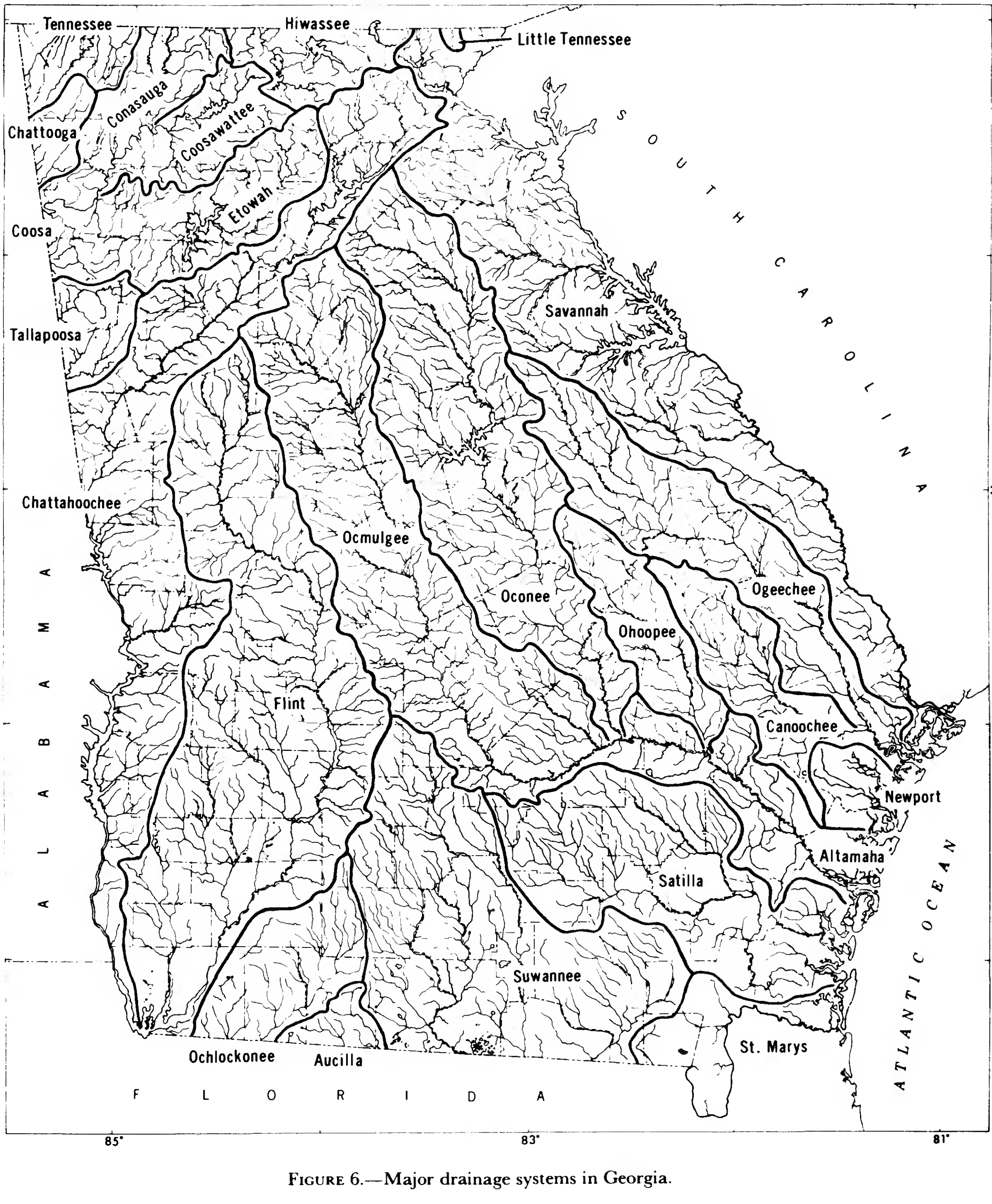


FIGURE 6.—Major drainage systems in Georgia.

TABLE 2.—Summary of crayfish distribution in major river basins and physiographic provinces of Georgia

CRAYFISH		RIVER BASIN																
	Endemic	Little Tennessee	Hiwassee	Tennessee	Chattooga	Coosa	Tallapoosa	Chattahoochee	Flint	Ochlockonee	Aucilla	Suwannee	Saint Marys	Satilla	Altamaha	Newport	Ogeechee	Savannah
Cambarus																		
(A.) hamulatus				A?														
(C.) bartonii		B	B	AR		BPR		BP							P			BP
(C.) howardi								P										
(D.) cymatilis						R												
(D.) englishi							P											
(D.) halli							P											
(D.) harti	●							P	P									
(D.) latimanus			BR		R	BPR	P	Pf	P						Pf		Psv	Psv
(D.) reflexus																	fv	sv
(D.) striatus				AR	R	BPR	P	Pf	Pdf						Pfv			P
(D.) strigosus	●																	P
(D.) truncatus	●														f			
(H.) coosawattae	●					BR												
(H.) fasciatus	●					P												
(H.) girardianus				AR														
(H.) longirostris			B	A	R													
(H.) manningi	●					R												
(H.) speciosus	●					BR												
(J.) asperimanus																		BP
(J.) conasaugaensis						BPR												
(J.) cryptodytes									d									
(J.) distans				A														
(J.) nodosus			B					BP										B
(J.) parvoculus				A														
(J.) unestami				AR	A													
(L.) acanthura			B	R	R	BR	P	P							P			
(L.) d. diogenes								Pdf	Pdf						P			s
(P.) chaugaensis																		B
(P.) coosae						BPR												
(P.) extraneus				R														
(P.) georgiae		B																
(P.) hiwasseensis			B															
(P.) parrishi			B															
(P.) scotti					R													
Fallicambarus																		
(C.) hedgpethi								f	df									
Faxonella																		
clypeata								Pd	df			t			fv		sv	

TABLE 2.—Continued

CRAYFISH	Endemic	RIVER BASIN																
		Little Tennessee	Hiwassee	Tennessee	Chattooga	Coosa	Tallapoosa	Chattahoochee	Flint	Ochlockonee	Aucilla	Suwannee	Saint Marys	Satilla	Altamaha	Newport	Ogeechee	Savannah
Orconectes																		
erichsonianus				AR	R	P												
forceps				R														
spinosus					R	R												
Procambarus																		
(D.) devexus	●																	P
(H.) advena	●														sv	s	s	s
(H.) caritus	●													b	sv			
(H.) pygmaeus												ot		bs	sv	s	s	s
(H.) talpoides									d	t		ot	s	bs				
(H.) truculentus	●														v		v	
(L.) barbatus															sv	s	sv	sv
(L.) pubischelae deficiens	●													bs	sv			
(L.) p. pubischelae												ot	o	bs				
(O.) acutissimus								f										
(O.) a. acutus									P*				b*		fv		fv	Pv
(O.) angustatus	●																	
(O.) enoplosternum															sv		sv	fv
(O.) epicyrtus	●																sv	s
(O.) fallax												ot	os	bs				
(O.) leonensis										t?	t?							
(O.) litosternum	●															s	sv	
(O.) lophotus				R	R	R												
(O.) lunzi														s	sv	s	s	
(O.) pubescens															fv		Psv	Pv
(O.) seminolae									df			ot	s	bs	sv		s*	
(Pe.) gibbus	●								df									
(Pe.) petersi	●																Pfsv	
(Pe.) raneyi															P			Pfv
(Pe.) spiculifer						PR	P	Pdf	Pdf	dt		t	s	bs	Pfv			P
(Pe.) versutus								f										
(S.) howellae	●								f						fsv			
(S.) paeninsulanus								d	df	t	t	ot	s	bs				
(S.) troglodytes															sv	s	fsv	fsv

PHYSIOGRAPHIC PROVINCES * Introduced

A - **Appalachian Plateau**
B - **Blue Ridge**
P - **Piedmont**
R - **Ridge and Valley**

Coastal Plain ***(Districts in italics)***

b - ***Bacon Terraces*** o - ***Okefenokee Basin*** v - ***Vidalia Upland***
d - ***Dougherty Plain*** s - ***Barrier Island Sequence***
f - ***Fall Line Hills*** t - ***Tifton Upland***

O. forceps, and *Procambarus (O.) lophotus.*

Chattooga: *Cambarus (D.) latimanus, C. (D.) striatus, C. (H.) longirostris* (introduced?), *C. (L.) acanthura, C. (P.) scotti, Orconectes erichsonianus, O. spinosus*, and *Procambarus (O.) lophotus.*

Conasauga: *Cambarus (C.) bartonii, C. (D.) cymatilis, C. (D.) latimanus, C. (D.) striatus, C. (H.) coosawattae, C. (H.) manningi, C. (H.) speciosus, C. (J.) conasaugaensis, C. (L.) acanthura, C. (P.) coosae, Orconectes spinosus, Procambarus (O.) lophotus*, and *P. (Pe.) spiculifer.*

In Georgia the following are not found outside of the Ridge and Valley Province: *Cambarus (D.) cymatilis, C. (P.) extraneus, C. (P.) scotti, Orconectes forceps, O. spinosus*, and *Procambarus (O.) lophotus.*

The Blue Ridge Province.—In Georgia this physiographic region encompasses the mountainous areas in the northeastern part of the state. Clark and Zisa (1976) recognize three districts within it: the western one comprising the Cohutta Mountains, which attain altitudes of 1000 to 1334 meters above sea level; the west-central McCaysville Basin, for the most part with elevations of 530 to 600 meters and bisected by a narrow strip of the Piedmont; and the eastern, the largest of the three, occupied by the Blue Ridge Mountains, with elevations ranging between 600 and 1567 meters. The watersheds of this province include the Conasauga, Coosawattee, and Etowah (all three tributaries of the Coosa River) on the west and southwest, the Chattahoochee and Savannah on the southeastern and eastern slopes, and the Little Tennessee and Hiwassee on the north. These mountainous districts consist primarily of metamorphic and igneous rocks (Precambrian and Paleozoic ages); consequently the streams flowing within and from the province are low in carbonates. Virtually all of the streams originate in seeps, springs, and upland bogs and flow over either bedrock or rock-littered beds; in the valleys they have cut through clay deposits and the stream beds contain much rubble.

The drainage basins and the crayfishes frequenting them are as follows.

Coosa: *Cambarus (C.) bartonii, C. (D.) latimanus, C. (D.) striatus, C. (H.) coosawattae, C. (H.) speciosus, C. (J.) conasaugaensis*, and *C. (L.) acanthura.*

Chattahoochee: *Cambarus (C.) bartonii* and *C. (J.) nodosus.*

Savannah: *Cambarus (C.) bartonii, C. (J.) asperimanus, C. (J.) nodosus*, and *C. (P.) chaugaensis.*

Little Tennessee: *Cambarus (C.) bartonii* and *C. (P.) georgiae.*

Hiwassee: *Cambarus (C.) bartonii, C. (D.) latimanus, C. (H.) longirostris, C. (J.) nodosus, C. (L.) acanthura, C. (P.) hiwasseensis*, and *C. (P.) parrishi.*

In Georgia the following are not known to occur outside of the Blue Ridge Province: *Cambarus (P.) chaugaensis, C. (P.) georgiae, C. (P.) hiwasseensis*, and *C. (P.) parrishi.*

The Piedmont Province.—Encompassing approximately one-third of the area of the state, this province forms a broad band some 160 to 220 kilometers wide between the Blue Ridge–Ridge and Valley provinces and the Fall Line Hills District of the Coastal Plain Province. The predominating rocks of the Piedmont Province are granite, schist, and gneiss and are largely Precambrian in origin, although wedges of metamorphosed Paleozoic sediments are also present. A few ridges in the western part of the province rise to heights of 800 meters; elsewhere elevations range from about 167 to 567 meters above sea level. Relief varies from as much as 267 meters in the northeast to as little as 17 in areas of the southwestern part of the province. Several of the larger rivers of the state course through or originate in the Piedmont Province: the Coosa, Tallapoosa, Chattahoochee, and Flint draining into the Gulf of Mexico, and the Savannah, Ogeechee, and Altamaha (Oconee and Ocmulgee) into the Atlantic Ocean.

The crayfish faunas of the Piedmont Province sectors of the several river basins are as follows.

Coosa: *Cambarus (C.) bartonii, C. (D.) latimanus, C. (D.) striatus, C. (H.) fasciatus, C. (J.) conasaugaensis, C. (P.) coosae, Orconectes erichsonianus*, and *Procambarus (Pe.) spiculifer.*

Tallapoosa: *Cambarus (D.) englishi, C. (D.) halli, C. (D.) latimanus, C. (D.) striatus, C. (L.) acanthura*, and *Procambarus (Pe.) spiculifer.*

Chattahoochee and Flint: *Cambarus (C.) bartonii, C. (C.) howardi, C. (D.) harti, C. (D.) latimanus, C. (D.) striatus, C. (J.) nodosus, C. (L.)*

diogenes diogenes, *Faxonella clypeata*, *Procambarus (O.) acutus acutus*, and *P. (Pe.) spiculifer*.

Altamaha: *Cambarus (C.) bartonii*, *C. (D.) latimanus*, *C. (D.) striatus*, *C. (L.) acanthura*, *C. (L.) diogenes diogenes*, *Procambarus (Pe.) raneyi*, and *P. (Pe.) spiculifer*.

Ogeechee: *Cambarus (D.) latimanus*, *Procambarus (O.) pubescens*, and *P. (Pe.) petersi*.

Savannah: *Cambarus (C.) bartonii*, *C. (D.) latimanus*, *C. (D.) striatus*, *C. (D.) strigosus*, *C. (J.) asperimanus*, *Procambarus (D.) devexus*, *P. (O.) a. acutus*, *P. (O.) pubescens*, *P. (Pe.) raneyi*, and *P. (Pe.) spiculifer*.

In Georgia the following are known to occur only in the Piedmont Province: *Cambarus (D.) englishi*, *C. (D.) halli*, *C. (D.) harti*, *C. (D.) strigosus*, and *Procambarus (D.) devexus*, and the latter three, insofar as is known, are endemic in the state.

THE COASTAL PLAIN PROVINCE.—Encompassing almost 13,760 square miles, the Coastal Plain Province occupies about three-fifths of the area of the state. The surface formations range from Cretaceous sediments in the Fall Line Hills to Recent unconsolidated deposits along the Atlantic coast and coastal islands. In addition to the Cretaceous sands, clays, and gravel (in the Fall Line Hills District), there are also clays, limestone, marl, and sand deposited during the Paleocene, Eocene, and Oligocene. Limestone formations of Eocene and Oligocene ages constitute conspicuous elements of the Dougherty Plain District. To the southeast from the Fall Line Hills and Dougherty Plain districts, these early Cenozoic sediments are tilted downward and overlain by Miocene deposits consisting of clay, limestone, marl, sand, and some dolostone. Miocene sediments form most of the surface layers of the Tifton Upland, Vidalia Upland, and much of the Bacon Terraces districts. Pliocene deposits are very limited or lacking, and Pleistocene sediments involving six shorelines characterize the Barrier Island Sequence District. The elevations of the Coastal Plain Province range from approximately 167 meters to sea level.

Traversing or lying wholly within (latter noted by asterisks) the Coastal Plain Province are the following river basins together with the crayfishes that occur in the respective watersheds within the province.

Chattahoochee: *Cambarus (D.) latimanus*, *C. (D.) striatus*, *C. (L.) diogenes diogenes*, *Fallicambarus (C.) hedgpethi*, *Faxonella clypeata*, *Procambarus (O.) acutissimus*, *P. (Pe.) spiculifer*, *P. (Pe.) versutus*, and *P. (S.) paeninsulanus*.

Flint: *Cambarus (D.) striatus*, *C. (J.) cryptodytes*, *C. (L.) diogenes diogenes*, *Fallicambarus (C.) hedgpethi*, *Faxonella clypeata*, *Procambarus (H.) talpoides*, *P. (O.) seminolae*, *P. (Pe.) gibbus*, *P. (Pe.) spiculifer*, *P. (S.) howellae*, and *P. (S.) paeninsulanus*.

*Ochlockonee: *Procambarus (H.) talpoides*, *P. (Pe.) spiculifer*, and *P. (S.) paeninsulanus*.

*Aucilla: *Procambarus (S.) paeninsulanus*.

*Suwannee: *Faxonella clypeata*, *Procambarus (H.) pygmaeus*, *P. (H.) talpoides*, *P. (L.) pubischelae pubischelae*, *P. (O.) fallax*, *P. (O.) seminolae*, *P. (Pe.) spiculifer*, and *P. (S.) paeninsulanus*.

*Saint Marys: *Procambarus (H.) talpoides*, *P. (L.) pubischelae pubischelae*, *P. (O.) acutus acutus*, *P. (O.) fallax*, *P. (O.) seminolae*, *P. (Pe.) spiculifer*, and *P. (S.) paeninsulanus*.

*Satilla: *Procambarus (H.) caritus*, *P. (H.) pygmaeus*, *P. (H.) talpoides*, *P. (L.) pubischelae deficiens*, *P. (L.) pubischelae pubischelae*, *P. (O.) fallax*, *P. (O.) lunzi*, *P. (O.) seminolae*, *P. (Pe.) spiculifer*, *P. (S.) paeninsulanus*.

Altamaha: *Cambarus (D.) latimanus*, *C. (D.) striatus*, *C. (D.) truncatus*, *Faxonella clypeata*, *Procambarus (H.) advena*, *P. (H.) caritus*, *P. (H.) pygmaeus*, *P. (H.) truculentus*, *P. (L.) barbatus*, *P. (L.) pubischelae deficiens*, *P. (O.) acutus acutus*, *P. (O.) enoplosternum*, *P. (O.) lunzi*, *P. (O.) pubescens*, *P. (O.) seminolae*, *P. (Pe.) spiculifer*, *P. (S.) howellae*, and *P. (S.) troglodytes*.

*Newport: *Procambarus (H.) advena*, *P. (H.) pygmaeus*, *P. (L.) barbatus*, *P. (O.) litosternum*, *P. (O.) lunzi*, and *P. (S.) troglodytes*.

Ogeechee: *Cambarus (D.) latimanus*, *C. (D.) reflexus*, *Faxonella clypeata*, *Procambarus (H.) advena*, *P. (H.) pygmaeus*, *P. (H.) truculentus*, *P. (L.) barbatus*, *P. (O.) acutus acutus*, *P. (O.) enoplosternum*, *P. (O.) epicyrtus*, *P. (O.) litosternum*, *P. (O.) lunzi*, *P. (O.) pubescens*, *P. (O.) seminolae*, *P. (Pe.) petersi*, and *P. (S.) troglodytes*.

Savannah: *Cambarus (D.) latimanus*, *C. (D.) reflexus*, *C. (L.) diogenes diogenes*, *Procambarus (H.) advena*, *P. (H.) pygmaeus*, *P. (L.) barbatus*, *P. (O.) acutus acutus*, *P. (O.) enoplosternum*, *P. (O.) epicyrtus*, *P. (O.) pubescens*, *P. (Pe.) raneyi*, and *P. (S.) troglodytes*.

Those species that in Georgia are confined to the Coastal Plain Province are as follows (those that seem to be endemic in the state are preceded by an asterisk): *Cambarus (D.) reflexus*, **C. (D.) truncatus*, *C. (J.) cryptodytes*, *Fallicambarus (C.) hedgpethi*, **Procambarus (H.) advena*, **P. (H.) caritus*, *P. (H.) pygmaeus*, *P. (H.) talpoides*, **P. (H.) truculentus*, *P. (L.) barbatus*, **P. (L.) pubischelae deficiens*, *P. (L.) pubischelae pubischelae*, *P. (O.) acutissimus*, *P. (O.) enoplosternum*, **P. (O.) epicyrtus*, *P. (O.) fallax*, **P. (O.) litosternum*, *P. (O.) lunzi*, *P. (O.) seminolae*, **P. (Pe.) gibbus*, *P. (Pe.) versutus*, **P. (S.) howellae*, *P. (S.) paeninsulanus*, and *P. (S.) troglodytes*.

Ecological Considerations

In exploiting the diverse aquatic and semiaquatic habitats existing in the state, the crayfishes exhibit an adaptive radiation that is not surpassed by any crayfish assemblage occupying a comparable area elsewhere in the world. At least a part of the diversity demonstrated by the sixty-odd species has been influenced by the environments invaded by the ancestral stocks, and, to be sure, there is strong evidence of channelization in the response of distantly related stocks to the same or similar habitats.

For convenience of discussing the crayfishes and the environments in which they live, four ecological groups are recognized: (1) the stream dwellers, (2) the lake, pond, and ditch inhabitants, (3) the burrowers, and (4) the cave dwellers. That the species occurring in Georgia are not all limited to a single type of habitat implied by these categories is obvious when it is realized that at least one, *Cambarus (D.) striatus*, occupies not only lentic and lotic habitats but also burrows, and it has been found in caves. Other species with a more limited ecological tolerance, however, are much more restricted in their habitat distribution.

THE STREAM DWELLERS.—With the availability of as wide a range of stream habitats as any geographic area in the eastern part of the United States, the opportunity for adaptations to varied lotic habitats has been extensive and surprisingly fully exploited by crayfishes occurring in the state. From the seeps, springs, and runoff in the Blue Ridge Province to the sluggish, muddy, or coffee-colored rivers of the Coastal Plain Province, there occurs a broad spectrum of lotic habitats. (Physical and chemical data obtained at several localities on most of the major streams in the state are summarized in a series of anonymous publications entitled *Water Quality Monitoring Data for Georgia Streams* and issued by the Georgia Department of Natural Resources, Environmental Protection Division, Atlanta. The most recent is for 1976, published in January 1977.)

In the small rills and tumbling brooks of the mountainous areas, several crayfishes have found congenial habitats. There they live among rocks in pools, or they dig intricate tunnel systems between the rocks, even in cascading areas. As a result of water coursing through such tunnels, the path of the channel of streams is frequently altered. Likewise, the water flowing in subterranean courses may follow a crayfish burrow, thus shifting the place of emergence to the surface. Such habitats are almost exclusively populated by members of the genus *Cambarus* that have been assigned to the nominate subgenus and to *Jugicambarus*. In such habitats *C. (C.) bartonii*, *C. (J.) asperimanus*, and *C. (J.) conasaugaensis* are found.

The larger mountain and valley streams (Figure 7*a,b*), with clear, cool, swiftly to moderately flowing water passing through alternating riffles and pools, have been invaded by members of three additional subgenera (*Hiaticambarus*, *Puncticambarus*, and *Depressicambarus*). In these rapidly flowing streams, those species typical of the headwaters occur in far smaller numbers, most frequently being restricted to the shallow littoral part of the rocky stream bed, where they construct tunnels beneath rocks that jut from the shore into the stream. The riffles are dominated by members of the subgenus *Hiaticambarus*, and the pools and less turbulent waters by those of the subgenus

FIGURE 7.—Lotic habitats in Georgia: *a*, Tallulah River in NW part of Rabun Co (Savannah Basin, Blue Ridge Province), stream and adjacent seepage areas and bogs frequented by *Cambarus (C.) bartonii* and *C. (J.) nodosus*; *b*, Cane Creek at St Rte 151, Walker Co (Chattooga Basin, Ridge and Valley Province), inhabited by *Cambarus (D.) latimanus*, *C. (H.) longirostris*, *C. (P.) scotti*, and *Orconectes erichsonianus*; *c*, Tobler Creek at St Rte 74, Upson Co (Flint Basin, Piedmont Province), supporting populations of *Cambarus (D.) latimanus* and *Procambarus (Pe.) spiculifer*; *d*, Little Black Creek at St Rte 112, Baldwin-Wilkinson Co line (Oconee Basin, Fall Line Hills District), frequented by *P. (O.) enoplosternum*; *e*, Savage Creek (choked with *Pontederia* sp.) 2 mi S of Pembroke on St Rte 119, Bryan Co (Canoochee-Ogeechee Basin, Barrier Island Sequence District), creek and adjoining roadside ditch frequented by *Procambarus (H.) advena*, *P. (H.) pygmaeus*, *P. (L.) barbatus*, *P. (O.) litosternum*, *P. (O.) lunzi*, and *P. (S.) troglodytes*; *f*, Ogeechee River at St Rte 119, Bulloch-Effingham Co line (Ogeechee Basin, Barrier Island Sequence District), frequented by *Faxonella clypeata*, *Procambarus (O.) enoplosternum*, *P. (Pe.) petersi*, and *P. (S.) troglodytes*. (*a*, *d*, *e*, courtesy of Daniel J. Peters.)

Puncticambarus and of the genus *Orconectes.* More rarely, both such areas are frequented by species belonging to the subgenus *Depressicambarus* and very infrequently (only in the Ridge and Valley Province) by one member each of two subgenera of *Procambarus*: *Ortmannicus* and *Pennides.*

Typifying the crayfish fauna of the riffles of such streams are: *Cambarus (H.) coosawattae, C. (H.) fasciatus, C. (H.) girardianus, C. (H.) longirostris, C. (H.) manningi,* and *C. (H.) speciosus,* and in the littoral areas, *C. (C.) bartonii, C. (J.) conasaugaensis,* and *C. (D.) striatus.* Occupying the less turbulent reaches of these mountain and valley streams are: *C. (J.) distans, C. (J.) parvoculus, C. (J.) unestami, C. (P.) chaugaensis, C. (P.) coosae, C. (P.) extraneus, C. (P.) georgiae, C. (P.) hiwasseensis, C. (P.) parrishi, C. (P.) scotti, Orconectes erichsonianus, O. forceps, O. spinosus, C. (D.) latimanus, C. (D.) striatus,* occasionally *Procambarus (Pe.) spiculifer,* and very rarely *P. (O.) lophotus.*

Streams in the Piedmont Province are also varied in their physical characteristics and in the crayfish fauna supported by them. In addition to the larger creeks and rivers carrying runoff from the Plateau, Ridge and Valley, and Blue Ridge provinces are the smaller springs, brooks, and creeks that have their origins in the Piedmont Province.

In most sectors of streams in the Piedmont Province, the rate of flow is not so great as that in the mountainous areas, and, in general, they have a less rock-littered bed (Figure 8*a*). In a number of areas, however, the streams flow over bed rock (Figure 7*c*) and riffles with rather swift currents. Many of the streams flow through clay or sand deposits, and the bottom may consist of rock or clay, frequently overlain by sand and/or silt. In wooded areas the shaded stream beds lack vascular plants, but where exposed to light a number of emergent plants flank the *Vallisneria* beds growing in the mainstream of the current. *Podostemum* dominates many riffle areas of the large creeks and rivers exposed to full or almost full light. Erosion of the clay soil in much of the Piedmont Province turns most of the streams yellowish red following rains. Except in those streams in which the current becomes so sluggish that the silt and sand loads seal the rocks to the stream bed, the clay particles seem not to affect adversely the crayfish faunas. In the upper parts of the province, as well as in isolated streams elsewhere within it that resemble those of the mountains, the crayfish do not appear to recognize any appreciable differences from the conditions existing in the larger mountain streams. The springs and small runs at lower elevations, however, are dominated, if not occupied to the exclusion of all other crayfishes, by members of the subgenus *Depressicambarus.* The larger streams in particular, and, to some extent, even some of the smaller ones, are invaded by members of the subgenus *Pennides* and more rarely by those of the subgenus *Ortmannicus.* In the upper Piedmont Province, several of the species that also occur in the mountain and valley streams are present: *Cambarus (D.) latimanus, C. (H.) fasciatus, C. (P.) coosae,* and *Orconectes spinosus.* Others include *C. (C.) bartonii, C. (D.) englishi, C. (D.) halli, P. (Pe.) petersi, P. (Pe.) raneyi, P. (Pe.) spiculifer,* and rarely *P. (O.) acutus acutus* and *P. (O.) pubescens.*

Streams in the Coastal Plain Province are at least as varied as are those of the Piedmont Province. Perhaps the most conspicuous differences lie in the color of the water. Those streams originating in the more inland provinces (the Chattahoochee, Flint, Ocmulgee-Oconee-Altamaha), except during extended dry seasons, are silt laden, whereas those lying almost or wholly within the Coastal Plain Province are predominantly clear but most are amber to coffee-colored. In the Fall Line Hills District, the streams (Figure 7*d*) are not markedly different from those of the lower Piedmont Province, numbers of them gaining velocity in areas of steep gradient. In upland sections of the province there exist a large number of spring-fed, clear streams that flow primarily over sandy bottoms, but in lee areas dense aquatic vegetation supported by silt deposits rich in organic matter is a conspicuous feature, and the water in the larger creeks is often amber in color. Most of these creeks lack or have little rock litter on their beds, and the crayfishes find cover in the

FIGURE 8.—Lotic and lentic habitats in Georgia: *a*, Newberry Creek at Rte S1819, Burke Co (Savannah Basin, Vidalia Upland District), inhabited by *Cambarus (D.) latimanus*, *Procambarus (O.) pubescens*, and *P. (Pe.) raneyi*; *b*, tributary to Newberry Creek (mouth in right foreground of Figure 8*a*), frequented by *Cambarus (D.) latimanus* and *C. (D.) reflexus*, burrowing along banks and in seepage area (center); *c*, seepage area on Savannah River Bluff at boat landing 0.2 mi NW of Rte 119, Effingham Co (Savannah Basin, Barrier Island Sequence District), inhabited by *Cambarus (D.) reflexus* and *C. (L.) diogenes diogenes*; *d*, semipermanent pool in roadside ditch 0.2 mi SW of US Hwy 221 on St Rte 64, Atkinson Co (Satilla Basin, Bacon Terraces District), frequented by *Procambarus (H.) pygmaeus*, *P. (H.) talpoides*, *P. (L.) pubischelae pubischelae*, and *P. (O.) seminolae*; *e*, temporary pool and wet roadside ditch 2.6 mi NW of Lanier Co line on St Rte 168, Berrien Co (Suwannee Basin, Tifton Upland District), populated by *Procambarus (H.) talpoides*, *P. (L.) pubischelae* × *deficiens*, and *P. (O.) seminolae*; *f*, fluctuating pool in roadside ditch and borrow pit 15.4 mi N of Fargo on US Hwy 441, Clinch Co (Suwannee Basin, Okefenokee Basin District), frequented by *Procambarus (H.) pygmaeus*, *P. (H.) talpoides*, and *P. (O.) seminolae*.

organic debris and roots of shoreline plants exposed along undercut banks. In segments of the streams where light is sufficient to support aquatic vascular plants, some crayfishes are abundant among the vegetation and in the organic substrate. The lower-lying parts of the Coastal Plain Province are traversed by rather sluggish streams of reddish brown water (Figure 7*f*), in some areas (particularly in the Tifton Upland) flowing over sandy bottoms and in others through swamps with bottoms rich in organic debris and frequently choked with dense growths of vascular plants (Figure 7*e*). The larger streams of the Coastal Plain Province are often flanked by cypress swamps as much as four to six miles wide (Cooke, 1925:51); there channels often become divided, coursing between islands. A conspicuous, if not common, feature of the lower Coastal Plain Province is the presence of large springs, from which crystal clear water flows with a moderate to rapid current. Many of these streams support a rich vegetation and, concomitantly, a large crayfish population.

Most of the stream-dwelling crayfishes of the Coastal Plain Province are members of the genus *Procambarus* and belong to the subgenera *Pennides* (all of the members of which are restricted to lotic habitats) and the more ecologically diverse *Ortmannicus* and *Scapulicambarus*. Less frequently invading the streams of the province are members of the genera *Cambarus*, *Faxonella*, and *Procambarus*, subgenus *Leconticambarus*.

The widespread crayfish in the Coastal Plain Province of the state is *Procambarus (Pe.) spiculifer*, and other species frequenting lotic habitats within the province are: *P. (O.) acutissimus*, *P. (O.) acutus acutus*, *P. (O.) angustatus*, *P. (O.) enoplosternum*, *P. (O.) epicyrtus*, *P. (O.) fallax*, *P. (O.) litosternum*, *P. (O.) lunzi*, *P. (O.) pubescens*, *P. (O.) seminolae*, *P. (Pe.) gibbus*, *P. (Pe.) petersi*, *P. (Pe.) raneyi*, *P. (Pe.) versutus*, *P. (S.) howellae*, *P. (S.) paeninsulanus*, and *P. (S.) troglodytes*. Very rarely *Cambarus (D.) latimanus*, *Faxonella clypeata*, *P. (L.) barbatus*, *P. (L.) pubischelae deficiens*, and *P. (L.) pubischelae pubischelae* occur in very sluggish areas or backwaters of streams traversing the Coastal Plain Province.

THE LAKE, POND, AND DITCH DWELLERS.—The crayfish habitats in the state that have been most neglected in this study are the lakes and ponds. To determine the composition of the crayfish fauna in them, trapping must be employed, and collecting in the littoral area at night with the aid of a light would no doubt be fruitful in some lakes. During the course of this work, I have set no traps, and night collecting has been minimal. Consequently little is known of the fauna in such habitats.

Surely prior to impoundment, segments of the streams that are now converted to man-made lakes supported a rich crayfish fauna. (We know this to be true of the flooded section of Talking Rock Creek, a tributary of the Coosawattee River above the "reregulation dam" below Carter Reservoir in southeastern Murray County.) What effect these impoundments have had on the crayfishes, to my knowledge, is purely conjectural, but after repeatedly viewing the barren, broad, baked clay beds above low water level in several of them, I strongly suspect that the crayfish populations adapted to lotic habitats have been drastically reduced or even exterminated. The probability that populations of one or more less ecologically specialized species has become established in these fluctuating lakes seems slight. To most of the stream dwellers that formerly inhabited the riverbeds, these lakes must be as intolerable as a desert.

Except in certain districts of the Coastal Plain Province, there are few natural lakes in the state. Among them are several resulting from abandoned channels along the larger rivers, and even these are more common in the Coastal Plain Province than elsewhere. Far more extensive and conspicuous are those lakes derived from old sea floors—for example, standing water in the Okefenokee Swamp and at least one lake in Lanier County (Cooke, 1925:50)—and solution lakes and sinkhole ponds, which are common on the Dougherty Plain and Tifton Upland. None of the natural lakes are deep, and in many of them rooted vegetation occurs from shore to shore. To the south in Florida there are many solution lakes that occasionally drain underground and become dry within a few hours, and there is every reason to believe that at least some of the lakes and sinkhole ponds in the Tifton Upland and Dougherty Plain likewise have temporary or permanent continuity with subsurface water. Even though man-made, the extensive system of roadside and drainage ditches in the Piedmont and throughout most of the Coastal Plain provinces (Figures 8*d–f*, 9*f*) furnishes some of the most important crayfish habitats existing in the state. Certainly without these man-made scars traversing the ranges of so many species, we should know much less than we do about the crayfish fauna of the state, and were it not for those that contain water during most of the year, little would be known about these species that exploit lentic habitats.

Extrapolating from my limited knowledge of the Florida crayfishes that frequent lakes and ponds, and adding to this the few records of those occurring in Georgia lakes and the considerable data on the inhabitants of flooded ditches, I dare predict which species will be found to occur in the lakes and ponds of the Coastal Plain: in the Dougherty Plain and Tifton Upland, *P. (S.) paeninsulanus* and/or *P. (O.) leonensis* (which has not yet been found in the state) should be common in the littoral areas. East of the Suwannee River the latter should be replaced by *P. (O.) fallax* and *P. (O.) seminolae*. In and between the Altamaha and Savannah rivers, the dominant inhabitants of lentic habitats include *P. (O.) lunzi* and *P. (S.) troglodytes*. Within their ranges, *P. (O.) a. acutus* and *P. (S.) howellae* no doubt frequent natural lakes and ponds as they do small impounded farm ponds and permanent pools in roadside ditches. Almost certainly, the secondary burrowers (see below) existing in the vicinity of at least some of the lakes will invade them as they have some of the small cypress ponds and pools in roadside ditches.

THE BURROWERS (Figures 9, 10)—There is every reason to believe that all of the crayfishes of the state are not only able to burrow but actually engage in burrowing at least occasionally. Some species spend only a part of the year in these subsurface habitats, whereas others absent themselves for short seasons, and still others seldom or almost never leave them.

In constructing a burrow, the crayfish loosens the soil by using the ambulatory pereiopods. When sufficient material is free, the third maxillipeds are thrust below the loosened substrate. Once the maxillipeds are loaded, the chelipeds are pressed over the load, and the crayfish moves headfirst through a passageway to the surface, where the load (pellet) is either dropped or positioned and tapped into place with the chela. Afterward, the crayfish descends into the burrow tailfirst. Most of the digging is accomplished at night, but on overcast days, it is not unusual to find fresh (very wet) pellets of soil on chimneys at any hour.

Interest in the crayfish chimney was expressed as early as 1884 when, in describing the burrow and chimneys of *Cambarus d. diogenes*, Tarr (1884: 128) stated that he did not "... think the chimney is a necessary part of the nest but simply the result of digging." Abbott, later in the same year, took exception to this statement and countered Tarr's conclusion by stating: "On the contrary, I am convinced that the crayfish *builds* his chimney or tower; that he often studies the locality with care and *builds* to suit the chosen site" (Abbott, 1884:1157). Although Abbott was unaware of the function that the chimney might serve, I suggest that a clue to a possible explanation had been unwittingly furnished him in the article containing the conclusion with which he was in disagreement. Tarr (1884:128) stated:

> At first [the crayfish] burrows diagonally ... [and] when the burrow must be dug deeper the economy of a perpendicular burrow must immediately suggest itself.... Mud from this and also from the first part of the perpendicular burrow is carried out of the diagonal opening and deposited on the edge. If a freshet occurs before this rim of mud has a chance to harden, it is washed away and no mound is formed over the oblique burrow. After the vertical opening is made, as the hole is bored deeper, mud is deposited on the edge, and the deeper it is dug the higher the mound.

Had my attention not been called to Vogel's (1978) article on "Organisms that Capture Currents" by my colleague Thomas A. Bowman, I should have continued to overlook the possible significance of the chimneys marking the open-

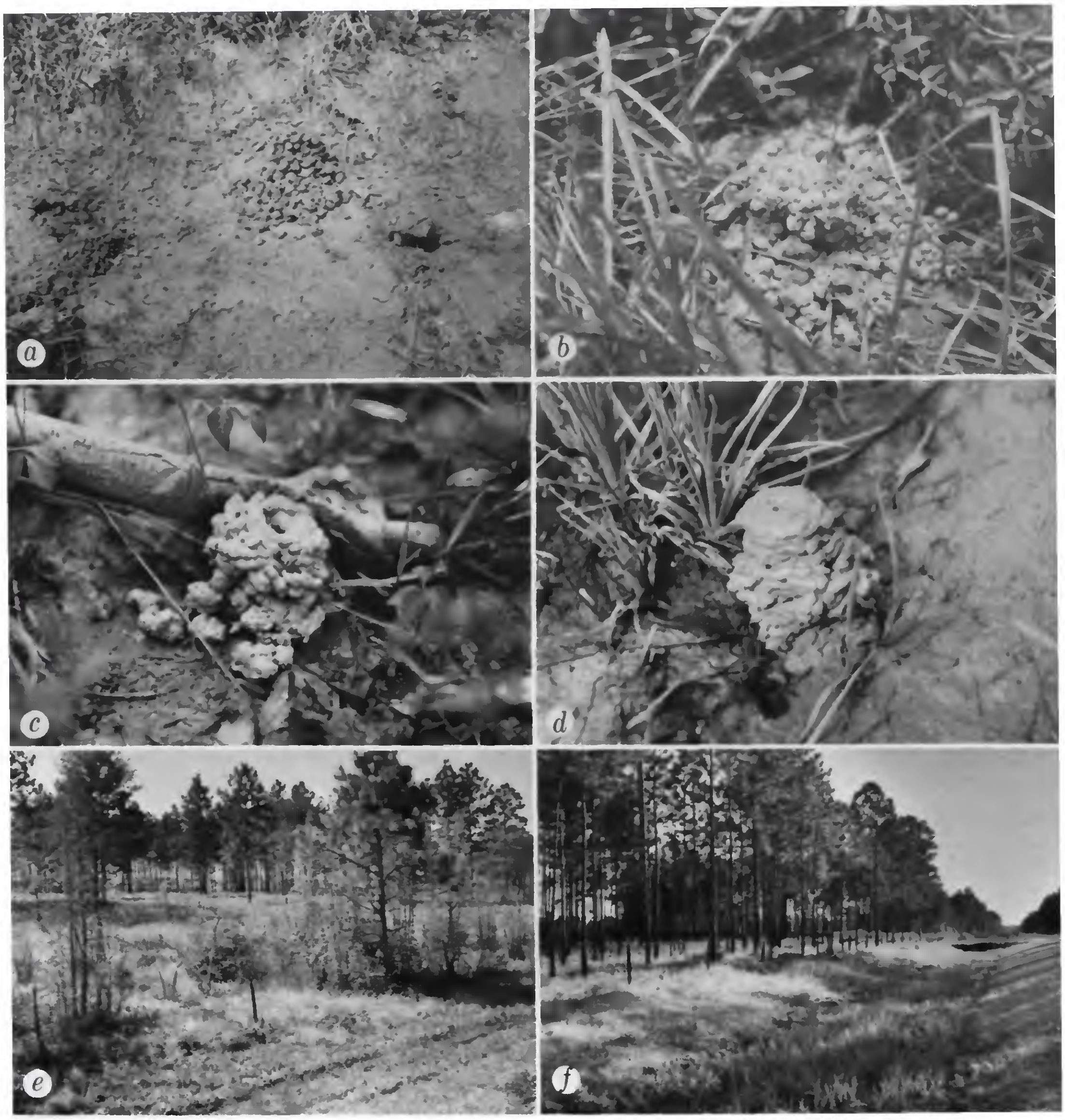


FIGURE 9.—Crayfish chimneys marking burrows, and habitats where they occur: *a*, burrow of *Procambarus (H.) talpoides* 8.1 mi N of US Hwy 280 on St Rte 215, Wilcox Co (Ocmulgee Basin, Tifton Upland District); *b*, burrow of *Procambarus (H.) advena* 0.1 mi S of Toombs Co line on St Rte 130, Montgomery Co (Altamaha Basin, Vidalia Upland District); *c*, burrow of *Procambarus (L.) barbatus* from along South Fork of Ogeechee Creek at US Hwy 301, Screven Co (Ogeechee Basin, Vidalia Upland District); *d*, same from 1.3 mi E of St Rte 80 and Rte C119, Bulloch Co (Ogeechee Basin, Barrier Island Sequence District); *e*, damp to wet areas in rolling hills 0.2 mi W of Irwin Co line on St Rte 32, Turner Co (Suwannee Basin, Tifton Upland District), inhabited by *Procambarus (H.) talpoides* and *P. (O.) seminolae*; *f*, flatwoods 2.9 mi SW of Alma on St Rte 64, Bacon Co (Satilla Basin, Bacon Terraces District), ditch inhabited by *P. (H.) talpoides* (*b*, courtesy of Daniel J. Peters.)

ings of crayfish burrows. Vogel pointed out that the burrows of many animals are so constructed as to take advantage of wind and water currents in being flushed. This has suggested to me that the differential heights of the mouths of crayfish burrows (see Tarr's description above) would at least seasonally effect a flow of air through some of the passageways within the tunnel systems of the animal. The importance that attaches to such an air current becomes evident when one realizes that the oxygen concentration of the water in the tunnel system is often less than 2 mg/l. Certainly the movement of air in the system would, except in times of drought or excessive cold weather, make the galleries more livable. During such adverse weather conditions the crayfish can and does plug one or more of the openings to its burrow.

Without data to demonstrate that the chimneys aid in venting the burrows, the possibility that these turrets do so inclines me to agree with Abbott (1884) that the chimneys of crayfish burrows are a functional part of the tunnel systems, and that many, if not most, are at least in part designed.

Hobbs (1942b) recognized three categories of burrowers among the crayfishes occurring in Florida, and while they cannot be accurately defined, such a classification has been found useful.

Primary Burrowers: Among those so categorized are crayfishes that spend almost their entire lives below the surface of the ground; occasionally they leave their lairs (Figures 9*a*,*b*, 10*a*,*d*) on brief forays on land, presumably searching for food, and, at times, the males for a mate. Seldom and in the burrows of few species, are the passageways in communication with bodies of open water. It is not surprising that the systems of galleries constructed by these crayfishes is more complex than those of species that spend less of their life below ground. The soil in which burrows are constructed varies from coarse sand through sandy loams, sandy clay, and red or blue white clays. Insofar as I have been able to determine, the only consistent generalized feature of these burrows is the presence of at least one spiraling-to-subvertical tunnel that extends downward below the water table and a series of near horizontal ones that radiate from the former (Figure 10*a*). One or several of the radial galleries may be as much as three meters in length, dip below the water table, and may or may not open to the surface. Most of the openings are marked by chimneys that may or may not exhibit a design. In wooded areas, the tunnels wind among and around roots that, in places, serve as one of the walls of the passageway. In areas devoid of shrubs and trees, the tunnel walls are not supported even in a soil that consists of little more than coarse sand.

When the burrows are being excavated, the crayfishes respond to being disturbed in a variety of ways, some of which are predictable if the identity of the occupant is known. For example, one can be reasonably certain that when the burrow of *Cambarus (D.) reflexus* or that of *C. (D.) harti* is opened, the crayfish is going to retreat to the end of one of the passageways and remain there until cornered or until long after the disturbance has ceased. In contrast, if individuals of *Procambarus (H.) talpoides* retreat to the deep subvertical passage and if this tunnel is opened to the water table and left undisturbed for a few minutes, the crayfish usually appears at the air-water interface.

During and following a rainy season, the activity of the primary burrower is clearly evident in the new chimneys, as well as by the pellets that are added to the old ones; furthermore, at this time the crayfish is more likely to be found in one of the horizontal passages. With the arrival of the dry season, it often begins to plug the superficial sections of the runways, presumably reopening or extending the deep passage, keeping ahead of the receding water table. To some degree, the same is true with the advent of cold weather and their moving to deeper warmer water. Many times I have removed chimneys in searching for a burrow, to find no passageway beneath or even near it, and if the subsoil is like that at the surface, the former course of the tunnel that once connected the passageways to the chimney cannot be ascertained; of course, if the crayfish is obtaining the "fill" from a subsoil that differs in texture or color

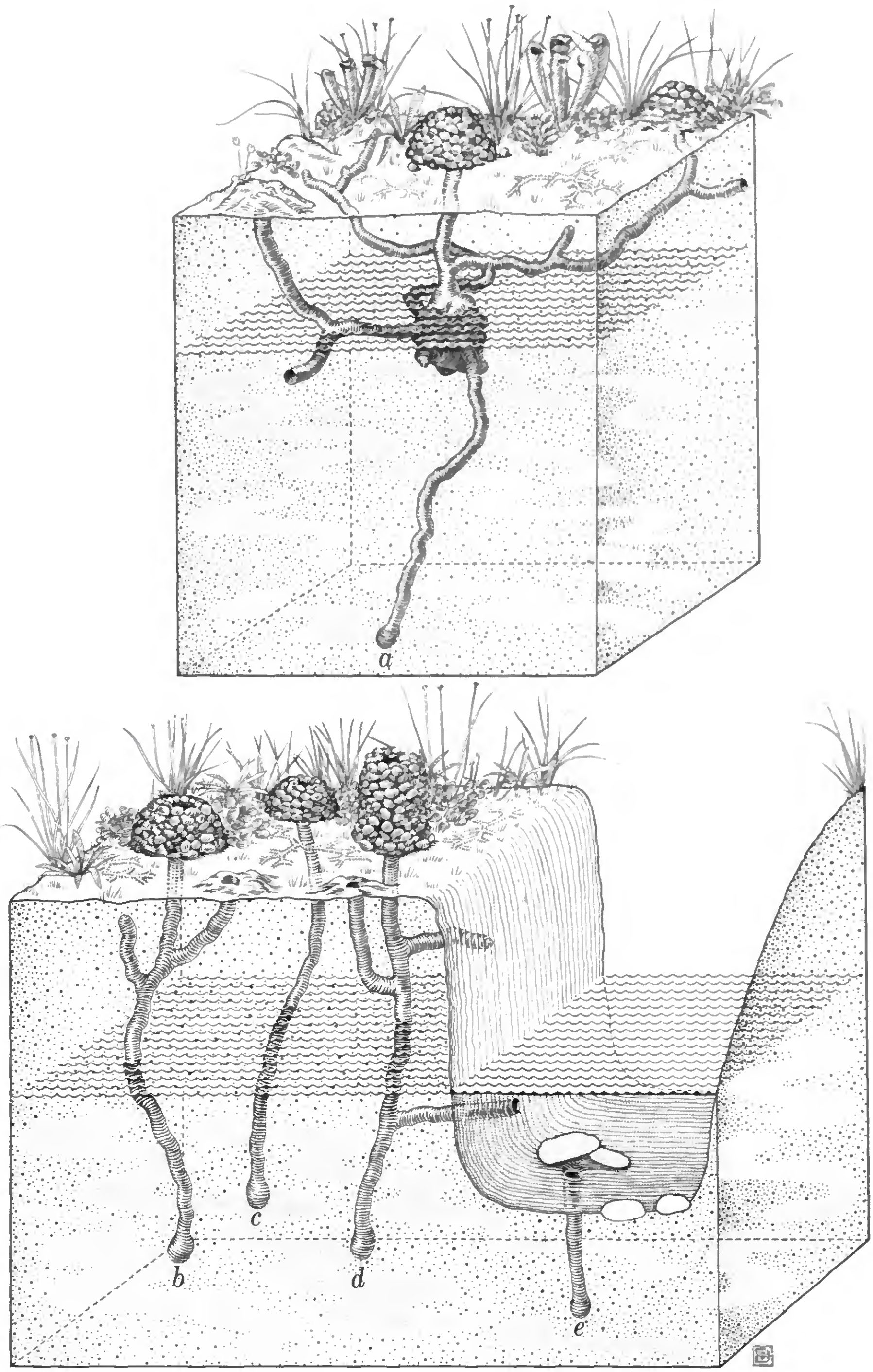


FIGURE 10.—Generalized crayfish burrows: *a*, *d*, those of primary burrowers; *b*, that of secondary burrower; *c*, *e*, those of tertiary burrowers.

from the more superficial layer, the position of the now obliterated tunnel can be discerned.

Whereas most of the primary burrowers avoid a confrontation with a person (or perhaps with any animal or object) digging into or destroying a part of their tunnel system by retreating to some gallery until the disturbance ends, at least some members of *C. (D.) cymatilis* move to the area being disturbed and face the intruder with upraised, gaping chelae, refusing to retreat.

Among the Georgia crayfishes, the following are considered by me to be primary burrowers: *Cambarus (D.) cymatilis, C. (D.) harti, C. (D.) reflexus, C. (D.) striatus* (in certain areas), *C. (D.) strigosus, C. (D.) truncatus, C. (J.) nodosus, C. (L.) acanthura, C. (L.) diogenes diogenes, Procambarus (D.) devexus, P. (H.) advena, P. (H.) caritus, P. (H.) talpoides,* and *P. (H.) truculentus.*

Cambarus (D.) striatus and the two members of the subgenus *Lacunicambarus* differ from the other species listed and should perhaps be designated as atypical primary burrowers. Throughout most of its range the former occurs in lentic and lotic habitats, but in much of Georgia, particularly in the lower Piedmont Province, many individuals and certain populations appear to spend virtually all of their lives in and around burrows. The excavations made by them are not nearly so highly branched as are those of most of the other primary burrowers. The burrows of *C. (D.) strigosus* are sometimes also rather simple. Whereas the only adult specimen of *C. (L.) acanthura* that I have observed in open water was an ovigerous female, juveniles are abundant in streams in the spring. Presumably they move from these lotic habitats and construct comparatively simple burrows along the stream bank or in the flood plains during the summer, afterward spending the greater part of their lives in the burrows. Much like the latter species, *C. (L.) d. diogenes* remains in burrows most of the year, but on a number of occasions in the spring I have collected juveniles, first form males, and ovigerous females from streams. Their burrows, resembling those of *C. (L.) acanthura*, consist of a subvertical passageway with two or three short branches to or approaching the surface and, when constructed near a body of water, one gallery communicating with it (Figure 10*d*). Most individuals respond to roiling of the water in the burrow by coming to the air-water interface rather quickly after agitation of the water ceases. The chimneys marking the mouths of their burrows are frequently, if not usually, beautifully tubuliform, often attaining heights of one-third of a meter.

There is evidence that at least to some degree the complexity of the tunnel system of the primary burrowers is influenced by the mean proximity of the water table to the surface: the deeper the table is situated, the less complex the burrow. Furthermore, the system of galleries occupied by females is usually more complex than that housing males, and concomitantly has more chimneys marking current and abandoned openings to the surface. Of the hundreds of burrows constructed by members of primary burrowing species that I have excavated, never have I found two individuals occupying a single tunnel system.

Although there is every reason to believe that among many of the tertiary burrowers the animals do not recognize, or at least exchange, their abodes, I suspect that most of the lives of at least the female members of the subgenus *Hagenides* (all except one of which are primary burrowers) are spent in a single tunnel system. Presumably when an occupant dies, the abode is taken over by a juvenile.

It is not known how and when the young are dispersed in these forms that infrequently or never enter open bodies of water. Perhaps they leave, or are driven from, the complex in which they hatch during or shortly after a rain and immediately begin construction of their own home burrow. In the spring, many chimneys are seen that consist of comparatively small pellets; these mark tunnel systems containing individuals of the subgenus *Hagenides* that hatched the previous year (late spring to fall). Whereas their abode might have had its origin in the walls of one of the radial galleries of the mother's burrow and the connection later plugged, I have never observed small lateral passageways. Perhaps such temporary tunnels are constructed below the water table. Inasmuch as my observations, particularly in recent years, have been restricted primarily to the spring and during a few very short periods in the fall, perhaps, if the young do leave their original home burrow through an underground passage, I have overlooked such small galleries.

In Georgia, the primary burrowers occur in several types of habitats in which the one feature shared in common by them is a water table that seldom, if ever, drops more than one to three meters below the surface of the ground. Such a condition obtains in the Blue Ridge Province along streams, in seepage areas and bogs, and in the vicinity of springs. Exploiting these habitats are *Cambarus (J.) nodosus* and *C. (L.) acanthura*. In the Ridge and Valley Province, the primary burrowers are *C. (D.) cymatilis, C. (D.) striatus,* and *C. (L.) acanthura*. Tunnel systems of these crayfishes have been found both adjacent to and in the flood plains of streams, as well as some distance from a stream in areas where the ground water, always within a meter of the surface, frequently is no more than a few centimeters beneath it. In the Piedmont Province, the primary burrowers are found in habitats not markedly different from those in the Ridge and Valley Province; however, they have also been found in swampy areas near springs and on seepage slopes but are especially common in low-lying areas adjacent to springs. Constituting the Piedmont assemblage of primary burrowers are *Cambarus (D.) harti, C. (D.) reflexus, C. (D.) striatus, C. (D.) strigosus, C. (L.) acanthura, C. (L.) diogenes diogenes,* and *Procambarus (D.) devexus*.

Within the Coastal Plain Province, the habitats that have been invaded by the primary burrowers range from low-lying areas along streams and seepage slopes (particularly in the Fall Line Hills and higher elevations of the Vidalia Upland districts (Figure 8*b*), but even in the Barrier Island Sequence District) on many of which pitcher plants, lycopods, and sundews abound, to pine flatwoods and poorly drained swamp lands of the Tifton Upland (Figures 8*e*, 9*e*), Bacon Terraces (Figures 8*d*, 9*f*), Okefenokee Basin (Figure 8*f*), and Barrier Island Sequence districts (Figure 8*c*). Found in this province are the following: *Cambarus (D.) reflexus, C. (D.) striatus, C. (D.) truncatus, C. (L.) diogenes diogenes, Procambarus (D.) devexus, P. (H.) advena, P. (H.) caritus, P. (H.) talpoides,* and *P. (H.) truculentus*.

A summary of the distribution of these primary burrowers in the state is presented in Table 2 and Figures 41, 53, 87, 105, and 120.

Secondary Burrowers: These crayfishes spend much of their lives in burrows but frequently move into open water during rainy seasons. Their abodes (Figures 9*c,d*, 10*b*) are comparatively simple ones, usually consisting of a single subvertical passageway that may slope gently or descend in an irregular spiral. Seldom are there more than two openings to the surface, and rarely is there a second passageway leading toward the water table.

Species that are so classified are most abundant in depressions such as swamp pools, borrow pits, and roadside ditches that during wet seasons are flooded but throughout much of the year contain no standing water. The secondary burrowers are rarely found in seepage areas or bogs in which the water table is at, or immediately below, the surface throughout the year.

The chimneys marking the burrows of these crayfishes are not always conspicuously different from those of the primary burrowers. Frequently I have opened a tunnel system believing it to be that of a secondary burrower only quickly to find horizontal passageways and a primary burrower in one of the galleries. Thus some of the chimneys are rather symmetrical while others are very irregular. The depth of the tunnels of the secondary burrowers varies markedly; they may or may not penetrate the water table. When I first encountered crayfishes that had failed in their digging to reach the groundwater level, I assumed that I had interrupted an act of excavation that would have continued until the occupant had at least reached water. After repeatedly håving found secondary and tertiary burrowers in tunnels that ended blindly above the water table—and sometimes the crayfish (even an ovigerous female) in them in a state of torpor—I am not at all certain that the crayfish would have dug deeper; rather it might await the elevation of the groundwater level before becoming active again. In all such burrows the surrounding soil was damp, and I assume that the humidity at the bottom of the tunnel was at or near saturation levels.

Frequently pairs of individuals, consisting of a first form male and a female, are found occupying the same burrow, and rarely I have found a forked burrow with an ovigerous female occupying one arm and a first form male occupying the other. Never, however, have I encountered a female carrying eggs or young sharing a single passageway with another adult of either sex. Only infrequently have I seen young remaining in the burrow with the mother after they had attained a total length of approximately 20 millimeters.

The secondary burrowers also are able to plug the superficial section of their tunnel system from below, and in dry seasons as much as or more than 30 centimeters of the upper part of the original tunnel may be filled.

Among the Georgia crayfishes, the following species may be categorized as secondary burrowers: *Fallicambarus (C.) hedgpethi*, *Faxonella clypeata*, *Procambarus (H.) pygmaeus*, *P. (L.) barbatus*, *P. (L.) pubischelae deficiens*, and *P. (L.) pubischelae pubischelae*.

Tertiary Burrowers: More than half of the crayfishes occurring in Georgia are so classified. These are those species that live in open water and retreat to burrows (1) in the winter, moving below the frost line, (2) (females) as the time of ovulation approaches, entering and remaining there to lay and brood the eggs, and (3) when the body of water begins to disappear, thus avoiding dessication and finding protective cover.

There is a wide spectrum of variation in the burrowing habits of the species referred to this category, ranging from such forms as the riffle-dwelling *C. (H.) longirostris* to *Cambarus (D.) latimanus* and *Procambarus (O.) acutus acutus*, which inhabit more sluggish areas of streams as well as lentic habitats. The former digs subvertical passages in the stream bed (Figure 10*e*) during the fall and retires to them before the water in the stream bed freezes; the males reappear in open water in the early spring, and the females emerge in the late spring or early summer after the young have become independent. In streams with adequate cover, *C. latimanus* may remain concealed among rocks most of the year, but much more often it constructs comparatively complex burrows in the banks, apparently beginning its digging below the mean water level and once in the bank extending galleries in all directions. In complexity, some of their tunnel systems rival those of the primary burrowers. Except when plugged from within, or during very low-water stages, the passageways are in communication with the water in the stream, and, after dark, the crayfish occupying them frequently wander about the stream bed.

Populations of *P. (O.) a. acutus* that frequent lentic habitats construct simple, subvertical burrows (Figure 10*c*) in or along the margin of the pool or pond in which they spend much of the year. Frequently the crayfish are found in pairs in such burrows, and judging from the few ovigerous females that have been found, most must remain in the excavation until the young have become at least semi-independent. If the water table retreats, the crayfish enter existing burrows or construct new ones, and if the body of water continues to disappear, they resume their digging, plugging the mouth of the excavation from below and filling the more superficial part of the tunnel with the soil removed from below as they follow the descending water table. In late fall, I have dug second form males of this species from burrows constructed at the edge of a drying roadside pond. The burrows had been plugged and were about one meter deep, sufficiently so as to have penetrated well below the frost line.

That no sharp demarcation exists between the three types of burrowers recognized herein is exemplified by the burrowing habits of *Procambarus (O.) seminolae*, which frequents a broad range of habitats, and by the males of some primary burrowers. Those members of *P. (O.) seminolae* sharing roadside ditches with secondary burrowers assume virtually the same burrowing habits as do the latter. Furthermore, members of the species that live in permanent streams reflect the habits of the stream dwellers; thus the species is represented by both secondary and tertiary burrowing individuals. Occasional males of *P. (H.) talpoides* have been found in burrows, perhaps newly constructed, that were no more complex than those of the secondary burrowers, possessing only one branch from the principal subvertical tunnel.

Soil types, except as they are indicative of the groundwater level, appear to have little or no influence on the distribution of the burrowing crayfishes. Representatives of each of the three types of burrowers have been found in soils ranging from virtually pure sand, sand and rocks, through sandy humus, sandy clay, and blue and red clays. Some of these soils are so hard at times that they resemble sandstone or fired clay!

THE CAVE DWELLERS.—The karst areas of the state lie in the extreme northwestern and in the southwestern parts. In the former, the subterranean passages occur principally in Ordovician limestones of Dade, Walker, and Chattooga counties. In the southwest, the subterranean passageways lie within much younger limestone deposits of Eocene and Oligocene age in the Dougherty Plain District of the Coastal Plain Province.

The only troglobite known to occur within the state, *Cambarus (J.) cryptodytes*, has been collected in a single cave in Decatur County. As pointed out in the section devoted to *C. (A.) hamulatus*, this crayfish almost certainly occurs in the subsurface waters in the northwestern corner of Dade County. In addition to the troglobites, however, three troglophilic species (*Cambarus (C.) bartonii*, *C. (D.) latimanus*, and *C. (D.) striatus*) have also been found in streams flowing through caves in the Appalachian Plateau and Ridge and Valley provinces.

Phylogenetic Considerations

To aid in visualizing the phylogenies as interpreted and discussed herein, Figures 11–25 are offered. The terminal illustrations of Figures 11 and 20 represent, for the most part, species groups and are repeated as the "stem forms" in the following figures. Inasmuch as the subgenus *Distocambarus* is monotypic, no further illustrations of this line are included.

Morphological Aspects

For reasons that have been presented elsewhere (Hobbs, 1962), the secondary sexual features, particularly those of the first pleopod of the male, seem to provide more reliable characteristics than others that aid in the assessment of relationships of members of the genus *Procambarus*. Nowhere is this better illustrated than among the Georgia crayfishes. Paradoxically, within species groups that have become adapted to similar habitats, the secondary sexual features are more diverse than are those features that seem to have been channelized by the environment. Such is clearly evident within several of the infrageneric groups occurring in the state. For example, if the secondary sexual features of the members of the subgenera *Ortmannicus* and *Scapulicambarus* are disregarded, one finds far more similarity between members of *Ortmannicus* that dwell in lentic habitats (the *blandingii* Group) and the three species assigned to the subgenus *Scapulicambarus* than between the lentic (the *seminolae* Group) and lotic (the *pictus* Group) members of *Ortmannicus* (cf. Figures 136, 137, 182). A comparison based on the first pleopod of the male, however, reveals that the presence of a well-defined shoulder on the cephalic surface (along with other features of the terminal elements) clearly sets the members of *Scapulicambarus* (Figure 16) apart from those of the subgenus *Ortmannicus* (Figures 13–15). At the same time, the only characteristics that I have observed to be unique in each species of both subgenera are features of the first pleopod and sometimes those of the annulus ventralis.

Certain characteristics of a hypothetical ancestor of the American cambarid crayfishes were enumerated and discussed by Hobbs (1962:273–278), and the first pleopod of the first form male is depicted in Figure 11*a*, herein. Among the Georgia species possessing the largest combination of these characteristics are members of the subgenus *Pennides*. All five representatives occurring in the state are more specialized in some respect than are some others that frequent streams in, or bordering, the Mississippi Embay-

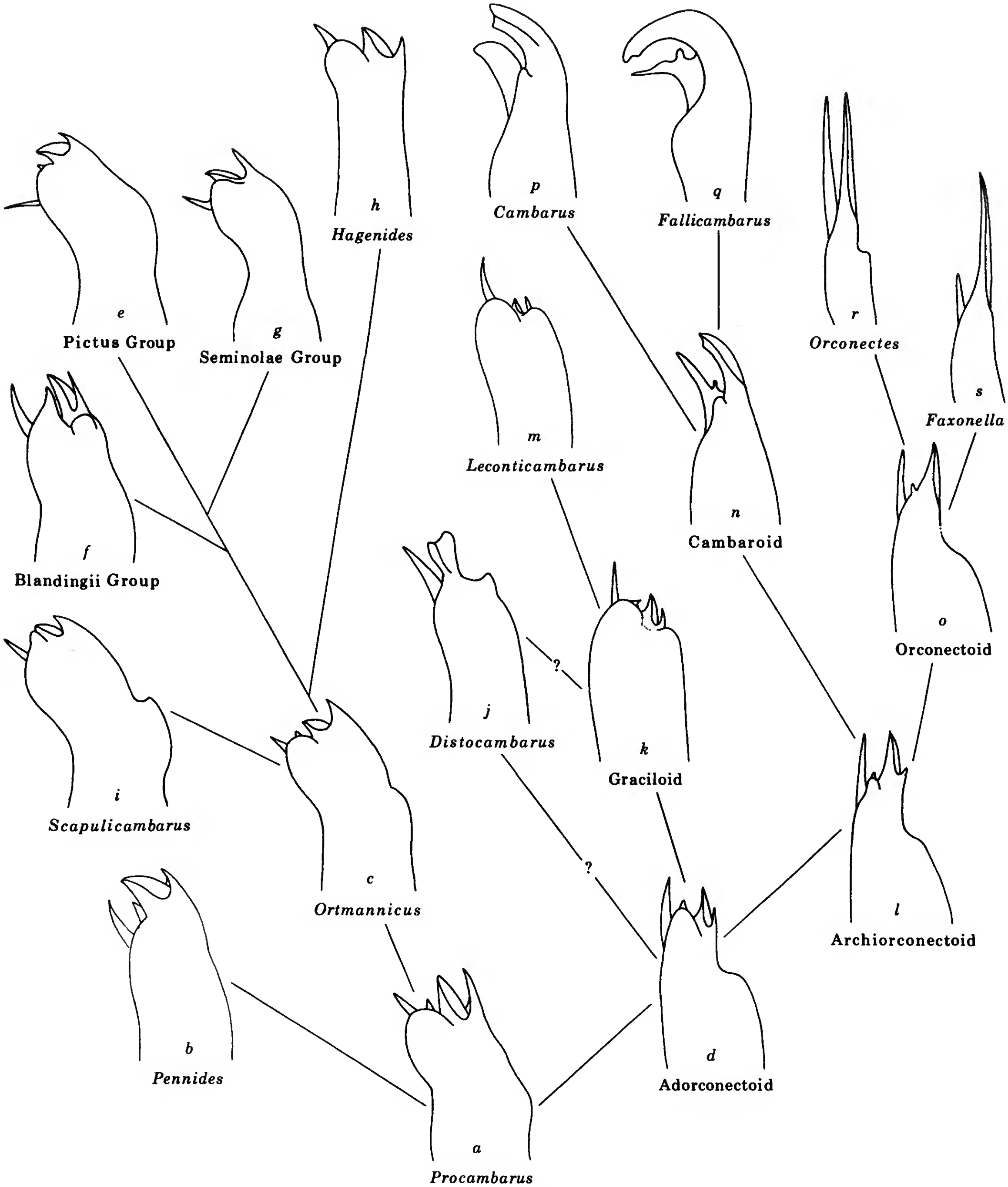


FIGURE 11.—Postulated relationships of the stem forms of the male first pleopod in the evolution of the crayfishes of Georgia. (Terminal figures are reproduced in dendrograms depicted in Figures 12–20.)

ment, which was flooded during the late Mesozoic and early part of the Cenozoic eras (*P. natchitochae* Penn, 1953:5; *P. ablusus* Penn, 1963:121; *P. elegans* Hobbs, 1969b:329; and *P. clemmeri* Hobbs, 1975a: 19). Considering the Georgia representatives of *Pennides* alone, clearly the most disjunct of the five is *Procambarus versutus* (Figure 12). The less robust, more densely tuberculate chela, the distally tapering first pleopod with a laterally displaced cephalic processs (Figure 12*f*), and an annulus ventralis partly obscured by widely gaping caudal projections of the sternum anterior to it (Figure 181*d*) make this crayfish stand alone. In some respects linking it with the other three is *P. petersi*, in which the first pleopod bears a small laterally situated cephalic process (Figure 12*b*), and the annulus ventralis is also partly hidden in ventral aspect by prominences extending caudally from the sternum anterior to it; however, only a trace of the median gap so conspicuous in *P. versutus* is present between the prominences

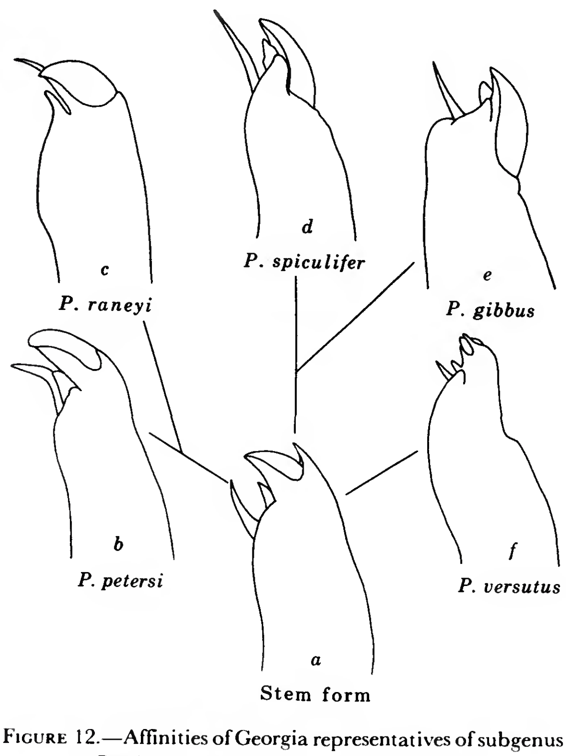


FIGURE 12.—Affinities of Georgia representatives of subgenus *Pennides* (stem form, *a*, from Figure 11*b*).

(Figure 176*d*). The first pleopod and annulus ventralis of *P. petersi* resemble the corresponding structures of *P. raneyi* more closely than they do those of *P. gibbus* and *P. spiculifer*. Similarities are strikingly evident in the disposition of the central projection and mesial process of the first pleopod as well as in the annulus ventralis and adjacent cephalic sternum. A comparison of the first pleopod of *P. gibbus* with that of the other three reveals convincing evidence that it is farther removed morphologically from *P. petersi* and *P. raneyi* than is *P. spiculifer*. The swollen caudodistal part of the first pleopod resembles that of *P. suttkusi* Hobbs (1953a:173), an inhabitant of the Choctawhatchee River basin in Alabama and Florida, but the presence of a mesially situated cephalic process and the extreme prolongation of the sternal projections over the annulus ventralis in the latter species suggest the probability of this resemblance in the two having arisen through convergence. Assuming the swollen caudodistal region to have arisen independently, then morphologically both the first pleopod and the annulus ventralis of *P. spiculifer* link the corresponding elements of *P. petersi* with those of *P. gibbus*.

Closely allied to these stream-dwelling *Pennides* are the members of the *pictus* Group of the subgenus *Ortmannicus*. In addition to being largely restricted to lotic environments, they have maintained the major facies typical of *Pennides*. Although losing one of the cervical spines, some members have retained a much more generalized first pleopod in the male than is present in most members of the latter subgenus—all of the terminal elements are present, including the three units of the caudal element (caudal knob, caudal process, and adventitious process). The most generalized condition among the Georgia representatives appears to exist in *P. enoplosternum* (Figure 13*e*). Inasmuch as the nonsecondary sexual characters of the members of this group are rather uniform, only features of the first pleopod of the male and of the annulus ventralis are considered in assessing relationships within the group. The first pleopod of *P. enoplosternum* approximates very closely that of the hypothetical generalized *Procambarus* as envisaged by Hobbs (1962, fig. 7).

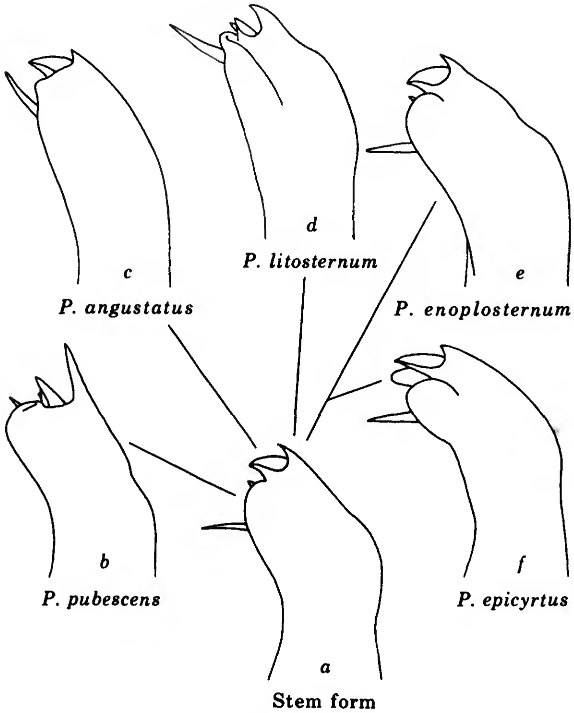


FIGURE 13.—Affinities of Georgia representatives of *pictus* Group of subgenus *Ortmannicus* (stem form, *a*, from Figure 11*e*).

Except for the terminal elements being disposed more caudally and a shorter cephalic process and central projection, there are almost no differences. Even though no generalized annulus ventralis has been described or depicted, that of *P. enoplosternum* appears to me to be as little modified as that of any other species in this or related subgenera. The affinities of this crayfish with *P. epicyrtus* are so clearly evident (Figures 13*e,f*, 150, 155) that it hardly seems necessary to mention specific features in which the similarities occur. The major differences are in the stronger caudal deflection of the terminal part of the first pleopod, the usually enlarged caudal process, and the caudomedian elevation of the annulus ventralis. With a reduction of the caudal knob, caudal and adventitious processes, and loss of the cephalic hump from the appendage, it could be converted to one that closely resembles the first pleopod of *P. angustatus*. The homologies that exist between the pleopods of *P. enoplosternum* and *P. litosternum* are readily discernible, and the most conspicuous modification in the latter occurs in the caudal knob, which is less bulbous and is curved around the base of the central projection and caudal process. There is little difference in the annuli ventrales of the two, but the projecting tubercles from the sternum over the annulus are not present in the latter. The first pleopod of *Procambarus pubescens*, the remaining Georgia member of the group, also resembles the hypothetical ancestor, differing primarily in possessing a far less inflated caudal knob, which forms a caudodistal ridge, and a reduced caudal process. The annulus ventralis exhibits no marked departure from that of *P. enoplosternum*, and the caudally projecting prominences from the sternum over the cephalic part of the annulus are, at best, comparatively small and inconspicuous. Certainly these five crayfishes were derived from a common crayfish stock, one exhibiting features strongly resembling those of *P. enoplosternum*.

Arising from this same ancestral *Ortmannicus* stock were the members of the *seminolae* Group, four of which have found congenial niches in the southern part of the state. Developing a broader ecological tolerance than that of their ancestors and related members of the *pictus* Group, they have invaded a wide range of habitats, including both lotic and temporary lentic bodies of water, the latter necessitating their being able burrowers. In most members of this group the rostral margins are more convergent and the areola narrower (Figures 164–166) than in members of the *pictus* Group, and in none of them is the saddle marking on the thoracic region represented by more than the lateral horns (Figure 136*e–g*). As in the members of the *pictus* Group, the nonsecondary sexual features are so markedly similar that intragroup relationships must be based almost exclusively on the secondary sexual features. The most generalized of the species occurring in Georgia is *Procambarus lunzi*, which, in respect to the terminal elements of the first pleopod of the male and the annulus ventralis of the female (Figures 14*c*, 166*d*), is somewhat intermediate between *P. seminolae* at one extreme and *P. fallax* and *P. leonensis*

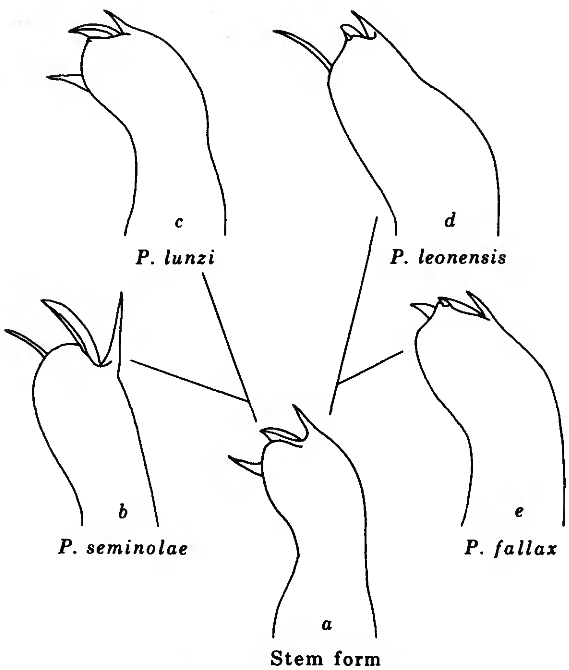


FIGURE 14.—Affinities of Georgia representatives of *seminolae* Group of subgenus *Ortmannicus* (stem form, *a*, from Figure 11*g*).

at the other. Linking *P. seminolae* with *P. lunzi* is *P. (O.) ancylus* Hobbs (1958b:164), the range of which lies to the northeast in North Carolina and South Carolina. The terminal elements of the first pleopods of the three are markedly similar, but they are shortest in *P. lunzi*, somewhat longer in *P. ancylus*, and yet longer and directed more nearly distally in *P. seminolae*. In comparing the terminal elements of the pleopod in *P. fallax* and *P. lunzi*, there is little difference in the cephalic process; the mesial process of the former is somewhat flattened and sublanceolate, and the central projection is shorter, appearing to have been retracted. In *P. leonensis*, the cephalic process resembles that of the latter two species; the mesial process is almost spiculiform; and the central projection, being much shorter than it is in either of the other two species, appears to have been withdrawn even more than in *P. fallax*. Thus in respect to the central projection, beginning with *P. lunzi*, it became progressively more elongate in *P. ancylus* and *P. seminolae* and progressively shorter in *P. fallax* and *P. leonensis*. Similarly, modifications in the annuli ventrales can be observed in comparing the illustrations of the respective species.

More distantly related to the members of the *pictus* Group is the assemblage of species assigned to the *blandingii* Group. Three of these occur in a wide range of habitats in Georgia. According to Hobbs (1962:275), the ancestors of this group arose from the same generalized *Procambarus* stock as did these of the *pictus* Group. The most obvious modifications from this hypothetical ancestor paralleled those of members of the *seminolae* Group (for example, the tapering rostrum and narrower areola), probably a channelizing effect resulting from becoming adapted to living in lentic habitats with fluctuating water levels. As in the previously discussed groups of *Ortmannicus*, one must turn to the secondary sexual features for evidence of intragroup relationships. The most obvious modification of the first pleopod (Figure 15) of the hypothetical ancestor that led to the "Blandingii" stock was in the caudal element: the caudal process shifted from a caudomesial to a caudal-to-caudolateral position, where it came to lie at the caudal or caudolateral base of the central projection; the caudal knob also assumed a lateral position, and, in the extreme transposition, was moved cephalically to the cephalic base of the cephalic process (in *P. (O.) blandingii* (Harlan, 1830:464)). Some of the intermediate positions it must have occupied in its migration are exemplified in the three members of the group occurring in the state, being situated more cephalically in *P. a. acutus* and *P. lophotus* than in *P. acutissimus*. The form of the knob is perhaps more generalized in *P. a. acutus*, but it is less far removed from its supposed ancestral position in the latter. The annulus ventralis of *P. acutissimus* is also more like that of members of the *pictus* Group than are those of *P. a. acutus* and *P. lophotus*.

The crayfishes assigned to the subgenus *Scapulicambarus* are almost certainly derived from an ancestor not markedly different from that believed to have given rise to the *pictus* Group,

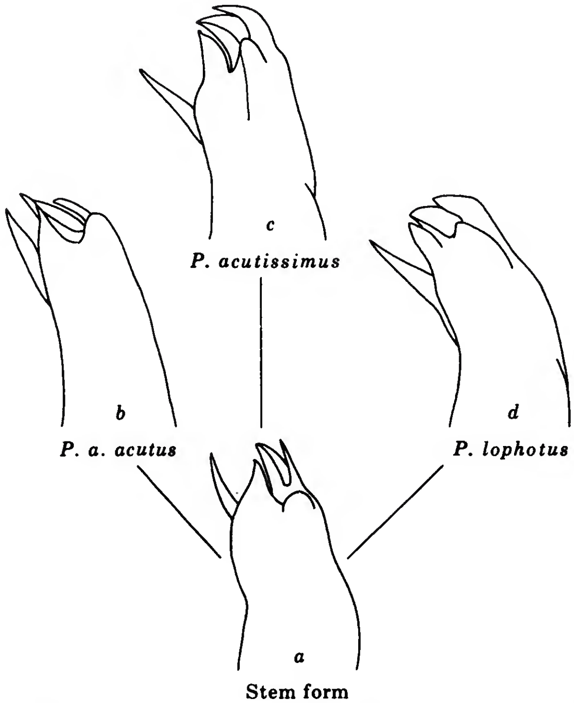


FIGURE 15.—Affinities of Georgia representatives of *blandingii* Group of subgenus *Ortmannicus* (stem form, *a*, from Figure 11*f*).

paralleling to a considerable degree the adaptive features of the members of the *seminolae* Group. The chief character that sets this species group apart from others in the genus *Procambarus* is the conversion of the ancestral hump on the cephalic surface of the first pleopod to a distinct shoulder that frequently is angular and sometimes produced in an acute projection (Figure 16). Among the three Georgia representatives, certainly *P. paeninsulanus* resembles members of the *pictus* Group more closely than do the other two, and *P. howellae*, in turn, resembles *P. paeninsulanus* more closely than does *P. troglodytes*. The broad compressed lobiform cephalic process of the first pleopod of the latter is markedly dissimilar to the corresponding element in the other two. Furthermore, the usual very narrow areola (sometimes virtually obliterated at midlength) of *P. troglodytes* represents a functional specialization, an enlargement of the gill chamber, that has not been so well developed in either *P. paeninsulanus* or *P. howellae*. The acute shoulder on the cephalic surface of the first pleopod of the latter, and the laterally shifted cephalic process together with the laterally twisted distal third of the appendage, render this crayfish clearly less like related congeners than is *P. paeninsulanus*. A comparison of the annuli ventrales of the three leads one to the same conclusion.

The affinities of the ecologically and morphologically disjunct members of the subgenus *Hagenides*, with those of other subgenera, seem to me to be far more obscure than in the other species groups of the genus occurring in Georgia. The characteristics of the first pleopod (Figure 17) appear at first glance to be so unique as to be impossible to fit into any scheme of lineage, but neglecting all members of the subgenus except *P. (H.) geodytes* Hobbs (1942b:80, which occurs in northeastern Florida) and *P. advena*, a tie with the *seminolae* Group of *Ortmannicus* not only seems possible but even probable. Except for their greater proportional length and a reduced cephalic process, the first pleopods of these cray-

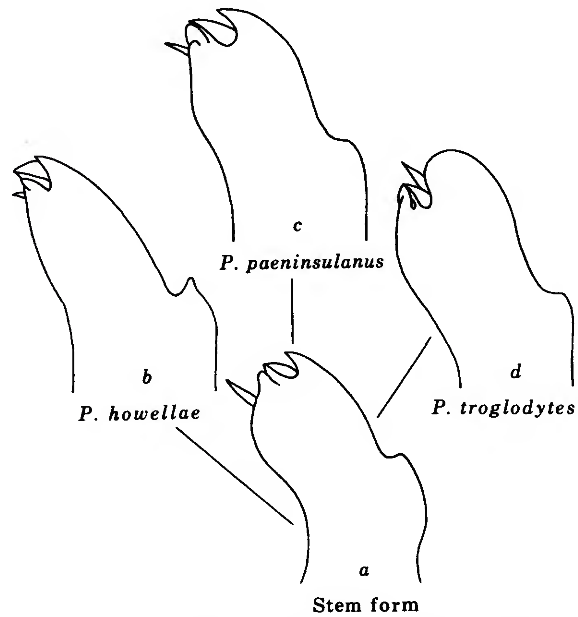


FIGURE 16.—Affinities of Georgia representatives of subgenus *Scapulicambarus* (stem form, *a*, from Figure 11*i*).

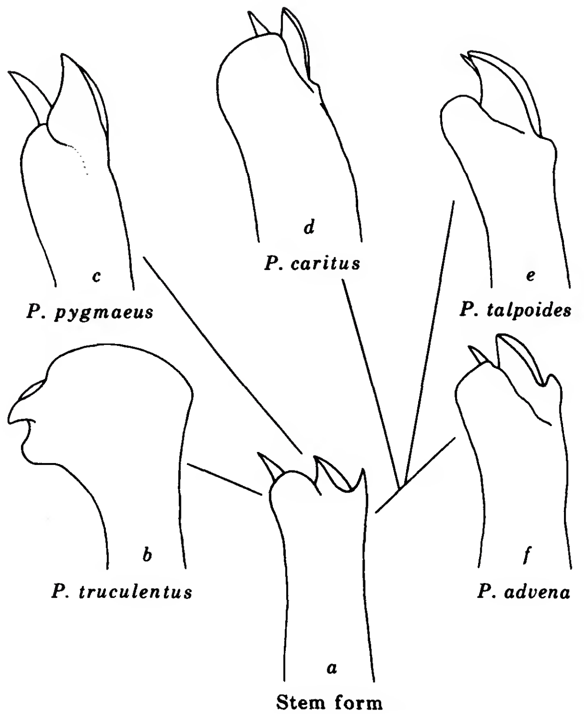


FIGURE 17.—Affinities of Georgia representatives of subgenus *Hagenides* (stem form, *a*, from Figure 11*h*).

fishes are not markedly different from those of *P. fallax*, and *P. geodytes* has retained hooks on the ischia of the fourth pereiopods, a feature that all other members of *Hagenides* lack. Other than in the characteristics of the first pleopod, and to a lesser degree those of the annulus ventralis, the crayfishes assigned to this subgenus resemble members of the specialized subgenera of the genus *Cambarus* more closely than they do the majority of their congeners. At least some of the advanced characteristics can be correlated with becoming adapted to spending almost their entire lives in complex burrows. Among these adaptations are smaller eyes, shorter rostra, with strongly convergent margins never bearing spines or tubercles, longer narrower areolae, great reduction of all spines on the carapace, depressed chelae, and a reduction in the size of the abdomen. Similar adaptations in members of the subgenera *Depressicambarus* and *Jugicambarus* of the genus *Cambarus* to a life in burrows are almost certainly responsible for the strong resemblances in these distantly related species to members of the subgenus *Hagenides*. As suggested above, the most generalized of the Georgia representatives of the latter appears to be *P. advena*, and in maintaining a reduced or rudimentary cephalic process, *P. talpoides* links this species to the more divergent *P. caritus*. The most conspicuous innovations within the subgenus are the swollen distal part of the pleopod of *P. truculentus*, in which the terminal elements arise from the caudal surface at right angles to the shaft of the appendage and the equally bizarre distal part of the pleopod in the four Floridian subspecies of *P. (H.) rogersi* (Hobbs, 1938:62). With respect to the first pleopod of the male in *P. pygmaeus*, the central projection consists of a prominent bladelike structure that spans almost the entire cephalocaudal plane of the distal end of the shaft of the appendage, a modification that places *P. pygmaeus* even farther from *P. advena* than *P. caritus*, in which the central projection is comparatively small. Despite this morphological feature that suggests a high degree of specialization, ecologically *P. pygmaeus* is much more broadly tolerant than any other member of the subgenus, for few, if any, individuals spend almost all of their lives in burrows.

Members of the two remaining subgenera of *Procambarus* represented in the crayfish fauna of Georgia are believed to have been derived from a postulated adorconectoid stock (Hobbs, 1969a: 119; 1967b, fig.14), which in turn arose from a primeval *Procambarus* stock postulated to have given rise to several lineages (Hobbs, 1969a:119): the graciloid, mexicanoid, and archiorconectoid, the latter subdividing into the orconectoid and cambaroid lines. In the graciloid line, "the distal portion of the appendage [= first pleopod of the male] was shortened, bringing the terminal elements and the subapical setae to the level of the cephalic shoulder" (Hobbs, 1967b:13). This stock was ancestral to the members of the subgenera *Girardiella* (Lyle, 1938:76; see Hobbs, 1972a:6), none of which occurs in Georgia, and *Leconticambarus*. The progenitors of *Leconticambarus* are believed to have differed from those giving rise to the assemblage referred to the subgenus *Girardiella* in possessing hooks on the ischia of the fourth pereiopod, a prominent boss on the coxa of the same appendage, and subapical setae on the first pleopod, characteristics shared by *P. p. pubischelae* and *P. barbatus*. None of these features are present in modern members of *Girardiella*, but all are features of most extant *Leconticambarus*, although certain species lack one or both of the former two characters. Among the Georgia representatives (Figure 18), *P. pubischelae deficiens* lacks both the hook and the boss on the fourth pereiopod, suggesting a derived condition. *Procambarus p. pubischelae* is almost certainly the most primitive of the three occurring in the state, for the cephalic shoulder on the first pleopod is present in the form of a rounded knob, and the annulus ventralis is far more similar to all of the remaining members of the subgenus than is that of *P. barbatus*, in which the cephalolateral regions are flared laterally. The cephalodistal part of the first pleopod of the male of the latter species slopes gently from the base of the terminal elements rather than forming an angle or a rounded knob, a feature that is less common in the subgenus.

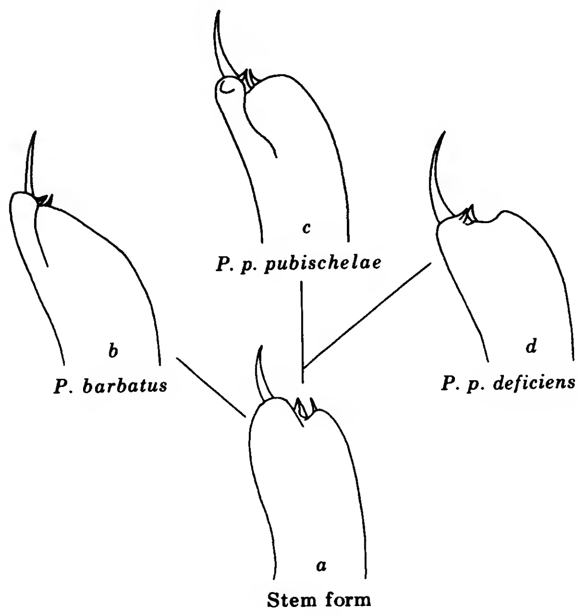


FIGURE 18.—Affinities of Georgia representatives of subgenus *Leconticambarus* (stem form, *a*, from Figure 11*m*).

It is very probable that *Procambarus (D.) devexus*, the only member of the subgenus *Distocambarus*, has descended from an adorconectoid ancestor through the graciloid line. Except for the unique form of the first pleopod of the male and the peculiarly hinged annulus ventralis, it shares a number of features with the more generalized members of the subgenus *Girardiella*. In contrast, however, the first pleopods of the male are markedly dissimilar in being rather strongly reflexed distally and in possessing no trace of a caudal element, one of the most prominent features of the first pleopod of all members of the latter subgenus. The annulus ventralis is also somewhat unique as is the cheliped in which the carpus is conspicuously long. Thus I visualize this crayfish as having been derived from a common graciloid ancestor shared by the members of both *Girardiella* and *Leconticambarus* but having more recent ties with the former than with the latter. Perhaps of significance is the fact that the limited range of *P. devexus* is isolated far from that of the subgenus *Girardiella*, with the range of *Leconticambarus* inserted south of, but between, them.

No representatives of the mexicanoid line occur in Georgia, but all of the remaining species are believed to have taken their origin in the archiorconectoid lineage—the descendant cambaroid line leading to the members of the genera *Cambarus* and *Fallicambarus*, and the orconectoid line leading to the genera *Faxonella* and *Orconectes*.

Hobbs (1969a:120) presented a hypothesis concerning what he considered to be important in the evolving archiorconectoid line, one that was expressed almost exclusively in terms of modifications of the first pleopod of the male. He pointed out that the major trend in the archiorconectoid stock's diverging from the adorconectoid ancestors was the reduction of the cephalic process and caudal element of this appendage. The disappearance of the cephalic process became complete in all modern representatives of the orconectoid line, and the caudal process occurs as a minute vestige in one troglobitic species; otherwise it, too, has been lost. The major trend in this line has been a lengthening of the central projection and usually a concomitant elongation of the mesial process.

Four of the Georgia crayfishes, belonging to two genera, are believed to have evolved from the orconectoid stock. Of the three members of the genus *Orconectes*, *O. erichsonianus* probably resembles the ancestral stock more closely than do the other two (Figure 19). One of its features supporting this conclusion is the relative length of the terminal elements of the first pleopod of the male; in this crayfish they are distinctly shorter than those of *O. forceps* and *O. spinosus*. In addition, the annulus ventralis of *O. erichsonianus* is markedly less sculptured than that of the other two, which are virtually indistinguishable. Among the nonsecondary sexual characters, *O. erichsonianus* exhibits several features that appear to be more generalized than are those of *O. forceps* and *O. spinosus*. With respect to these closely allied species, the first pleopod of the latter, while retaining the primitive cephalic shoulder, possesses a longer central projection, suggesting a more advanced condition. Suffice it to comment that both are more highly evolved than is *O. erichsonianus*.

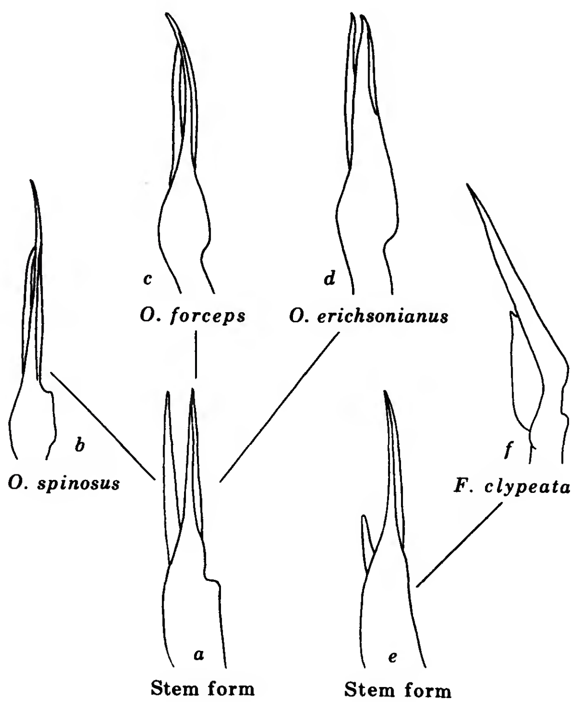


FIGURE 19.—Affinities of Georgia representatives of genera *Orconectes* and *Faxonella* (stem forms, *a*, *e*, from Figure 11*r*,*s*, respectively).

There seems little reason to question the assumption that the species assigned to the genus *Faxonella* are more closely allied to members of the genus *Orconectes* than to those of other species groups, but there is doubt concerning the remoteness of their common ancestry. This was emphasized by Hobbs (1969a, fig. 4). Two features of *Faxonella* raise questions that are difficult to resolve in assessing the kinship of its members to those of *Orconectes*. Whereas the trend in the development of the mesial process of the first pleopod of the male in the latter appears to have been toward an increase in length, in *Faxonella* the process is short and the trend seems to have been toward its reduction. In the Georgia representative, *F. clypeata*, it is usually vestigial but occasionally absent. The annulus ventralis of crayfishes belonging to the genus is more intricately sculptured than most, if not all, members of the genus *Orconectes*, and more importantly, unlike those of the latter it is not fused to the sternum immediately anterior to it. Even in the primitive troglobitic *Orconectes*, the annulus is fused with the sternum to the extent that no more than a hinge-like motion between them is possible. Whereas in *Faxonella* the first pleopod of the female is vestigial or absent, it is usually present in members of *Orconectes*. In view of these traits, I suggest that three lines diverged from the orconectoid ancestor, the most successful leading to the assemblage of species assigned to the genus *Orconectes* and the other two leading to the groups constituting the genera *Faxonella* and *Hobbseus* (no representatives of the latter are known to occur in Georgia). There seems to be little doubt that *F. clypeata* is the most advanced member of the group.

The remaining crayfishes of the state are believed to have been descended from the cambaroid stock, in which the comparatively short mesial process and central projection of the first pleopod began to turn caudally and in almost all of the descendants bent through an angle of at least 90 degrees. As suggested by Hobbs (1969a: 123), a divergence occurred in this stock, giving rise to two lineages culminating in the species groups *Fallicambarus* and *Cambarus*. In the cambaroid lineage from the archiorconectoid stock, both the cephalic and caudal elements of the pleopod, although reduced, persisted. Some primitive members of the genus *Fallicambarus* retain rudiments of a mesially shifted cephalic process, but all traces of the caudal element are lost throughout the genus. In that segment leading to species embraced by the genus *Cambarus*, a rudiment of the caudal element remained and is represented in a number of modern forms, but the cephalic process has disappeared.

In the nominate, more primitive, subgenus of *Fallicambarus* a reduced cephalic process on the first pleopod and hooks on the ischia of the third and fourth pereiopods occur in two of the species. These two features are of common occurrence in members of the genus *Procambarus* but are rare or nonexistent in other cambarid groups. Thus they serve to link the cambaroid line with the more primitive members of *Procambarus*. Whereas neither feature is present in *Fallicambarus (Creaserinus) hedgpethi*, the only representative of the genus occurring in Georgia, this crayfish (with a cambaroid first pleopod in the male bearing a somewhat twisted mesial process and a strongly depressed chela in which there is a concavity along the opposable proximal part of the dactyl, sharply terminated distally by a prominent tubercle) is clearly set apart from the descendants of the other cambaroid lineage occurring in the state.

The major features in the evolution of the genus *Cambarus* were discussed in some detail by Hobbs (1969a) and are briefly summarized here to place the elements of the genus occurring in the state in a phylogenetic perspective (Figures 11, 20). The most generalized of the *Cambarus* stock occurring in Georgia are the stream dwellers assigned to the subgenus *Puncticambarus*. These crayfishes are typified by a long rostrum with or without marginal spines or tubercles; a broad areola usually bearing many shallow punctations; and elongate chelae that are somewhat depressed, usually bearing two rows of tubercles on the palm, well-defined longitudinal ridges on the weakly gaping fingers, and the opposable base of the fixed one lacking a conspicuous tuft of setae. Two species groups are believed to have originated from the primitive *Puncticambarus* ancestor: the *extraneus* Group and the *coosae* Group (Figure 21). The most generalized of the species occurring in Georgia is probably *C. extraneus*, which, in addition to possessing marginal spines on the rostrum, shares more features in common with primitive members of the subgenus *Ortmannicus* than do the remaining species. The closely allied allopatric *C. georgiae* and *C. parrishi* have retained most of the *Ortmannicus*-like characteristics of *C. extraneus*, and indeed the shape of the chela of *C. georgiae* is more *Procambarus*-like than that of any member of the genus occurring in the state. With the loss of marginal spines from the rostrum, *C. hiwasseensis* seems clearly to have been derived from a common ancestor with *C. parrishi*, both of which lack cervical spines, and *C. chaugaensis* tends to link *C. georgiae* with the latter two. The affinities of the remaining two Georgia species of the subgenus, which are assigned to the *coosae* Group, suggest an early separation of their ancestors from those of the *extraneus* Group. Whereas *C. coosae* retains the primitive characters of the subgenus, several features, such as a thickening of the rostral margins, more strongly tuberculate carapace, more prominent punctations in the areola and on the chelae, have been added. With the absence of marginal spines on the rostrum, *C. scotti* is considered to be more advanced than *C. coosae*.

Cambarus (Hiaticambarus) speciosus combines characteristics of the subgenera *Hiaticambarus* and *Puncticambarus*, and, while creating a problem as to how to weigh these characters in assigning it to one of the two subgenera, such a combination of features lends credence to the belief that the primitive *Hiaticambarus* was derived from a *Puncticambarus*-like ancestor (Figure 22). This crayfish surely approximates the ancestral form of the primitive *Hiaticambarus*, and had it retained marginal spines on the rostrum (as have most individuals of *C. coosawattae*, *C. fasciatus*, and some pop-

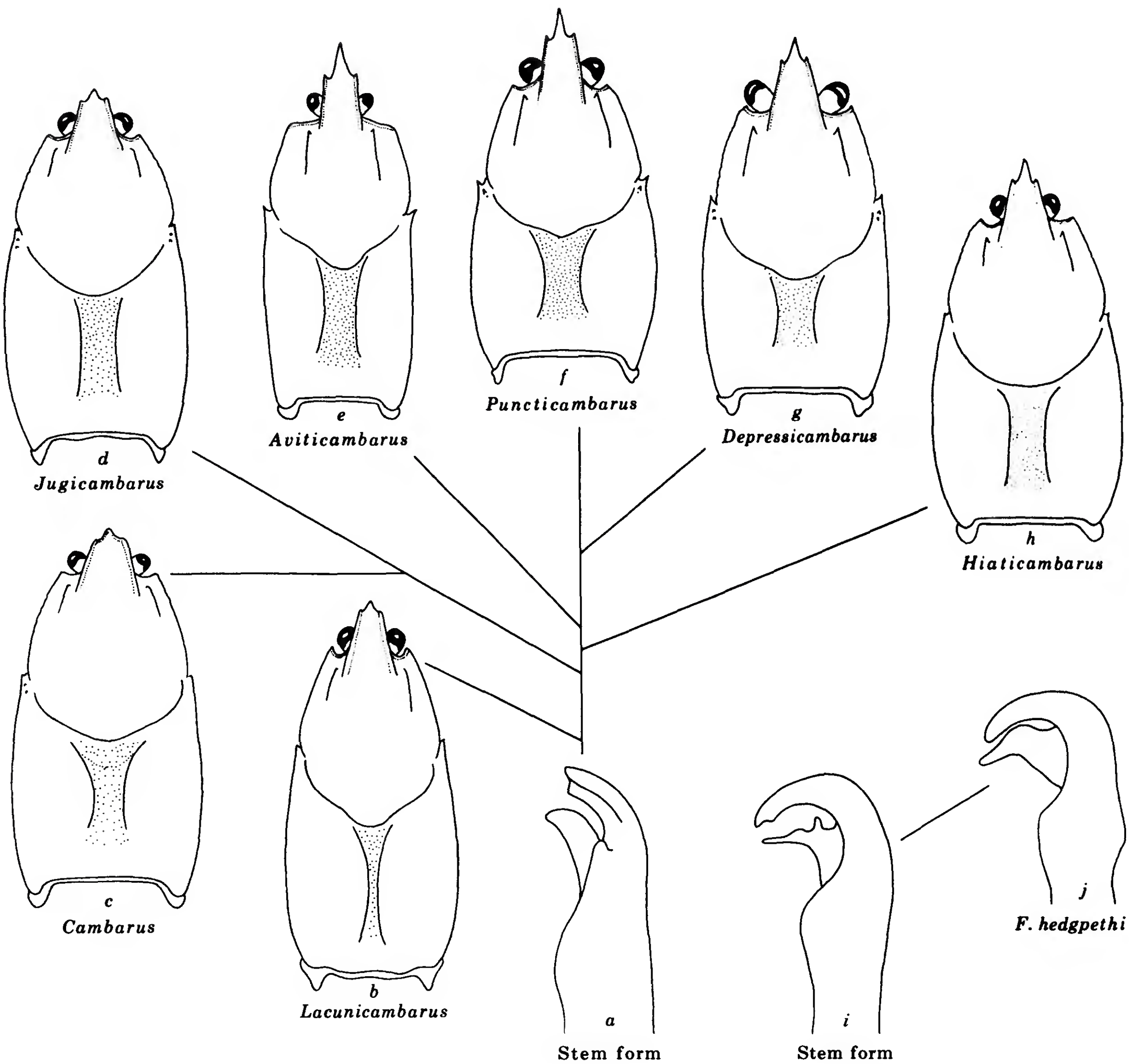


FIGURE 20.—Affinities of Georgia representatives of subgenera of genus *Cambarus* and genus *Fallicambarus* (stem forms, *a*, *i*, from Figure 11*p*,*q*, respectively).

ulations of *C. girardianus*), it would have had all of the characteristics I might have supposed to have been present in the prototype of *Hiaticambarus*. The primitive *C. speciosus*, *C. girardianus*, and *C. fasciatus*, all at least occasionally with two rows of tubercles on the mesial surface of the palm of the chela, are linked to the more advanced *C. longirostris* and *C. manningi* through *C. coosawattae*, which, unlike the two most advanced species, has retained marginal spines on the rostrum.

I know of no reason to question the statement of Hobbs (1969a:136) that the subgenus *Depressicambarus* "has had a history stemming from an *extraneus*-like (*Puncticambarus*) ancestor . . .," and the characters postulated by him and by Bouchard (1978:46) to be those of the ancestral stock

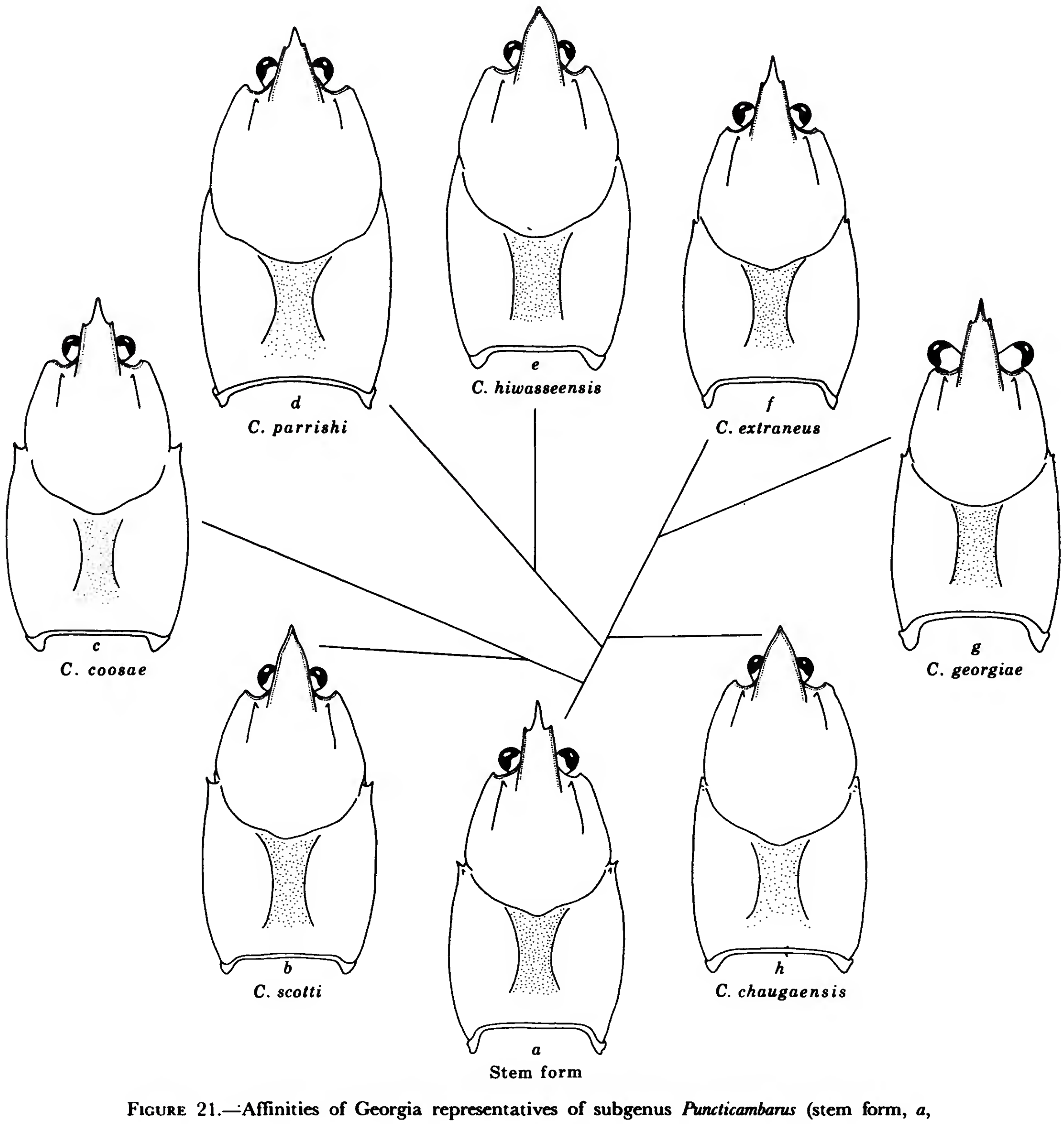


FIGURE 21.—Affinities of Georgia representatives of subgenus *Puncticambarus* (stem form, *a*, from Figure 20*f*).

of the subgenus support such a supposition (Figure 23). The features selected by Bouchard are essentially those found in members of *C. halli*, *C. obstipus* Hall (1959:221), and *C. englishi*, species that both he and Hobbs considered to be the most primitive of the extant members of the subgenus. Hobbs noted that "indeed *C. halli*, except for the shorter, broader chelae could well be assigned to the subgenus *Puncticambarus*." These three species constitute the *halli* Group (Bou-

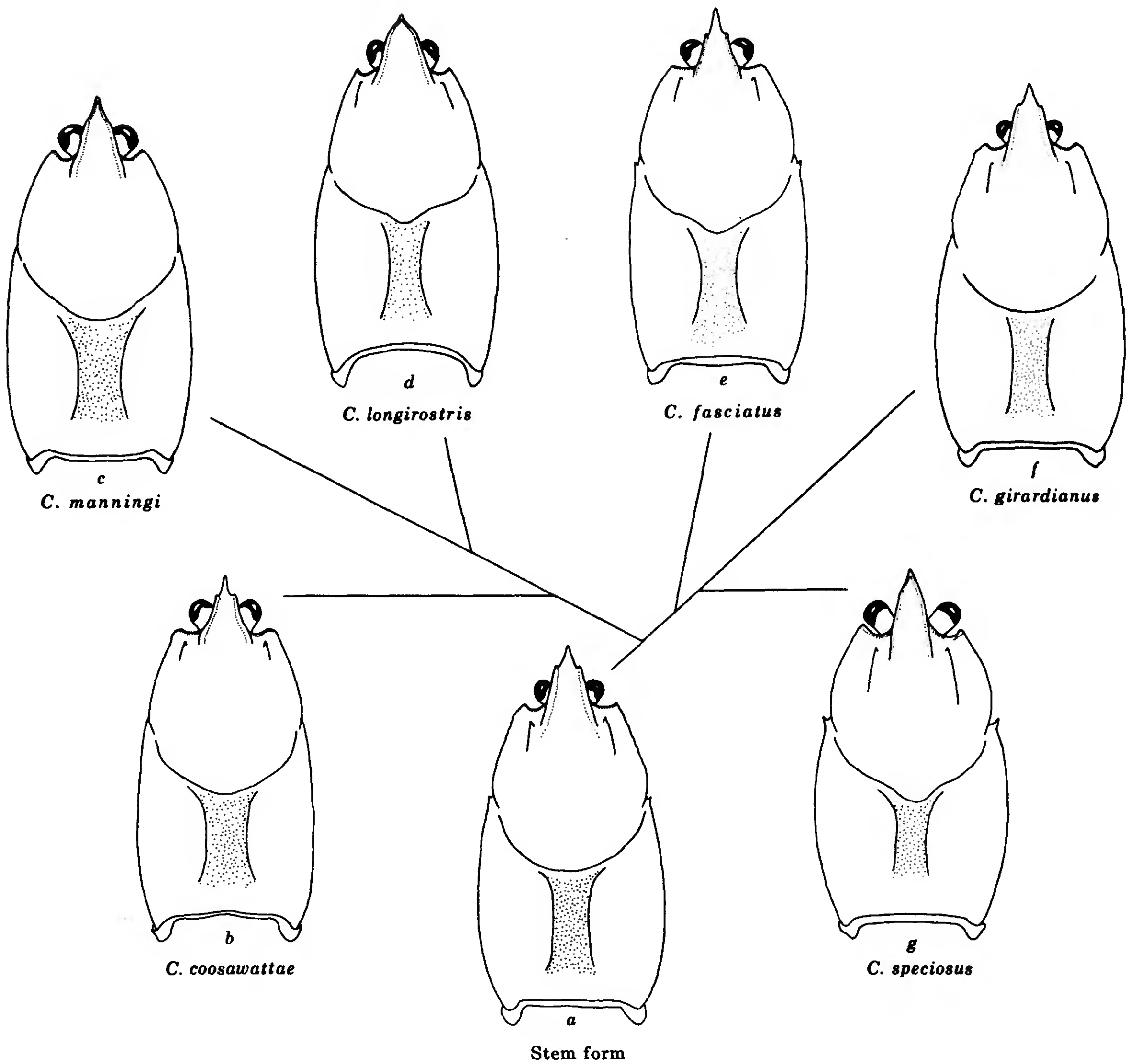


FIGURE 22.—Affinities of Georgia representatives of subgenus *Hiaticambarus* (stem form, *a*, from Figure 20*h*).

chard, 1978:44), and two of them, *C. englishi* and *C. halli*, occur in Georgia. In them, marginal spines or tubercles are usually present on the rostrum, the areola is broad and densely punctate, the suborbital angle is well developed, and the coloration is brilliant, involving strikingly contrasting greens, browns, and reds, reminding one of the bright color patterns in some members of *Puncticambarus* and *Hiaticambarus*. Unique, however, in the color pattern are the pale transverse bands on the caudal margins of the first five abdominal terga. Of the Georgia representatives, *C. englishi*, in lacking a subapical notch on the tapering central projection and apparently being restricted to riffle areas, has departed farther than has *C. halli* from their common ancestor.

The remaining members of the subgenus that had been described prior to or in his publication

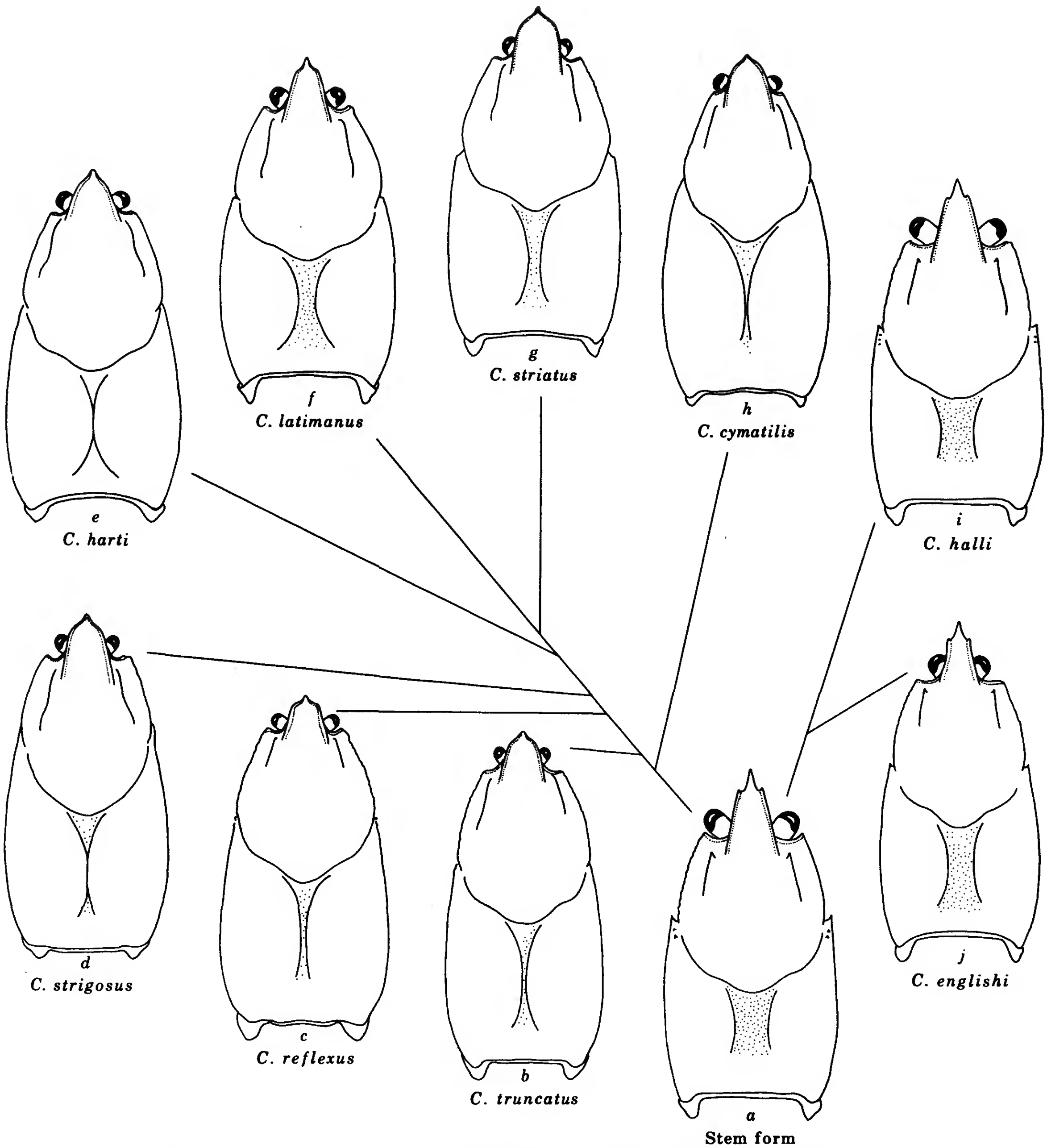


FIGURE 23.—Affinities of Georgia representatives of subgenus *Depressicambarus* (stem form, *a*, from Figure 20*g*).

were assigned by Bouchard (1978:44) to the *latimanus* Group. Added here are four additional species. The relationships of the seven Georgia representatives of this group are not clear to me, but surely *Cambarus latimanus* is the most generalized member. Some populations exhibit a spination similar to that of members of the *halli* Group, a condition that occurs in few of the young and in none of the adults of other members of the *latimanus* Group. Closely allied to *C. latimanus* is the sympatric *C. striatus*, which was surely derived from a *latimanus*-like stock, differing from it most conspicuously in possessing a longer narrower areola, and, in much of its range in Georgia, in becoming a primary burrower—an adaptation that was assumed by the remaining five species occurring in the state. The ranges of four of them overlap that of *C. striatus*. All five appear to me to have descended from the same common stock from which the latter and *C. latimanus* arose, and the fact that the ranges of none of the five are sympatric renders such a supposition at least not improbable. The most divergent member of the group is *C. cymatilis*. In addition to having a unique (within the subgenus) arrangement of tubercles along the opposable margin of the fixed finger, this crayfish also possesses a long disto-medial spine on the mesial ramus of the uropod, which extends beyond the margin; also the suborbital angle of *C. cymatilis* is better developed than in any other species of the *latimanus* Group. Although superficially *C. strigosus* resembles *C. striatus* more closely than do *C. harti*, *C. reflexus*, and *C. truncatus*, the first pleopod of the male of *C. reflexus* is more similar to that of *C. striatus*. The short central projection of the first pleopod of the bright orange red *C. truncatus* places this crayfish closer to *C. strigosus* than to the others of the group. Finally, the blue *C. harti*, possessing a dactyl of the cheliped resembling that of members of the genus *Fallicambarus* and of primary burrowers belonging to the genus *Procambarus*, seems to me to be as closely allied to *C. striatus* and *C. cymatilis* as to any of the other species of the subgenus.

As pointed out by Hobbs (1969a:129,130), *C. (Aviticambarus) hamulatus* (Figure 25*b*) is "rather closely related to the more primitive members of *Puncticambarus* . . . and was almost certainly derived from a primitive stock that was shared by *C. extraneus* . . . ." Most obvious of its distinctive features are those associated with its having become adapted to a troglobitic existence.

With the loss of marginal spines or tubercles from the rostrum, a tendency toward the suppression of the more lateral of the two rows of tubercles on the palm of the chela, and a retention of well-defined longitudinal ridges on the fingers, a stock derived from the primitive *Puncticambarus* lineage diverged to give rise to members of the subgenera *Cambarus* and *Jugicambarus* (Figure 24). In the stem form of the latter, the mesialmost row of tubercles remaining on the palm of the chela came to be cristiform, and the chela itself assumed a subrectangular shape; punctations on the palm were few in number but were large, rather deep, and in descendants often were studded with long stiff setae. Among the most generalized of the species occurring in Georgia is *C. distans*, in which the first pleopod of the male differs in no conspicuous way from those of members of the subgenus *Puncticambarus*. In *C. unestami* (which retained at least a remnant of the second row of tubercles on the palm of the chela) and *C. parvoculus*, the central projection of the pleopod became longer and more strongly recurved, heralding the climax that was reached in the pleopods of *C. conasaugaensis and C. asperimanus*, the latter being recurved almost 180 degrees and having lost the ancestral subapical notch. Almost equally divergent (more so in terms of its habitat) from the ancestral stock is the primary burrower, *C. nodosus*. The elongate terminal elements of the first pleopod of the male of this crayfish and its burrowing habit suggest a high degree of specialization, but the presence of two well-defined rows of tubercles on the palm of the chela must be considered to be either an atavistic trait or a retention of a character from its *Puncticambarus* ancestry.

Most individuals belonging to the subgenus *Cambarus* (Figure 25*d,e*) possess a single row of tubercles on the mesial surface of the palm of the chela that differs from that in *Jugicambarus* by being adpressed rather than elevated in a cristiform row. Some populations of the Georgia members of *C. bartonii*, however, have retained parts of the second row of tubercles on the mesial surface of the palm of the chela as have occasional individuals of some populations, most members of which lack a second row. Because the populations

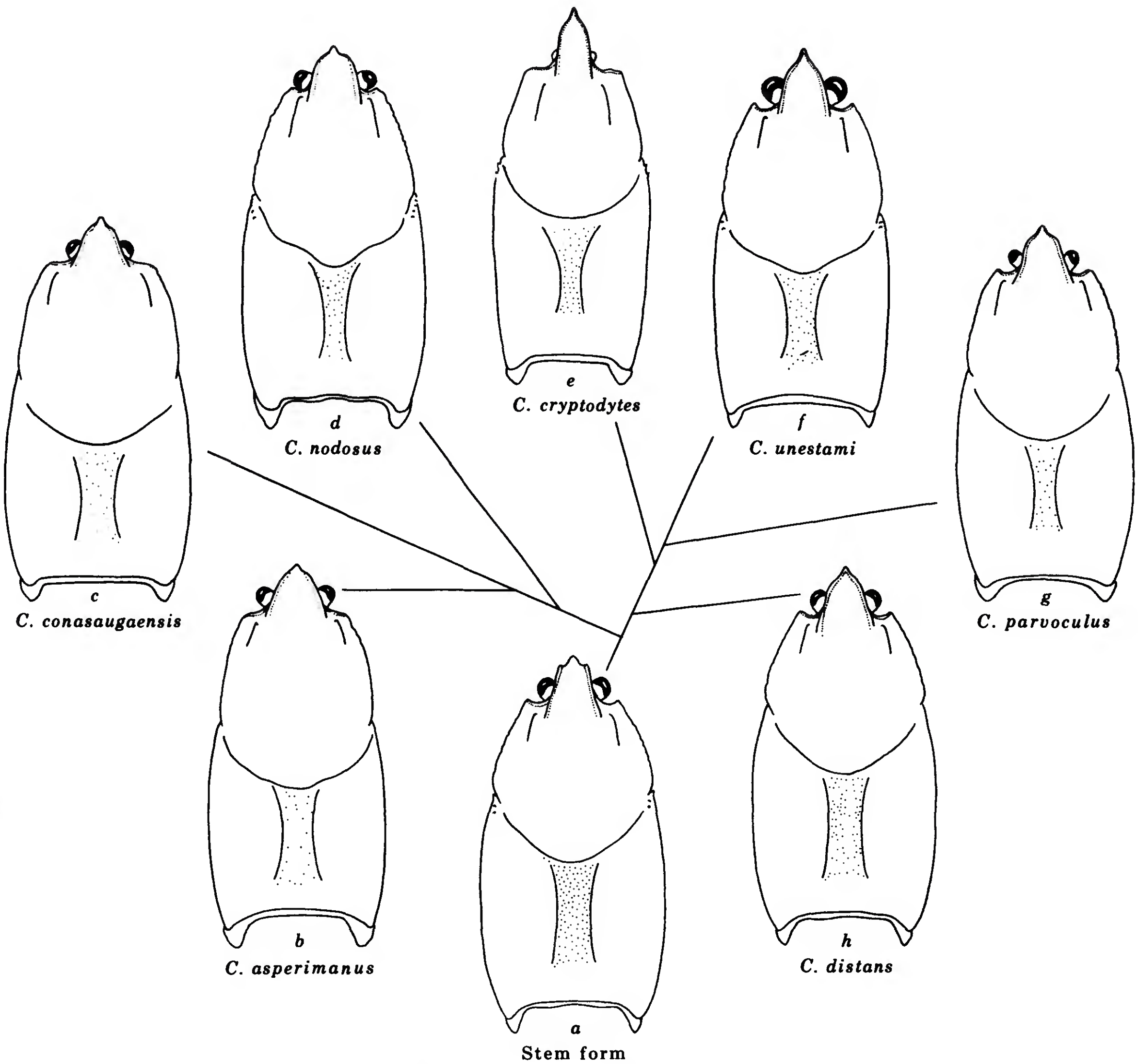


FIGURE 24.—Affinities of Georgia representatives of subgenus *Jugicambarus* (stem form, *a*, from Figure 20*d*).

of this highly variable species that are found in Georgia are treated in some detail in the section devoted to this crayfish, no elaboration is offered here beyond pointing out its close affinity to members of the subgenus *Jugicambarus*. *Cambarus howardi*, a close ally of *C. bartonii*, is the only other species occurring in the state that has been assigned to the subgenus *Cambarus*.

GEOGRAPHICAL AND TEMPORAL ASPECTS

Now that the affinities and morphological changes that are believed to have occurred in the evolution of the Georgia crayfishes have been presented, an orientation, insofar as possible, of these changes in space and time seems appropriate. As was suggested in an earlier reference to

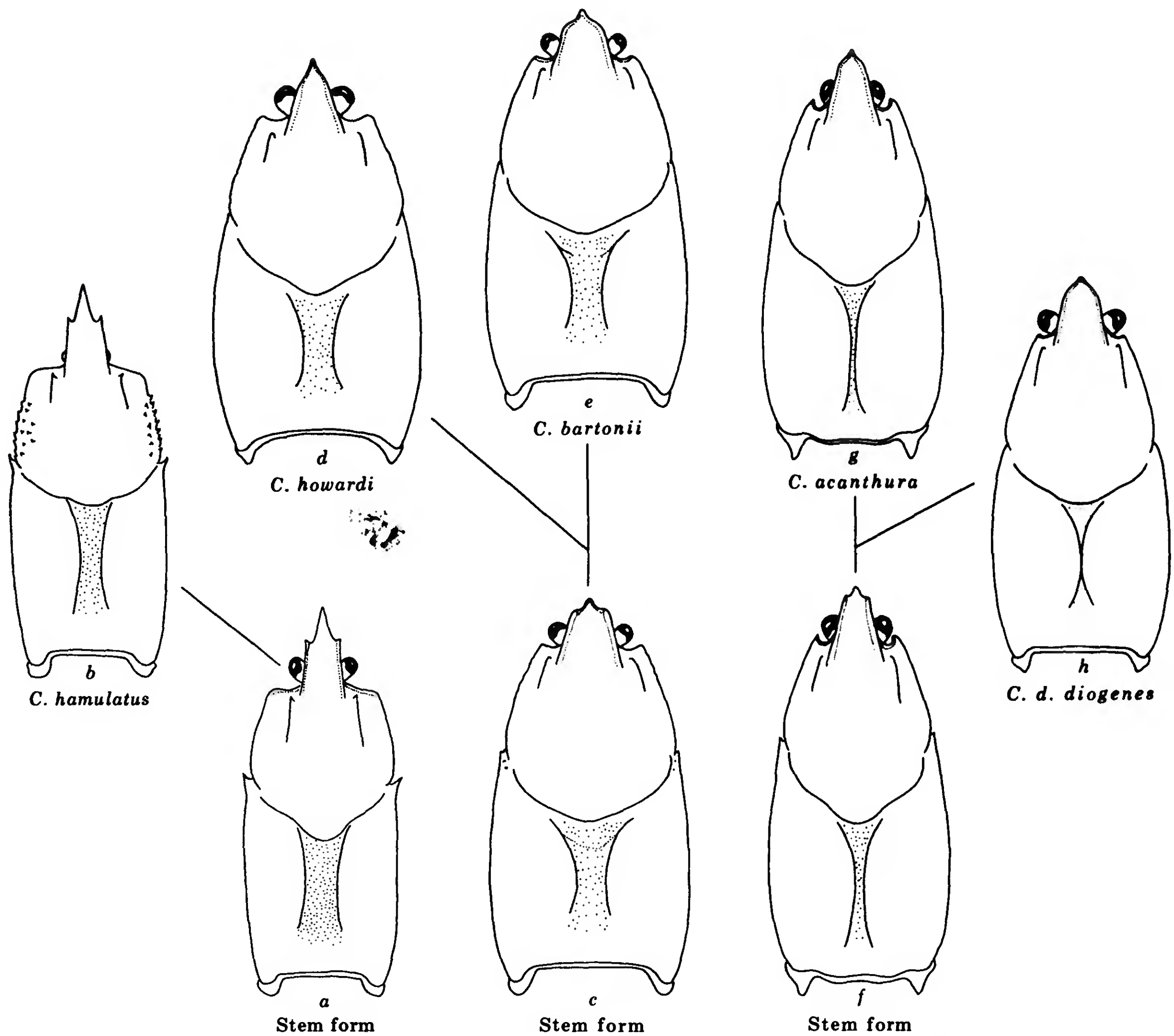


FIGURE 25.—Affinities of Georgia representatives of subgenera *Aviticambarus*, *Cambarus*, and *Lacunicambarus* (stem forms, *a*, *c*, *f*, from Figure 20*e*, *c*, *b*, respectively).

the evolution within the genera *Fallicambarus* and *Faxonella*, the more important events in the diversification in them, as well as in several other stocks, have occurred beyond the political boundaries of the state. This is especially true of the ancestral history of the genus *Orconectes*, to a lesser degree in that of *Cambarus*, and in a few species groups of the genus *Procambarus*. In marked contrast, virtually all important events in the evolving members of the latter genus occurred within or in the vicinity of the present boundaries of the state.

As a working hypothesis, I suggest that the ancestral cambarine stock (Figure 11*a*) entered the freshwaters of the southeastern part of the North American continent during the late Cretaceous or early Cenozoic eras. This ancestral *Procambarus* stock, moving through estuarine waters, may well have populated many of the streams flowing from the southern and southeastern slopes of the existing continent. At first they no doubt remained near or in the tidewater area but later ventured into waters of lesser salinity. Employing these assumptions, I envisage the early Cenozoic as a time during which these southward flowing streams were being populated by crayfishes (Figure 11*b–d*) undergoing an adaptive radiation that resulted in the exploitation of many, if not most, available habitats within the water courses.

Soon after the early *Procambarus* stock (typified by several modern members of *Ortmannicus* (Figure 11*e–g*) and *Pennides* (Figure 11*b*)) had populated the streams and had become largely limited to freshwater, stocks were isolated in their respective drainage systems. Exceptions came about through passive dispersal, resulting from headwater streams in one basin being captured by those of another, and perhaps on equally rare occasions by the crayfishes actively moving, during periods of low salinity, from one river mouth to another. For these stream dwellers, dispersal across drainage divides since the latter part of the Pleistocene has probably been minimal.

Before the close of the Miocene, perhaps as early as Eocene or Oligocene times, some of the stream inhabitants (Figure 11*c*; descendants) found a tolerable habitat in backwaters or in lowland sloughs that joined the rivers. From these adventurers arose the ancestors of the *seminolae* (Figure 11*g*) and *blandingii* (Figure 11*f*) groups of the subgenus *Ortmannicus* and of the subgenus *Scapulicambarus*. Once freed from flowing water, these crayfishes, now able to populate lentic habitats, were introduced to a tremendous ecological vacuum. On humid, cloudy days or evenings they no doubt made brief forays from their aquatic habitats, perhaps initially being forced to do so by the pools in which they were living becoming dry or by a lowering of the oxygen concentration of the water. For whatever reason, this overland trek led them to new ponds, lakes, and sloughs, and, having retained their ability to live in flowing water, these crayfishes were ultimately limited in their dispersal only by areas of dry land they could not cross before becoming desiccated, by salt water, and perhaps by cascading to swiftly flowing streams. One segment of the *Ortmannicus* stock, the ancestors of *Hagenides* (Figure 11*h*), having discovered through burrowing the availability of ground water, abandoned open water and invaded a habitat to which most of their descendants were destined to be restricted.

Another stock, derived from the adorconectoid ancestor and forerunners of the subgenera *Lecónticambarus* and *Distocambarus*, also found temporary lentic habitats open to them. By constructing burrows that penetrated the water table, they were enabled to escape protracted periods of drought as well as to find a refuge below the frostline during colder months.

The evolution of the stocks previously mentioned must have taken place at comparatively low elevations, perhaps comparable to the present Coastal Plain and lower Piedmont provinces. One of the stream-dwelling stocks (Figure 11*l*), however, moved upstream, reaching the vicinity of the Cumberland Plateau where two very successful lineages became established: the ancestors of members of the genus *Cambarus* (Figure 11*n*) and those of the genus *Orconectes* (Figure 11*o*). Representatives of both of these stocks (Figure 11*q,s*) also found congenial habitats in temporary pools and bogs and spread through lowland areas where there arose the species now assigned to the genera *Fallicambarus* and *Faxonella*. The more primitive descendants of both of these latter stocks occur in an area that during the early Cenozoic was situated on the western flank of the Mississippi Embayment, and the occurrence of representatives of both genera in Georgia must have resulted from comparatively recent migrations into the state from the west.

The major evolutionary lines had probably been established by Miocene times, and with modern drainage patterns having been developed shortly after the close of the epoch (Alt, 1974:21), the final stage was set for the refinement of evolutionary patterns that had begun during the earlier part of the Cenozoic.

By Pliocene times, all of the major streams flowing southward through the piedmont and coastal plain of Georgia were frequented by stocks derived from ancestors of *Pennides* and those of the *pictus* Group of *Ortmannicus*. Representatives of the former occurred in most of the river basins from San Luis Potosí, Mexico, to the Edisto River system in South Carolina. The stream-dwelling derivatives of the *pictus* Group, however, had a much more restricted range, one that extended from the Chattahoochee-Flint system to the Pee Dee watershed of North Carolina and South Carolina. The relictual occurrence of *Procambarus (O.) pictus* (Hobbs, 1940a:419) in the Saint Johns River basin in Florida and of *P. (O.) youngi* Hobbs (1942b:131) in the Florida panhandle, as well as the absence of members of the group in the Satilla, Saint Marys, Suwannee, Aucilla, Ochlockonee, and Chattahoochee-Flint basins, lead to the conclusion that the Pleistocene inundation of the area now drained by the Satilla, Saint Marys, and most of the Suwannee rivers was responsible for the extinction of almost all representatives of the group to the south and west of the Altamaha watershed. Five species of the group have become differentiated in the Georgia coastal plain bounded by the Altamaha and Savannah rivers. Throughout this area the streams are shared with members of the subgenus *Pennides*, suggesting the improbability that a member of one group excludes a representative of the other. Thus the question is posed as to what explanation exists for the occurrence of members of *Pennides* in all of the streams in the Georgia coastal plain except the Aucilla River (a stream that in Georgia frequently becomes dry), whereas the *pictus* Group has such a limited range. I can offer no explanation for the absence of a representative of the group in the Ochlockonee and Chattahoochee-Flint basins in Georgia, but a reasonable explanation of their absence in the Satilla, Saint Marys, and Suwannee basins does exist.

Prior to the retreat of the sea from the coastal area (perhaps as early as late Miocene or Pliocene times), a stock of the primitive *pictus* Group had gained access to lentic habitats, but, as noted above, they were still able to exist in streams. These ancestors of *P. (O.) seminolae* were in the Pleistocene coastal area between the Altamaha and Ochlockonee rivers, and as the sea retreated from the inundated areas, descendants of this stock not only moved into the newly developing lentic habitats but also invaded the streams where they still vicariate for members of the *pictus* Group. Apparently not only has *P. seminolae* been able to impede the invasion of members of the *pictus* Group into these river systems but also has indeed become established, probably recently, in the domain of the latter group north of the Altamaha River, where eventually it will encounter its closest relative, *P. (O.) lunzi*.

In Georgia, the descendants of the *Pennides* ancestors, although undoubtedly excluded from the lower coastal plain that was flooded during the Pleistocene invasions of the sea, have gained access to all of the streams that developed following the retreat of the sea at the end of the period. The fact that *P. spiculifer* is the commonest crayfish in all of the major southward-flowing streams in the state, except in the Ogeechee and Savannah basins, attests to its probable longtime successful occupation of the lotic habitats in the state. Surely it moved downstream through the developing drainage systems over the land newly exposed as the sea retreated from the continental mass, and no doubt it gained access to streams like the Saint Marys River through piracy of headwaters or perhaps across low divides at times following heavy rains when broad areas became inundated, linking adjacent watersheds.

Returning to the ancestors of the *seminolae* Group, surely they had become differentiated from the stream-dwelling *pictus* stock before the close of the Tertiary, and I visualize their occupying most lentic habitats in the coastal plain from the Carolinas southward into the peninsula and panhandle of Florida during the Pliocene. In Georgia, following the incursion of the Pleistocene sea, the ancestors of *P. lunzi* were occupying the coastal zone between the Savannah and Altamaha rivers, those of *P. seminolae*, the area between the Altamaha and Suwannee rivers, and those of *P. (O.) leonensis*, the area bounded by the Suwannee and Chattahoochee (perhaps as far west as the Choctawhatchee River in Alabama and northern Florida) rivers. Considerable doubt surrounds the Pleistocene refugium of *P. (O.) fallax*; however, it is possible, if not probable, that, like *P. (O.) pictus* and *P. (H.) geodytes*, it found a tolerable habitat on one or more of the islands that must have persisted throughout the Pleistocene and now constitutes a part of the "Trail Ridge" elevation in southeastern Georgia and northeastern Florida. Following the withdrawal of the sea, keeping somewhat abreast as the shoreline receded, the four stocks came to occupy their present ranges. Somehow *P. seminolae* and *P. fallax* have not only shared parts of their ranges, but also they not infrequently occur together in the same habitat. The nature of the barrier that separates the ranges of the former and *P. leonensis* is not at all understood, but I suspect that the comparatively well drained soils of the southwestern part of the Tifton Upland have offered obstacles that are less effective in the more eastern part of the upland and in the adjacent Bacon Terraces and Okefenokee Basin districts.

To be sure, the ancestors of the subgenus *Pennides* and those of the *pictus* and *seminolae* groups of *Ortmannicus* did not have the emerging Georgia coastal plain to themselves, and simultaneously four other crayfish stocks were claiming niches within the area. These were the forerunners of the subgenera *Hagenides*, *Leconticambarus*, and *Scapulicambarus*, as well as those of the *blandingii* Group of the subgenus *Ortmannicus*. The latter group probably became differentiated from the ancestral *Ortmannicus* stock in the coastal plain or lower piedmont to the west of the Chattahoochee Basin, perhaps within the Mobile River watershed, sometime during the middle to late Tertiary. The migration eastward of the ancestors of *P. blandingii* and *P. a. acutus* occurred during or since Pleistocene times. The latter appears to have such a broad ecological tolerance, being almost equally at home in temporary lentic and sluggish-to-moderate lotic habitats, that it is probably much better able to extend its range than those crayfishes that are more restricted in their habitat distribution. With little doubt, *P. a. acutus* is more common in Georgia than is evident in Figure 140, but despite my restricted knowledge of the ecology of crayfishes, it seems unlikely to me that it and *P. seminolae* could long share the same habitat. The apparent absence of the species (except its recent introduction in Meriwether County) from the Chattahoochee-Flint drainage system, if real, however, presents a problem for which I have no explanation. It is unlikely that competitive exclusion by *P. (S.) howellae* can be called upon to be responsible for its absence, for their ranges overlap in the Tifton Upland District, and they have been found together in three localities. Suggesting that the absence of *P. a. acutus* in the Chattahoochee-Flint system is perhaps an artifact of collecting is the apparent lack of any ditch- or pond-dwelling species in the upper Fall Line Hills District or in the lower Piedmont Province within the basin.

The presence of *Procambarus acutissimus* (a rather commonly occurring species in Alabama and eastern Mississippi) in the Chattahoochee Basin almost certainly represents a recent invasion into the state, as does the presence of *P. lophotus*. The latter has moved into Georgia through the Coosa Basin and in some manner, perhaps from headwaters of the Chattooga River, crossed the divide into the South Chickamauga Creek watershed.

The most primitive member of the subgenus *Scapulicambarus*, *P. paeninsulanus*, occurs in Georgia and neighboring parts of Alabama and Florida, and its range is flanked on the east and west by those of more highly derived relatives. Thus one might well conclude that the stem form, taking its origin from the primitive *Ortmannicus* stock in or adjacent to the lower Chattahoochee-Flint Basin during the middle to late Tertiary, subsequently spread eastward into South Carolina and westward as far south as San Luis Potosí, Mexico. Differentiating from this stock in Georgia was the primitive *P. paeninsulanus* in the Chattahoochee-Flint Basin; in late Pleistocene and recent times the ancestors of this crayfish moved eastward in Georgia, south of the Altamaha River, and southward into Florida. In the Altamaha Basin (Ocmulgee and Oconee watersheds), the closely allied

P. howellae became one of the dominant species, and, in the Ogeechee and Savannah basins, the more distantly related *P. troglodytes* became the ecological counterpart of the wide-ranging *P. (S.) clarkii* (Girard, 1852:91) of the Mississippi and neighboring basins. These two crayfishes appear to be more closely allied than either is to other species, and it is surprising that the ranges of three other species of the group (*P. howellae*, *P. (S.) okaloosae* Hobbs (1924b:100), and *P. paeninsulanus*) lie between their respective strongholds.

As pointed out earlier, the affinities of the members of the subgenus *Hagenides* to other members of the genus *Procambarus* are not so obvious as are those of the species groups that have just been discussed. Nevertheless the stem form (Figure 11*h*) of the subgenus was probably derived from a lineage including the ancestral *Ortmannicus* stock. By the late Tertiary, this crayfish must have become both genetically and ecologically isolated from its relatives and well on its way to changing its abode from surface lentic and sluggish lotic habitats to groundwater that was reached by burrowing. This venture almost assuredly took place in Georgia and likely somewhere in the Altamaha River basin. The descendants of this stock are confined to the coastal plain of Georgia and Florida (although there is a questionable record for South Carolina), and the most divergent members occur on the northeastern and southwestern limits of the range of the subgenus. It is probable that in Pliocene times the range of the stock was at least as great as it is today, but most of it disappeared during the Pleistocene with the encroachment of the sea. Safely above sea level and north of the Altamaha River in what is now the Vidalia Upland District, two segments of the primitive stock were preserved: the ancestors of the comparatively primitive *P. advena*, which were located nearer the coast (in the Ogeechee and Savannah watersheds), and those of the highly evolved *P. truculentus*, which were entrenched farther inland and east of the Oconee River, perhaps in the Ohoopee Basin. West of the Oconee River in the Vidalia Upland, the ancestors of *P. caritus* had become established, and closer to the Pleistocene coastline in the Bacon Terraces District were the forerunners of *P. talpoides*. The ancestors of the Floridian *P. (H.) geodytes* were almost certainly preserved, as were those of *P. (O.) pictus* and *P. (O.) fallax*, on one of the islands in the Trail Ridge chain. Lurking in the coastal area of the Tifton Upland during the Pleistocene were the ancestors of the several subspecies of *P. (H.) rogersi*, and sharing their ranges as well as perhaps those of *P. talpoides* and *P. advena* was the ancestral *P. pygmaeus*. With the retreat of the seas during the latter part of the Pleistocene, these four stocks moved into the newly emerging land: *P. advena*, impeded by the developing lower Altamaha and Savannah rivers, occupied the smallest range of the four; *P. talpoides* spread through the region between the Altamaha and Ochlockonee rivers, thus claiming a much larger area; as ecological conditions changed, *P. (H.) rogersi* abandoned its ancestral range in the southwestern part of Georgia as well as much of it in the adjacent part of Florida and emigrated along the developing Ochlockonee Basin into the coastal flatwoods of the Florida panhandle; and *P. pygmaeus* eventually spanned the ranges of the other three. *Procambarus caritus* and *P. truculentus* have remained (perhaps hemmed in by *P. talpoides* and *P. advena*, respectively) in the Vidalia Upland District.

In view of the striking parallelism that exists in the present ranges of the members of the subgenera *Hagenides* and *Leconticambarus*, one must conclude that whatever physical features of the environment influenced the distribution of the ancestors of one must have impinged almost equally on those of the other. Therefore a recounting of the postulated events in the evolution of the Pleistocene and Recent history of *Leconticambarus* would be so repetitious that, following a brief account of the origin of this stock, only the sympatric species pairs in the two subgenera are identified.

The species of the subgenus *Leconticambarus* appear to me to have had an early history quite different from that of other members of the genus *Procambarus* occurring in the state. According to Hobbs (1967b:13; 1969a:119), the ancestral "Barbatus-Gracilis" stock (graciloid line) took its origin in pre- or early Miocene times from a hypothetical adorconectoid ancestor that must have been dispersed along the coastal area of the early Tertiary Mississippi embayment. A segment of this stock is believed to have moved eastward with the retreat of the epeiric sea, and by Pliocene times it had reached across most, if not all, of the middle and lower coastal plain of Georgia and well into peninsular Florida. By early in the Pleistocene, the ancestral stocks leading to the currently recognized taxa occupied areas comparable to those believed to have been inhabited by three such stocks of *Hagenides*: that of *P. (L.) barbatus* sharing the range of ancestral *P. (H.) advena*, the ancestral *P. (L.) pubischelae deficiens* that of *P. (H.) caritus*, and the forerunners of modern *P. (L.) p. pubischelae* that of *P. (H.) talpoides*. As noted, Pleistocene and Recent migrations of each of the pairs appear to have been so markedly similar that the reader is referred to the accounts of the three members of the subgenus *Hagenides*, substituting the names of the sympatric *Leconticambarus*. Only one difference seems to be important. Whereas there is no evidence of intergradation between *P. caritus* and *P. talpoides*, there is good reason to believe that *P. (L.) p. deficiens* is likely sharing in a common gene pool with members of the nominate subspecies where their ranges are contiguous.

The disparate monotypic member of the subgenus *Distocambarus*, *P. (D.) devexus*, is believed to have a closer evolutionary tie with members of the graciloid assemblage than with any other group in the genus, but these affinities are remote at best. Surely the presence of this lone species in a small area of the Piedmont Province of the state represents a remnant of a stock that probably occupied a much larger range than does its descendants, but no evidence of its extent exists.

According to Hobbs (1969a:119), there were three major evolutionary lines emanating from the adorconectoid stock: the graciloid line, the Georgia descendants of which have just been discussed; the mexicanoid line, which is not represented in the Georgia fauna; and the archiorconectoid line that " . . . diverged further into two major lines—the orconectoid, from which arose the genera *Orconectes*, *Faxonella*, and *Hobbseus*; and the cambaroid, in which an early dichotomy separated the ancestors of *Fallicambarus* from *Cambarus*." As pointed out earlier, no representative of the genus *Hobbseus* occurs in the state, and the presence of single species of the genera *Faxonella* and *Fallicambarus* is believed to have resulted from comparatively recent emigrations from the west into the southeastern coastal plain.

Fitzpatrick (1977:373) expressed a slightly different interpretation of the origin of the genus *Hobbseus*, based chiefly on the presence of a comparatively well developed caudal "eminence at the base of the central projection" in *Hobbseus petilus* Fitzpatrick (1977:367). He suggested that the members of the genus *Hobbseus* may be closer to those of *Cambarus* than Hobbs had supposed and concluded that "evidences from this new species [*H. petilus*] strengthen the belief that *Hobbseus* arose from the cambaroid line . . . rather than the orconectoid line," and that "the genera *Cambarus*, *Hobbseus* and *Orconectes* . . . [were] contemporaneous, or nearly so, in their emergence from the archiorconectoid (= Adorconectoid stock) line."

The three species of the genus *Orconectes* have almost certainly entered Georgia from the northwest through the Tennessee River basin. Ortmann (1905a:114) pointed out, "From the Tennessee River two species (*spinosus* and *erichsonianus*) have crossed over into the Gulf and Atlantic drainages." Furthermore, ample evidence exists among the fishes (Smith-Vaniz, 1968:122–123) and mollusks (Simpson, 1900:135; Ortmann, 1913:289) that a part of the fauna of the Coosa watershed was derived from the Tennessee. Smith-Vaniz, for example, listed 10 species (thought not to have been introduced) that occur only in the Tennessee and Alabama basins, the latter of which includes the Coosa River. In addition, he cited three more occurring in the Alabama system that were believed by him to have had their ancestry in stocks that still exist in the Tennessee River system.

That the Tennessee River once continued southward along the flank of Walden Ridge to join the Coosa and was later captured by a headwater stream that cut its way across the ridge, opening Walden Gorge and deflecting the flow westward, has long been held possible by some geologists (Fenneman, 1938:276–277). Fenneman, however, considered such a sequence of events improbable, but he pointed out a possible breach in the divide between the two river systems in concluding that through headwater growth of the Coosa, it could well have captured the Conasauga River at the Georgia-Tennessee state line. Surely such an act of piracy by the Coosa could account for the presence in it of *O. spinosus*. Indeed this is a common species in the Conasauga River system at the present time. There are no records of *O. erichsonianus* from the Conasauga; if that species gained access to the basin by this route, it has been displaced by the present crayfish fauna.

The occurrence of *O. erichsonianus* and *O. forceps* in the South Chickamauga Creek basin in Georgia, a tributary to the Tennessee River, amounts to nothing more than their wandering upstream, a feat that, in the absence of pollutants, might even be accomplished today. There is no evidence that *O. forceps* occurs outside of this drainage system, but *O. erichsonianus*, which is rather widespread in the Coosa Basin, might have breached the divide between the headwaters of South Chickamauga Creek and the Chattooga River, thereby gaining access to the Coosa watershed. The syntopic occurrence of *O. erichsonianus* and *O. spinosus* in many parts of the Coosa Basin, however, and the absence of the latter in South Chickamauga Creek seem to favor another source of entry into the Coosa, and the Conasauga route seems to be the most obvious possibility.

In remarking on the mid-Cenozoic *Cambarus* stock, Hobbs (1969a:125) stated: "In remaining in streams, it retained most of the non-secondary sexual (somatic) features of the hypothetical ancestor, traits which are still preserved to a remarkable degree in several species occurring in the Green, Cumberland, Tennessee, and Coosa river systems." The most primitive of the Georgia members of the genus are those assigned to the subgenus *Puncticambarus*, a group that was believed by Hobbs (1969a:133–135)

> to have had its origin on the Cumberland Plateau where ... to the north and west ... this stock, like the others of the genus, very likely encountered considerable competition with the expanding genus *Orconectes* and to the east lay the Appalachian barrier; thus it could only expand to the northeast and south. The coastal plain was already dominated by a number of stocks of *Procambarus*, so that while some *Cambarus* were able to become established in *Procambarus* country, few ventured below the fall line.

All of the Georgia members of *Puncticambarus* arose from that stock that moved southward in the Great Valley and around the southern flank of the Smokies no later than Pliocene times. Of the representatives that remained in Georgia segments of the Tennessee Basin, those populating South Chickamauga Creek were ancestral to *Cambarus extraneus*; those in the Hiwassee River, to *C. hiwasseensis* and *C. parrishi*; and those in the Little Tennessee River, to *C. georgiae*. The stock that gained access to the Coosa watershed, probably accompanying *O. spinosus* and *O. erichsonianus* through the pirated Conasauga River, gave rise to *C. coosae* and *C. scotti*. Ancestors of the latter probably became at least temporarily isolated in the Chattooga River after migrating upstream from the mouth of the latter in Alabama. The ancestors of *C. chaugaensis* could well have reached the Savannah Basin through the capture of segments of the Little Tennessee Basin by the Savannah. The divide between the two in Rabun County, Georgia, is indeed a low one, and I should be surprised if there has not occurred a shift in the direction of flow in one or more small tributary streams from one basin to the other, even in very recent times. Surprising, however, is the apparent absence of *C. chaugaensis* in the adjacent Savannah tributaries that so closely resemble the Little Tennessee, in which *C. georgiae* is present as an uncommon inhabitant.

The precursors of *Cambarus (Aviticambarus) hamulatus*, which are believed to have been descended from a primitive *Puncticambarus* stock, must have invaded the subterranean waters of the Sequatchie uplift on the Cumberland Plateau "... subsequent to late Miocene times" (Hobbs, Hobbs, and Daniel, 1977:21). While there are no records of the occurrence of the species in Georgia, almost certainly it is present in the northwesternmost part of Dade County where the Paleozoic limestone formations are the same as those in the adjacent parts of Tennessee and Alabama where this crayfish has been found.

The progenitors of the subgenus *Depressicambarus* also are believed to have been derived from a primitive *Puncticambarus* stock. As to the area of divergence of these stocks, Hobbs (1969a:136) suggested rather vaguely " . . . the slopes of the Cumberland Plateau from which it moved through the Tennessee system above Walden Gorge to the Coosa and Black Warrior drainages and subsequently to the Savannah," implying that the ancestors of the primitive *C. halli*, which he referred to as a "relict of the ancestral stock of the subgenus," *C. obstipus*, and *C. (D.)* species F (see below) had moved away from the place of origin of the stem form. More recently, Bouchard (1978:45) offered an alternative hypothesis that the "ancestral stock of the subgenus arose in the southern end of the Piedmont" Province and moved northward "along the strikes of the Piedmont, Ridge and Valley and Cumberland Plateau." He believed that *C. halli* and *C. englishi* represented remnants of two invasions of the Tallapoosa Basin on the Piedmont and *C. obstipus* was left in the Black Warrior River basin on the southern end of the Cumberland Plateau. The most primitive segment of Bouchard's *latimanus* Group is a local variant of *Cambarus (D.) latimanus* (= *C. (D.)* species F, Hobbs, 1969a:104), which occurs commonly in the Broad River watershed (Savannah Basin) and less abundantly in nearby tributaries. The occurrence of this variant (which Hobbs grouped with *C. halli* and *C. obstipus* as the most primitive members of the genus) led Bouchard (1978:46) to state that "the *latimanus* group . . . probably arose on the Piedmont province, but further to the northeast than the *halli* group in the Georgia-South Carolina area, and utilized several corridors of migration." Of the several "corridors" of dispersal proposed by Bouchard, attention here is drawn only to what must have occurred in Georgia. Assuming that the primitive features of the variant in the Savannah Basin represent retentions rather than atavistic traits, then one must conclude that at one time a stock provided with them once occupied the upper parts of the Chattahoochee and Coosa basins (unless in the unlikely event it reached the Savannah via the Little Tennessee Basin) and later became extinct. Inasmuch as both the atypical (more primitive) variant and the typical form of *C. latimanus* exist in the Savannah, the presence of the former should perhaps be regarded, as suggested for the other members of the *halli* Group, a relict population. In some unknown area, perhaps in the Savannah or adjacent basins, a much more successful stock came into existence, and, in crossing low divides between drainage systems, spread throughout the piedmont sector of the state (moving elsewhere along paths suggested by Bouchard). This stock, ancestral to typical *C. (D.) latimanus*, while not shunning the larger streams, was particularly successful in the smaller ones entering the headwaters. From the outset, the members were able burrowers, tunneling into the banks of the streams, and some moved into seepage areas where eventually certain local populations became totally dependent upon groundwater. Concomitantly, in different areas they underwent similar modifications in their adaptations, though not all attained the same degrees of divergence from the ancestral stock. *Cambarus (D.) striatus* appears to me to represent one such stock that while becoming better adapted to subterranean habitats than did the ancestral *C. latimanus*, it nevertheless did not become overly specialized and thus acquired a broader ecological tolerance than the parent stock. Where this took place may never be determined, for the descendants are so widespread now, and apparently the species vagility has been so great, that it could have occurred in one (or more?) of many areas in Alabama, Georgia, and Tennessee. If it occurred in Georgia, I suspect the Coosa (or perhaps the Tennessee) Basin would have been the most likely. As to the time, the fragmentation of the *C. latimanus* stock could have been as recent as Pleistocene times, although I suspect that the stage of development attained by *C. striatus* may have been accomplished earlier. As for the remaining Georgia representatives of the subgenus *Depressicambarus*, these species were derived from populations that extended the adaptations similar to those that were begun by the ancestors of *C. striatus*. In becoming more specialized, however, they were decidedly less successful, thus limited in their distribution to small isolated areas where they became confined to seepage slopes or poorly drained soils, rejecting nearby bodies of open water. *Cambarus cymatilis* is confined to a part of the Conasauga Basin, *C. harti* to the Chattahoochee-Flint, *C. reflexus* to the middle Savannah and Ogeechee, *C. strigosus* to the piedmont sector of the Savannah, and *C. truncatus* to the Oconee Basin.

Another group of the genus *Cambarus* demonstrating close ties with members of the subgenus *Puncticambarus* are those of the subgenus *Hiaticambarus*. There seems to be little doubt that the most generalized species of the subgenus occur in the Tennessee (*C. girardianus*) and Coosa (*C. speciosus*) river basins. It is equally probable that the Tennessee Basin is the ancestral home of the subgenus, one that probably dates to Miocene times, when a *Puncticambarus*-like ancestor underwent adaptations leading to a life in swift water, and ultimately extended its conquest to the exploitation of riffles. The distribution of the several species in Georgia suggests a pattern of invasion of the state similar to that postulated for *Orconectes* and *Puncticambarus*. The presence of *C. girardianus* in Lookout and South Chickamauga creeks might represent either or both old or recent invasions. The same is true (although likely old) of the presence of *C. longirostris* in Lookout Creek and in the Hiwassee Basin. (The presence of this crayfish in a single locality in the Chattooga drainage system perhaps resulted from an introduction by man.) Surely in whatever manner early stocks of *Orconectes* and *Puncticambarus* gained access to the Coosa Basin, two stocks of *Hiaticambarus* also arrived with them, and the distribution of the latter is such that the Conasauga corridor was a likely one. The more generalized stock was to become ancestral to *C. speciosus*, *C. coosawattae*, *C. fasciatus*, and the more specialized *C. manningi*. In the presence of the ancestors of *C. (P.) coosae*, only those of *C. (H.) manningi* were able to become established, but in the Etowah Basin, where the former is rare, *C. fasciatus* became one of the more common species. In the Coosawattee Basin, the primitive facies of *Hiaticambarus* were preserved in the less ecologically restricted *C. (H.) speciosus*, and the more advanced riffle-dwelling *C. (H.) coosawattae* abounds in such habitats.

Representatives of the subgenus *Jugicambarus* reached Georgia along at least two routes: the Appalachian (Cumberland) Plateau and through the Blue Ridge Province. Two of the species, *C. distans* and *C. parvoculus*, have broad ranges on the plateau in the Cumberland and Tennessee watersheds and almost certainly reached the northwestern corner of Georgia along the Tennessee River. *Cambarus unestami*, in having retained certain primitive features, might represent an early (Miocene?) isolate of the ancestral *Jugicambarus* that populated most of the plateau. The three remaining species, primarily inhabitants of brooks and/or seepage areas in the mountains, represent divergences in an ancestral stock that had crossed the Tennessee Valley from the Appalachian Plateau and by (or at) the close of the Pleistocene had populated the southern part of the Blue Ridge Province: ancestors of *C. conasaugaensis* on the southwest, those of *C. nodosus* in the southern part, and those of *C. asperimanus* in the southeast. The seemingly enigmatic occurrence of *C. cryptodytes* in the southwestern part of the state, if its relationships are correctly understood, can be explained only as a relictual population of a Pleistocene invasion by a *Jugicambarus* stock along the Chattahoochee Basin. With warming climates, the epigean members in the coastal plain and piedmont were unable to survive (Hobbs and Barr, 1960:15–16).

Closely allied to the *Jugicambarus* stem form was that stock ancestral to members of the subgenus *Cambarus*. This stock, being less inclined to burrow and therefore living in open water and seeking refuge under rocks, is believed to have shared mountain brooks and smaller streams with the

Jugicambarus stock. Of the two species recognized here, *C. bartonii* may well represent a species complex, and no doubt stocks have populated the state along at least three routes. The populations occurring in the Appalachian Plateau Province are so distinct from those in the Blue Ridge Province that were there not others in eastern Tennessee and in North Carolina that suggest an amalgamation of the features of the two, they would most assuredly be recognized as separate species. Even in the Blue Ridge Province, there are variants suggesting divergence of two or more stocks that reached Georgia through the Hiwassee and Little Tennessee basins. Suggestions of migratory routes and temporal conjectures related to this crayfish are best left until the interrelationships of the southern components of the "species" are better understood. *Cambarus howardi*, an endemic species in the Chattahoochee Basin, is obviously a near relative, perhaps even a regional variant of *C. bartonii*, the ancestors of which gained access to the basin during the Pleistocene. Unlike the ancestral stock of *C. cryptodytes*, which also followed the Chattahoochee from the mountains, populations of *C. howardi* have persisted as far downstream in the basin as Lee County, Alabama.

Our knowledge of the subgenus *Lacunicambarus* (Figure 25*g,h*) has progressed little since Hobbs (1969a:148) stated:

> The origin of this group is obscure, and there is little reason for selecting any one of the three taxa as representing more nearly the ancestral stock. The fact that the areola of *C.* species J [= *C. acanthura*] is linear instead of obliterated suggests that it is the more primitive, but some populations of *C. d. diogenes* . . . have a similar areola. At present, little can be said about its origin or the migratory paths it followed, but it is suspected that it probably had a common ancestry with the members of the subgenus *Cambarus*.

Family CAMBARIDAE Hobbs, 1942a

Subfamily CAMBARINAE Hobbs, 1942a

Key to Genera of Subfamily Cambarinae

1. Male 2
   Female 7
2. First pleopod terminating in more than 2 parts .... **Procambarus**
   First pleopod terminating in no more than 2 parts (occasionally small caudal knob at caudomesial base of central projection in some members of *Cambarus*) 3
3. First pleopod with terminal elements bent at 90 or more degrees to shaft of appendage 4
   First pleopod with terminal elements extending distally from end or arising from caudal side of swollen distal part of shaft 5
4. Opposable margin of dactyl of chela with abrupt excision in proximal half marked distally by large tubercle .... **Fallicambarus**
   Opposable margin of dactyl of chela without abrupt excision in proximal half .... **Cambarus**
5. First pleopod straight; central projection never so much as 4 times as long as mesial process; both terminal elements forming at least one-fifth of total length of appendage .... **Orconectes**
   First pleopod inclined caudally, or with central projection at least 4 times as long as mesial process, or with short central projection arising from caudal side of swollen distal part of shaft; mesial process never forming as much as one-fifth of total length of appendage 6

6. First pleopod with central projection at least 4 times as long as mesial process .... **Faxonella**
   First pleopod with central projection subequal in length to, or shorter than, mesial process .... **Procambarus**
7. Annulus ventralis freely movable although sometimes partly hidden in ventral aspect by projections from sternum immediately anterior to it 8
   Annulus ventralis inflexibly fused with sternum immediately anterior to it or capable of slight hingelike motion 9
8. Dactyl of chela distinctly longer than mesial margin of palm; tubercles on mesial surface of latter well developed and conspicuous ..**Procambarus**
   Dactyl of chela subequal in length to, or shorter than, mesial margin of palm; tubercles on mesial surface of latter very small and inconspicuous .... **Faxonella**
9. Annulus ventralis inflexibly fused to sternum anterior to it .. **Orconectes**
   Annulus ventralis capable of slight hingelike motion 4

Genus *Cambarus*

Astacus.—Fabricius, 1798:407.

Cambarus Erichson, 1846:97. [Type-species by subsequent designation (Faxon, 1898: 644), *Astacus Bartonii* Fabricius, 1798:407. Proposed as subgenus of *Astacus*; elevated to generic rank by Girard, 1852:88. Gender: masculine.]

Gambarus.—Huxley, 1880:81 [erroneous spelling].

Orconectes.—Cope, 1881:881 [in part].

Camburus.—Faxon, 1885b:358 [erroneous spelling].

Camberus.—Miller, 1895:336 [erroneous spelling].

Camparus.—Williamson, 1899:47 [erroneous spelling].

S[ambarus].—Steele, 1902:11 [erroneous spelling].

Bartonius Ortmann, 1905a:97. [Type-species by original designation, "*C. bartoni*" Fabricius, 1798:407. Proposed as subgenus of *Cambarus*, treated unintentionally as generic name by Williamson, 1907:749, and declared a synonym of *Cambarus* by Fowler, 1912:341. Gender: masculine.]

Bartontius.—Rioja, 1941:193 [erroneous spelling].

Cambaus.—Okada, 1948:133 [erroneous spelling].

Canbarus.—Thompson, 1967:47 [erroneous spelling].

Cambaroides.—Unestam, 1969:204 [lapsus calami].

cambarus.—Padgett, 1970:19 [lapsus calami].

Cambaras.—Bouchard, 1973a:106 [erroneous spelling].

Cambraus.—Peters, 1975:iii [erroneous spelling].

Carbarus.—Bouchard, 1976c:17 [erroneous spelling].

Camabarus.—Huner, 1977:12 [erroneous spelling].

Subgenus *Aviticambarus* Hobbs, 1969a:96, 99. [Type-species, by original designation, *Orconectes hamulatus* Cope, 1881: 881. Gender: masculine.]

Subgenus *Depressicambarus* Hobbs, 1969a:96, 102. [Type-species by original designation, *Astacus latimanus* LeConte, 1856:402. Gender: masculine.]

Subgenus *Erebicambarus* Hobbs, 1969a:95, 99. [Type-species, by original designation, *Cambarus bartoni tenebrosus* Hay, 1902b:232. Gender: masculine.]

Subgenus *Hiaticambarus* Hobbs, 1969a:95, 105. [Type-species, by original designation, *Cambarus longulus* Girard, 1852:90. Gender: masculine.]

Subgenus *Jugicambarus* Hobbs, 1969a:95, 106. [Type-species, by original designation, *Cambarus bartonii asperimanus* Faxon, 1914:391. Gender: masculine.]

Subgenus *Lacunicambarus* Hobbs, 1969a:96, 110. [Type-species by original designation, *Cambarus diogenes* Girard, 1852: 88. Gender: masculine.]

Subgenus *Puncticambarus* Hobbs, 1969a:96, 101. [Type-species, by original designation, *Cambarus extraneus* Hagen, 1870:73. Gender: masculine.]

Subgenus *Veticambarus* Hobbs, 1969a:95, 96. [Type-species, by original designation, *Cambarus pristinus* Hobbs, 1965: 268. Gender: masculine.]

Subgenus *Exilicambarus* Bouchard and Hobbs, 1976:2. [Type-species by original designation, *Cambarus (Exilicambarus) cracens* Bouchard and Hobbs, 1976:2. Gender: masculine.]

DIAGNOSIS.—Antenna without conspicuous fringe on mesial border. Third maxilliped with teeth on mesial margin of ischium. Mesial margin of palm of chela with row of fewer than 12 tubercles except in albinistic species in which more present; lateral margin of fixed finger never bearing spiniform tubercles; opposable margin of dactyl almost never with prominent excision. Areola broad to obliterated or linear at midlength. Ischium of third pereiopod of male with hook. Coxa of fourth pereiopod of male with caudomesial boss, latter lacking basal setiferous pit ventrally. First pleopods of first form male symmetrical, seldom widely separated basally, with distal portion of shaft never inclined caudally, and terminating in 2 or 3 distinct parts (mesial process, central projection, and occasionally caudal knob; cephalic process always absent), 2 prominent ones bent caudally or caudolaterally between 45 and 100 degrees or with central projection forming arc approaching 180 degrees; central projection bladelike or tapering from base, with or without subapical notch; mesial process subconical, bulbiform, or conspicuously inflated at base, seldom corneous, never appearing twisted or subspatulate distally, and lacking eminence on cephalic (morphological) border; caudal element seldom present, but occasionally represented by knoblike prominence at caudolateral base of central projection. Female with annulus ventralis immovable or with caudal half or two-thirds capable of hingelike motion; first pleopod present, rudimentary, or absent. Branchial count 17 + ep. (Slightly modified from Hobbs, 1974a:11–12.)

RANGE.—From Minnesota and the coastal region of New Brunswick southward to Texas and the panhandle of Florida.

SPECIES.—Thirty-three of the 77 currently recognized members of the genus are known to occur in Georgia, and there is good reason to believe that, in addition, the troglobitic *Cambarus (Aviticambarus) hamulatus* (Cope, 1881:881) also occurs in the extreme northwestern part of the state. Six of the subgenera are represented, the numbers of species are noted in parentheses: *Cambarus* (2), *Depressicambarus* (9), *Hiaticambarus* (6), *Jugicambarus* (7), *Lacunicambarus* (2), and *Puncticambarus* (7).

The following is included to account for the number of species cited above. In his checklist of the North and Middle American crayfishes, Hobbs (1974b:10–22) included all of the members of the genus that had been described when the manuscript went to press. Since that time the following species assigned to the genus *Cambarus* have been added or are described herein: *Cambarus (Depressicambarus) pyronotus* Bouchard (1978: 37); *C. (D.) harti*, new species; *C. (D.) reflexus*, new species; *C. (D.) strigosus*, new species; *C. (D.) truncatus*, new species; *C. (Exilicambarus) cracens* Bouchard and Hobbs (1976:2); *C. (Hiaticambarus) coosawattae*, new species; *C. (H.) fasciatus*, new species; *C. (H.) manningi*, new species; *C. (H.) speciosus*, new species; *C. (Jugicambarus) batchi* Schuster (1976:225); *C. (J.) crinipes* Bouchard (1973a:103); *C. (J.) nodosus* Bouchard and Hobbs (1976:8); *C. (Lacunicambarus) acanthura*, new species; *C. (Puncticambarus) buntingi* Bouchard (1973b: 407); *C. (P.) coosae*, new species; *C. (P.) cumberlandensis* Hobbs and Bouchard (1973:41); *C. (P.) georgiae*, new species; *C. (P.) hiwasseensis*, new species; *C. (P.) parrishi*, new species; and *C. (P.) scotti*, new species.

The following species included in the checklist have been declared synonyms as follows: *C. (C.) bartonii cavatus* Hay (1902a:435) and *C. (C.) bartonii carinirostris* Hay (1914:384) were synonymized with the nominate subspecies by Bouchard (1976b:587); in the same publication (p. 592), Bouchard indicated that *C. Bartonii*, var. *longirostris* Faxon (1885a:64) [= *C. (H.) longirostris*] is a junior synonym of *C. (H.) girardianus* Faxon (1884:117); however, I am not convinced that the two are identical and recognize them as distinct species (see "Remarks" under the Subgenus *Hiaticambarus*). That *Cambarus jordani* (Faxon, 1884: 119) is a junior synonym of *C. (D.) latimanus* (LeConte, 1856:402), as is *C. (D.) floridanus* Hobbs (1941b:114) of *C. (D.) striatus* Hay (1902a:437), was pointed out by Bouchard (1978:28, 29).

Cambarus (D.) graysoni Faxon (1914:393) was recognized as a distinct species by Bouchard (1976b:589) who removed it from the synonomy of *C. (D.) striatus*.

REMARKS.—Chief among the systematic problems engendered by the crayfish fauna of Georgia are those involving members of the genus *Cambarus*. Attempting to decipher what species are present, determining the ranges of variation among them, and arriving at a decision as to what taxonomic disposition should be made of the several variants of certain species have consumed many of the hours devoted to the present study. Attention is called to several of the numerous problems that appear to me to persist.

My treatment of *Cambarus (C.) bartonii* leaves much to be desired. A detailed examination of this apparently highly variable and comparatively wide-ranging species (if indeed the many recognized variants are all members of a single species) is sorely needed. For example, I am tremendously puzzled by such extreme differences noted in populations of *C. (C.) bartonii* in Lookout Creek in Dade County, in the Ocoee watershed, and in headwaters of the Chattahoochee, Little Tennessee, and Savannah basins.

Bouchard (1978), in his fine treatment of the subgenus *Depressicambarus*, and I are in general agreement concerning the ranges of variation in *C. (D.) latimanus* and *C. (D.) striatus*; however, both species need further attention in Georgia. Certainly samples of many more of the burrowing populations of the latter should be acquired. With so few burrowing representatives from Georgia available, I have suppressed my inclination to introduce other taxa to receive certain distinctively appearing variants.

Need for a detailed analysis of this species group is indicated by the fact that Bouchard and I are not in agreement concerning the identities of *C. (H.) girardianus* and *C. (H.) longirostris* and the added problem of the occurrence of members of the subgenus in the Coosa Basin in Alabama that I am unable to refer to previously described species.

The single lot of specimens from Dade County and others from the Cumberland Plateau in Alabama that I have identified as *Cambarus (Jugicambarus) distans* Rhoades (1944:136) do not appear to be typical when compared with the types and topotypes of the species. Because of the lack of information on the variability of the species throughout its range, the specific determination of this material must be considered tentative.

Key to Subgenera of Cambarus Occurring in Georgia

1. Pigmented members with tubercles on mesial surface of palm forming cristiform or serrate row, if latter, chela subrectangular; palm and fingers often studded with long setae. Albinistic members with antennal scale less than twice as long as broad .... ***Jugicambarus***

   Pigmented members with tubercles on mesial surface of palm never forming cristiform row, if row serrate then chela subtriangular; palm and fingers never studded with long setae. Albinistic members with antennal scale more than twice as long as broad 2

2. Rostral margins distinctly thickened; areola with crowded deep punctations; fingers of chela with poorly defined longitudinal ridges, usually strongly gaping and almost always with conspicuous tuft of setae at base of opposable margin of fixed finger .... **Hiaticambarus**

   Rostral margins seldom distinctly thickened; areola rarely, except in members of *Puncticambarus*, with crowded punctations; fingers of chela with clearly defined longitudinal ridges and seldom strongly gaping, if so, never with conspicuous tuft of setae at base of opposable margin of chela 3

3. Albinistic; maximum width of palm of chela less than length of mesial margin .... **Aviticambarus** [*C. (A.) hamulatus*]

   Pigmented; maximum width of palm of chela greater than length of mesial margin 4

4. Mesial surface of palm of chela with single row of strongly depressed tubercles; areola moderately broad and sparsely punctate .. **Cambarus**

   Mesial surface of palm of chela usually with at least 2 rows of tubercles, if only 1, tubercles not strongly depressed; areola variable, broad to obliterated at midlength, if sparsely punctate, then chela always bearing 2 well-defined rows of tubercles 5

5. Areola obliterated to 28 times as long as broad at midlength; dactyl of chela with broad concavity on basal half of opposable margin; central projection of first pleopod of first form male very short, not tapering, and rounded apically .... ***Lacunicambarus***

   Areola of variable widths, rarely obliterated at midlength or sublinear; if so, then dactyl of chela lacking concavity on basal half of opposable margin; central projection of first pleopod of first form male short or long; if not distinctly tapering, always with subapical notch 6

6. Width of palm of chela less than 1.5 times length of mesial margin. First form male with central projection of first pleopod always bearing subapical notch; basis of third pereiopod almost invariably with tubercle opposing hook on ischium .... ***Puncticambarus***

   Width of palm of chela almost always at least 1.5 times length of mesial margin. First form male with central projection of first pleopod tapering or with subapical notch; basis of third pereiopod very rarely with tubercle opposing hook on ischium .... ***Depressicambarus***

Subgenus *Aviticambarus*

Subgenus *Bartonius* Ortmann, 1905a:97 [in part].
Subgenus *Cambarus* Fowler, 1912:341 [in part; not Erichson, 1846:97].
Subgenus *Aviticambarus* Hobbs, 1969a:99 [type-species: *Orconectes hamulatus* Cope, 1881:881].—Hobbs, Hobbs, and Daniel, 1977:76.

DIAGNOSIS.—Body and reduced eyes without pigment. Rostrum with marginal spines, margins not thickened. Postorbital and cervical spines (latter multiple in *C. (A.) hamulatus* and sometimes obsolete in *C. (A.) jonesi*) well developed. Suborbital angle lacking. Branchiostegal spine strong. Areola moderately broad (5.4 to 8.0 times as long as wide), constituting 40.0 to 45.0 percent of entire length of carapace and with many moderately deep punctations. Chela slender and elongate; mesial surface of palm with scattered or several rows of tubercles and dorsal surface polished or with setiferous punctations; lateral margin of fixed finger weakly costate with row of setiferous punctations; fingers not gaping and with well-defined longitudinal ridges dorsally; proximal opposable margin of dactyl never deeply concave; conspicuous tuft of setae never present at mesial base of fixed finger, lateral base never deeply impressed. First pleopods comparatively widely separated basally and with distal portion of shaft almost straight or undulating; terminal elements consisting of (1) long, bladelike tapering central projection, with shallow subterminal notch, recurved at no less than 90 degrees to shaft, and (2) long, comparatively slender mesial process directed caudally or curved throughout length with apex pointed proximally; caudal knob lacking. (Modified from Hobbs, 1969a:99.)

RANGE.—"Along the Sequatchie Uplift, from the upper part of the Sequatchie Valley in Bledsoe County, Tennessee, southward to Blount County, Alabama, and in the Tennessee River basin between Florence and Guntersville" (Hobbs, Hobbs, and Daniel, 1977:76).

SPECIES OCCURRING IN GEORGIA.—None; however, it is highly probable that *C. (A.) hamulatus* occurs at least in the Appalachian Plateau Province of the extreme northwestern corner of the state.

HABITAT.—See "Ecological Notes" under *C. (A.) hamulatus*.

Cambarus (Aviticambarus) hamulatus (Cope)

FIGURES 25*b*, 26, 195

Orconectes hamulatus Cope, 1881:881–882.—Bouchard, 1976a: 571.

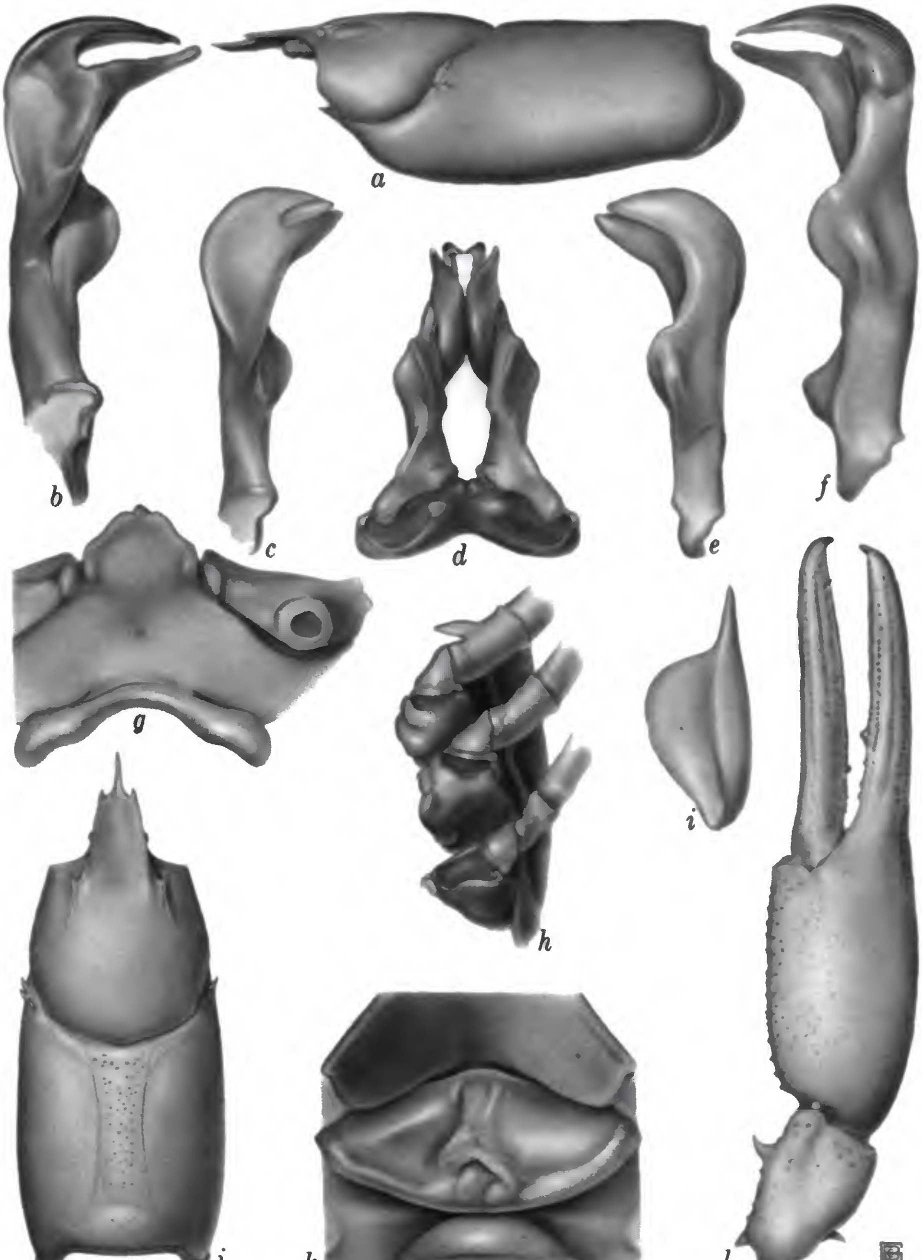


FIGURE 26.—*Cambarus (Aviticambarus) hamulatus*, topotypes (all from first form male except *c*, *e*, from second form male, and *k*, from female): *a*, lateral view of carapace; *b*, *c*, mesial view of first pleopod; *d*, caudal view of first pleopods; *e*, *f*, lateral view of first pleopod; *g*, epistome; *h*, proximal podomeres of third, fourth, and fifth pereiopods; *i*, antennal scale; *j*, dorsal view of carapace; *k*, annulus ventralis; *l*, dorsal view of distal podomeres of cheliped.

Cambarus hamulatus.—Faxon, 1884:145.—Hay, 1902a:435-437, fig. 8.—Hobbs and Barr, 1960:13, 14, 16-19, 23, figs. 1-10.—Bouchard, 1972:106; 1976a:571-574; 1976b:585.
Cambarus (Bartonius) hamulatus.—Ortmann, 1905a:120.
Cambarus (Cambarus) hamulatus.—Fowler, 1912:341 [by implication].—Bouchard, 1972:103.
Oronectes hamulatus.—Stiles and Hassall, 1927:219 [by implication; erroneous spelling].
Orconetes hamulatus.—Wolf, 1934:104 [erroneous spelling].
Cambarus (Faxonius) hamulatus.—Fleming, 1938:301.
Cambarus (Cambarus) hamueatus.—Fleming, 1938:303 [erroneous spelling].
Cambarus (Aviticambarus) hamulatus.—Hobbs, 1969a:99, 102, 127, 129, 130, 161, figs. 2e, 5, 13f, 14f, 17j; 1974b:10, fig. 21.—Bouchard, 1972:26, 28, 39, 102, 103; 1976a:572-575; 1976b:587.—Hobbs, Hobbs, and Daniel, 1977:76-78, fig. 37.
Cambarus (cf. *hamulatus*).—Cooper and Cooper, 1970:23.

The above is a selected bibliography (a nearly complete one is included in Hobbs, Hobbs, and Daniel, 1977:76); only synonyms, summary works, omissions, and references appearing since 1 January 1976 are included.

DIAGNOSIS.—

Body and eyes without pigment, latter lacking facets. Rostrum with marginal spines. Areola 7 to 8 times as long as wide. One to several cervical spines present on each side of carapace. Central projection of first pleopod of first form male moderately long, tapering, bearing weak subapical notch, and directed caudally at approximately 90 degrees to shaft of appendage; mesial process similarly oriented and extending slightly farther caudally than central projection (Hobbs, Hobbs, and Daniel, 1977:76).

COLOR NOTES.—This crayfish is albinistic, thus translucent to white.

TYPES.—Syntypes (♂II, ♀), MCZ 3678.

TYPE-LOCALITY.—Nickajack Cave, 0.5 mile south of Shellmound, latitude 34°59′23″N, longitude 85°36′38″W, Marion County, Tennessee. (Much of the cave is now flooded by an impoundment of the Tennessee River.)

RANGE.—From the upper Sequatchie Valley in Bledsoe County, Tennessee, southwestward to Blount County, Alabama.

GEORGIA SPECIMENS EXAMINED.—This crayfish has not been found in Georgia; however, there is every reason to believe that it occurs in subterranean waters in the extreme northwestern part of the state in Mississippian limestones underlying Sand Mountain. The type-locality, as noted above, lies only a short distance from the Georgia line.

SIZE.—The largest specimen available has a carapace length of 35.2 (postorbital carapace length 28.5) mm.

LIFE HISTORY NOTES.—"First form males have been collected in February, April, July, August, September, and November. Females carrying eggs or young have not been reported" (Hobbs, Hobbs, and Daniel, 1977:78).

ECOLOGICAL NOTES.—This crayfish is limited to subterranean habitats, and all available data are summarized by the authors just cited.

RELATIONSHIPS.—Nothing can be added to the remarks of Hobbs (1969a:129):

Although the two members of the troglobitic *Aviticambarus* (*C. (A.) hamulatus* and *C. (A.) jonesi* Hobbs and Barr (1960: 19)) probably are rather closely related to the more primitive members of *Puncticambarus*, they have become so highly modified that it seems appropriate that they be relegated to a separate subgenus. Were the differences all associated with adaptations to a spelean environment, as indeed are the most obvious ones, I should propose that they be included with *C. extraneus* and its relatives, but both the structure of the annulus ventralis (which is strikingly similar in the two and quite distinct from that of any other crayfish) and the first pleopods of the male are unique.

Of the two, *C. hamulatus*, which more nearly resembles *C. extraneus* and has retained the primitive multiple cervical spines, is considered to be the more primitive.

GEORGIA CRAYFISH ASSOCIATES.—Inasmuch as this crayfish has not been collected in Georgia, no associates are recorded.

Subgenus *Cambarus*

Subgenus *Cambarus* Erichson, 1846:97 [in part].—Fowler, 1912:341 [in part].—Hobbs, 1969a:109 [type-species, *Astacus Bartonii* Fabricius, 1798:407].
Subgenus *Bartonius* Ortmann, 1905a:97 [in part].

DIAGNOSIS.—Eyes small to moderate in size. Rostrum without marginal spines or tubercles and margins moderately to strongly thickened. Postorbital and cervical spines absent, sometimes represented by tubercles. Suborbital angle subacute to obsolete. Branchiostegal spine usually small or tuberculiform. Areola 3.0 to 7.3 times as long as broad and constituting 34.1 to 44.0 percent of entire length of carapace (40.5 to 46.4 percent of postorbital carapace length). Chela usually elongate, not strongly depressed, and with mesial margin of palm comparatively short (width of palm 1.3 to 1.6 times length of its mesial margin) and bearing single row (rarely 2) of tubercles; lateral margin of fixed finger costate or rounded; fingers seldom widely gaping, with well-defined longitudinal ridges dorsally, proximal opposable margin of dactyl never deeply concave; opposable base of fixed finger lacking conspicuous tuft of setae. First form male with hook on ischium almost always opposed by small tubercle on corresponding basis; first pleopod consisting of (1) bladelike central projection, bearing subapical notch, curved at angle of at least 95 degrees and occasionally so strongly curved that subapical notch directed toward proximal end of appendage; (2) inflated mesial process tapering to simple acute tip or subtruncate apically with 2 or 3 short rounded or acute tips; and (3) caudal knob usually absent, sometimes represented by low corneous ridge at caudomesial base of central projection. Female with annulus ventralis subsymmetrical, cephalic area usually not conspicuously less sclerotized than caudal, slightly movable but not hinged; caudal portion with tilted S-shaped sinus; first pleopod usually reaching midlength of annulus when abdomen flexed.

Range.—New Brunswick, Canada, to northern Georgia (in the Chattahoochee River basin, extending as far south as Lee County, Alabama), and from Indiana, Kentucky, and Tennessee to the Atlantic Ocean; along the Atlantic slope largely restricted to the mountains and upper piedmont south of Virginia.

Species Occurring in Georgia.—*Cambarus (Cambarus) bartonii* and *C. (C.) howardi*.

Habitat.—See "Ecological Notes" under *C. (C.) bartonii*.

Remarks.—Hobbs and Hall (1969) in describing *Cambarus (C.) howardi* were convinced that the members of the subgenus that frequent the Chattahoochee Basin from the vicinity of Lake Sidney Lanier downstream were clearly different from

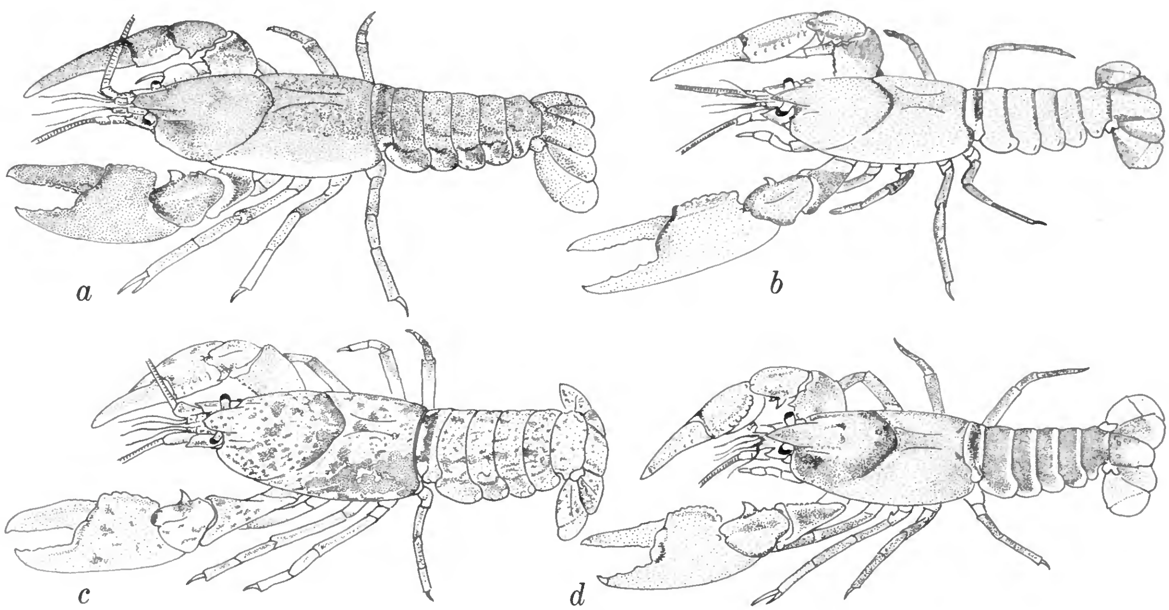


Figure 27.—Color patterns in *Cambarus (Cambarus) bartonii* (*a–c*) and *C. (C.) howardi* (*d*) by localities: *a*, Tennessee Basin in Dade Co; *b*, Toccoa (Hiwassee) Basin in Fannin Co; *c*, Savannah Basin in Stephens Co; *d*, Chattahoochee Basin in Hall Co.

any population of *C. (C.) bartonii* they had found within the state. Because no intergrades appeared to exist between this form and populations of *C. bartonii* occurring in headwaters of the Chattahoochee, they accorded it specific status. At the same time, they suggested that it might prove to be the most southern subspecies of *C. (C.) bartonii.* As more specimens of *C. howardi* from additional localities have been accumulated, the observed range of variation, as might have been anticipated, has become greater. Now, whereas the shape of the rostrum still will serve to distinguish this crayfish from all populations of *C. bartonii* occurring in the state, except for one of the variants in the Hiwassee Basin, the only character that I have discovered that will distinguish it from all members of the species in Georgia is the color. The rather drab, often mottled brown to olive, *C. bartonii* is readily separable from the lavender to forest green *C. howardi* bearing vermilion to scarlet ridges, condyles, and splotches on the dorsum of the body and chelipeds.

Considerable study of populations of the subgenus *Cambarus* is needed in the Chattahoochee Basin upstream from Lake Sidney Lanier in both the Chestatee and Chattahoochee watersheds of Lumpkin and the southern parts of Habersham and White counties.

Key to Georgia Members of Subgenus *Cambarus*

Dorsum of body and chelipeds lavender to forest green marked with scarlet or vermilion; rostral margins strongly tapering from base (restricted to Chattahoochee River basin) .... ***howardi***

Dorsum of body and chelipeds brown to olive, reddish markings if present limited to distal part of fingers of chela; rostral margins, except in one variant occurring in Hiwassee Basin, never strongly tapering from base (widespread in northern Georgia) .... ***bartonii***

Cambarus (Cambarus) bartonii (Fabricius)

FIGURES 25*e*, 27*a–c*, 28–30, 31*a,b*, 32, 33*a–h*, 34*a–j*, 35, 196

Astacus Bartonii Fabricius, 1798:407.

Astacus ciliaris Rafinesque, 1817:42. [Types not extant. Type-locality, brooks near Fishkill, Dutchess County, and Newburg, Orange County, New York.]

Astacus pusillus Rafinesque, 1817:42. [Types not extant. Type-locality, brooks in New York, near "Saratoga, Lake George, Lake Champlain, Utica, Oswego, &c."]

Astacus bartonii.—De Kay, 1844:22.

Astacus Bartoni.—Tellkampf, 1845:85.

Astacus (Cambarus) Bartonii.—Erichson, 1846:97.

Cambarus Bartonii.—Girard, 1852:88.

Cambarus montanus Girard, 1852:88. [Types destroyed in the Chicago fire in 1871; paratype (?), ANSP 322 (♂II), from James River, Virginia. Type-locality, restricted by Ortmann, 1931:114, "Tributary of James River, Rockbridge County, Virginia."]

Cambarus Bartoni.—Hagen, 1870:30.

Cambarus bartonii.—Packard, 1880:222.—Anonymous, 1971: 154*; 1973b:(55, 58, 63, 65, 70, 71, 76)*.—Hart and Hart, 1974:88*, 134*.—Wharton, 1978:46*.

Cambarus Bartonii Bartonii.—Faxon, 1885a:61 [by implication].

Cambarus bartoni.—Shufeldt, 1898:227.—Sprague, 1950:46*. —Sprague and Couch, 1971:530*.—Wharton, 1978:22*.

Cambarus bartonii bartonii.—Hay, 1899b:959 [by implication].—Hobbs and Walton, 1960a:18*; 1961:384*.—Holt, 1968b:(23, 26, 32)*.—Hobbs, 1968b:K-15*.—Hobbs and Hall, 1969:286*-287*.—Anonymous, 1970a:(22, 23, 27–29)*; 1971:153*.—Hart and Hart, 1974:(61, 79, 134)*.—Wharton, 1978:220*.

Camparus bartonii.—Williamson, 1899:47 [erroneous spelling].

Cambarus bartoni bartoni.—Hay, 1902a:435.—Crocker, 1957: 42, pl. 1: figs. 2, 3, 6; pl. 2: figs. 5–7.—Unestam, 1969: 203*, 205*.

Cambarus bartoni cavatus Hay, 1902a:435. [Syntypes, USNM 25017 (♂II, ♀, 2 juv. ♂). Type-locality, Powell River, Tazewell, Claiborne County, Tennessee.].—Cooper and Iles, 1971:46*.

Cambarus (Bartonius) bartoni.—Ortmann, 1905a:117, 120.

Astacus bartoni.—Ortmann, 1906b:348.

Cambarus bartoni typicus.—Ortmann, 1906b:450.

Cambarus bartonius bartoni.—Chidester, 1908:710.

Cambarus (Cambarus) bartonii.—Fowler, 1912:341.—Bouchard, 1976b:587–588.

Cambarus (Cambarus) bartonii cavatus.—Fowler, 1912:341 [by implication].—Hobbs, 1969a:109, figs. 5, 19n; 1974b:11*, fig. 25.

Cambarus bartonii montanus.—Faxon, 1914:385.

Cambarus bartonii cavatus.—Faxon, 1914:425.

Cambarus bartonii carinirostris Hay, 1914:384. [Types and paratypes, USNM 23962 (♂I, 7♂II, 15♀); paratypes, MCZ 7399 (♂I, ♂II, ♀). Type-locality, Gandy Creek at Osceola, Randolph County, West Virginia.]

Cambarus (Cambarus) bartoni cavatus.—Ortmann, 1931:104 [by implication].

Cambarus montanus montanus.—Ortmann, 1931:106.

Cambarus (Cambarus) bartoni carinirostris.—Ortmann, 1931:107 [by implication].

Cambarus bartoni montanus.—Ortmann, 1931:114.

Cambarus (Cambarus) bartoni bartoni.—Ortmann, 1931:130.

Cambarus (Cambarus) bartonii bartonii.—Fleming, 1938:303.—Hobbs, 1969a:109, 110, 144–146*, figs. 2b, 5, 13e, 14e, 19 l; 1972b:(111, 146, 154)*, figs. 5r, 86b, 88d, 89 l, 90a, 94b, 96c; 1974a:11, fig. 5; 1974b:10–11*, fig. 23.

Cambarus bartonius.—Roberts, 1944:370 [erroneous spelling].

Canbarus bartoni.—Thompson, 1967:47 [erroneous spelling].

Cambarus (Cambarus) species L.—Hobbs, 1969a:109, fig. 5.

Cambarus (Cambarus) bartonii carinirostris.—Hobbs, 1969a:109, fig. 19m.

Cambarus bartonni.—Coleman, 1972:21 [erroneous spelling].

Cambaras bartoni.—Bouchard, 1973a:106 [erroneous spelling].

Cambarus (Cambarus) bartoni bartonii.—Hobbs III, 1975:298 [erroneous spelling].

The above bibliographic citations embrace all of the synonyms (including incorrect spellings) known by me to have been applied to this species. Cited also are sources of illustrations, summary treatments, and all references to the occurrence of this crayfish in Georgia, the latter marked with an asterisk. It is by no means a complete bibliography for the species.

Summary of Literature Pertaining to Georgia.—Sprague (1950:46) cited the first specific locality for this crayfish in Georgia (head waters of Sneaking Creek on Garland Ridge approximately three miles north of Hiwassee, Towns County), where it was infected with *Thelohania cambari*, a microsporidian that affects the muscular system of its host. Ten years elapsed before Hobbs and Walton (1960a:18) recorded the presence of *C. (C.) bartonii* in Dunn Creek, 1.9 miles west of Fightingtown Creek on Hell's Hollow Road, Fannin County. There it served as one of the hosts to the entocytherid ostracod, *Entocythere simondsi* Hobbs and Walton, 1960a (= *Uncinocythere simondsi*). In 1961 (p. 383), they cited a second locality in Towns County where this crayfish was found to be infested by an ostracod described therein by them as *Entocythere hiwasseensis* (= *Donnaldsoncythere donnaldsonensis* (Klie, 1931)).

Holt (1968b) recorded the species from tributaries of the Ocoee River in Fannin County and from a tributary of the Nottely River in Union County, where it was a host of the branchiobdellid worm, *Pterodrilus simondsi* Holt (1968b). He also cited two additional localities for this crayfish in Union County where it harbored an unidentified member of the genus *Pterodrilus*. Hobbs (1968b) noted that the range of *C. (C.) bartonii* extended into Georgia. In 1969(a), he discussed the range of the species and illustrated the typical form.

Unestam (1969) noted the resistance of this crayfish, specimens of which were collected from the Savannah drainage system in Georgia, to the ascomycete, *Aphanomyces astaci* Schikora.

In a report of a biological survey of the Chattooga River in Rabun County (Anonymous, 1970a), five localities for this species are cited, and, in a similar study (Anonymous, 1971), one locality each from White and Habersham counties are included. Cooper and Iles (1971) reported the occurrence of *Cambarus bartoni cavatus* in Twin Snakes Cave, along Allison Creek, in Dade County. Hobbs (1972b), in his key to the North and Middle American crayfishes, included Georgia within the range of the species and presented several illustrations. In a survey of the Tennessee River Basin in Georgia (Anonymous, 1973b), seven additional localities are listed for the species.

Hobbs (1974a, b) included *C. (C.) bartonii bartonii* in both his synopsis of the families and genera of crayfishes and in his checklist of the North and Middle American species. Hart and Hart (1974), in their monograph of the entocytherid ostracods, reported one locality each from Banks, Hart, Union, and White counties, Georgia, in which this crayfish served as host to *Dactylocythere leptophylax* (Crawford, 1961). In the Banks County locality, it also harbored *Donnaldsoncythere donnaldsonensis* (= *D. hiwasseensis*) as did those in one locality each in Dade and Lumpkin counties. The same Fannin County locality cited by Hobbs and Walton (1960a) was included where *Cambarus (C.) bartonii* was infested with *U. simondsi*, and a second one was added in which the crayfish was host to *Entocythere elliptica* (Hoff, 1944).

While not mentioning Georgia, Bouchard (1976b) synonymized the subspecies *Cambarus (C.) bartonii carinirostris* and *C. (C.) bartonii cavatus* with the nominate subspecies, thus eliminating the last of the previously existing subspecific taxa that had been assigned to the species.

DIAGNOSIS.—(As pointed out above, the two Georgia members of the subgenus *Cambarus* occurring in Georgia are so markedly similar that only the following need be added to the subgeneric diagnosis.) Convergence of rostral margins highly variable, but strongly convergent from base in only one variant inhabiting streams in Hiwassee Basin. Areola 3.4 to 5.2 (average 4.3) times as long as broad, comprising 33.8 to 38.3 (average 36.2) percent of entire length of carapace (41.1 to 44.3, average 42.4, percent of postorbital carapace length), and bearing 2 to 6 punctations across narrowest part. Color brown to olive and often mottled; red coloration limited to distal part of fingers of chela.

COLOR NOTES.—Both the color and color patterns are so variable in Georgia that three rather distinctive types are briefly described:

Tennessee Basin (Lookout Creek) (Figure 27*a*): Dorsum of carapace olive tan with irregular pattern of small anastamosing chocolate markings, particularly in thoracic region; cephalic region with pale tan rostral and postorbital ridges; cream band extending posteroventrally from antennal region over most of mandibular and anteroventral branchiostegal areas; hepatic region grayish tan with cream tubercles; dorsolateral part of branchiostegites with paired broad, irregular, pale olive tan stripe flanked ventrally by light greenish ventrolateral part of branchiostegites. Abdomen mostly olive with chocolate flecks; first tergum darker than remaining ones, latter bearing paired irregular dorsolateral spots converging and becoming smaller and paler on successive segments. Pleura set off from terga by faint, dark, broadly V-shaped markings, and each pleuron with cream spot anteriorly, spot sometimes L-shaped with lower arm of L on ventral margin. Lateral quarters of telson dark greenish gray, median half lighter but mottled. Both rami of uropods with lateral half dark, more conspicuously so on mesial ramus. Antennular and antennal peduncles mottled greenish gray on cream, flagella banded with dark gray and cream. Third maxilliped cream with few grayish markings. Chelipeds mostly greenish gray from midlength of merus distally, all tubercles cream to white, proximal and distal marginal areas of carpus and dorsal condyle and ridges on propodus dark gray to black, and tips of fingers yellowish cream. Remaining pereiopods shades of olive green from proximodorsal part of merus distally. Sternum cream with some ridges and knobs suffused with yellow.

Hiwassee Basin (Figure 27*b*): Carapace olive brown, sometimes with pinkish suffusion and often irregularly mottled with small pale tan to pinkish cream splotches. Rostral margins buff; cervical groove and posterior margin darker than other areas of carapace; antennal area pink. Abdomen with dark transverse bar on first tergum, and all terga with reddish brown posterior margin, remainder of terga and pleura either concolorous, assuming predominant color of carapace, or mottled. Telson with lateral fourths darker than middle half, and lateral parts of rami of uropods darker than remaining areas. Antennular and antennal peduncles mottled brown on dark olive or tan, flagella ringed with olive brown and tan. Third maxilliped cream with olive suffusion on 3 distal podomeres. Chelipeds basically olive brown from distal half of merus to yellowish cream tips of fingers; distal part of merus, mesial and distal parts of carpus, tubercles along mesial margin of palm, and ridge on propodus at base of dactyl darker than other surfaces. Remaining pereiopods dark olive from ischium distally. Sternal area pinkish cream.

Hiwassee and Savannah Basins (Figure 27*c*): Carapace olive to dark tan with conspicuous mot-

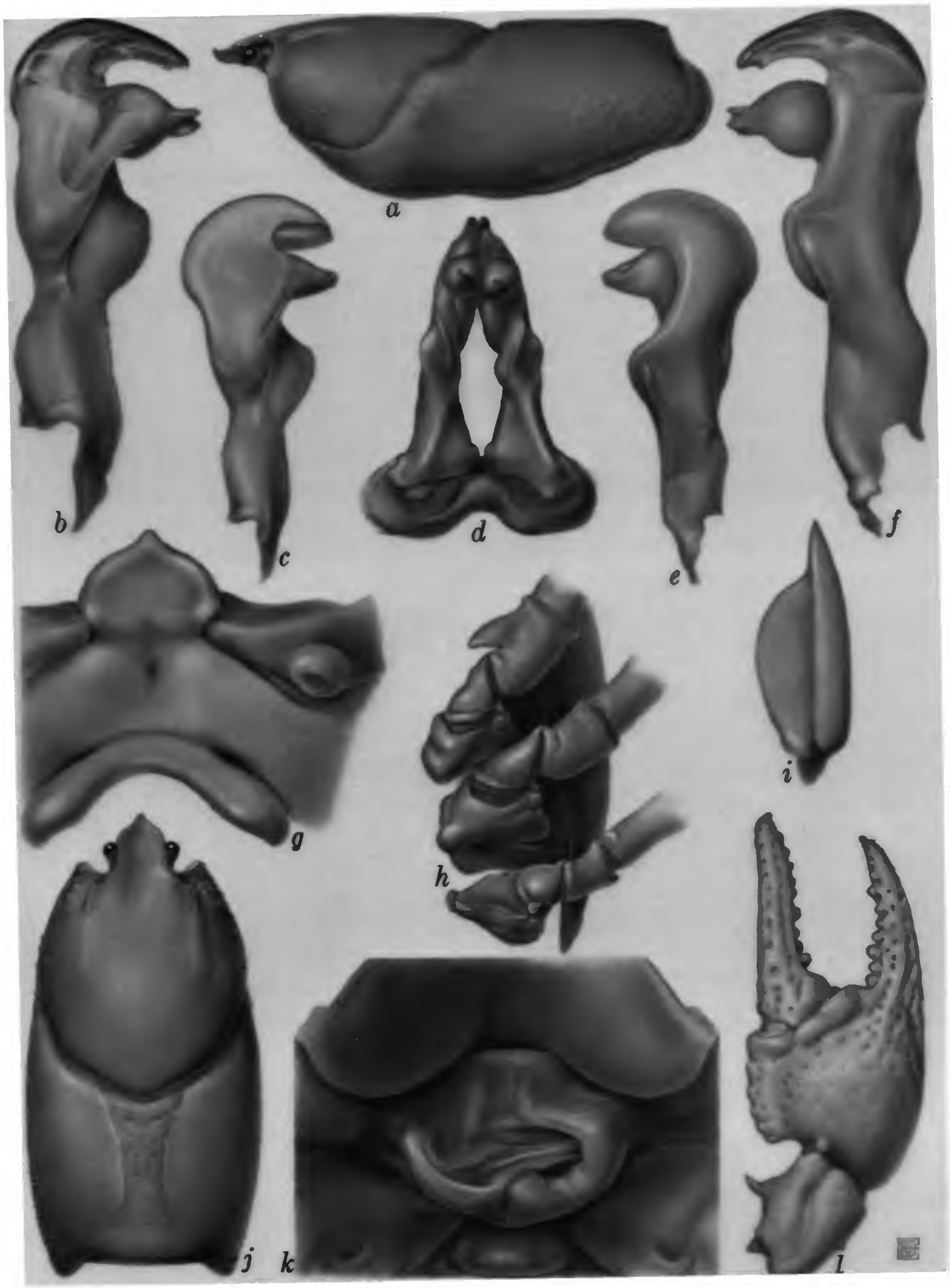


FIGURE 28.—*Cambarus (C.) bartonii* from the Little Tennessee Basin, Rabun Co (all from male, form I, except *c*, *e*, from male, form II, and *k*, from female): *a*, lateral view of carapace; *b*, *c*, mesial view of first pleopod; *d*, caudal view of first pleopods; *e*, *f*, lateral view of first pleopod; *g*, epistome; *h*, proximal podomeres of third, fourth, and fifth pereiopods; *i*, antennal scale; *j*, dorsal view of carapace; *k*, annulus ventralis; *l*, dorsal view of distal podomeres of cheliped.

tlings of dark brown, those on dorsolateral surfaces of branchiostegites anastomosing, forming broad sublinear series; cervical tubercles and those in hepatic region cream to white; margins of rostrum and postorbital ridges sometimes fused with orange; antennal, mandibular, and anteroventral branchiostegal regions often at least partially cream or white; cervical groove dark brown, with color occasionally bleeding slightly onto adjacent parts of branchiostegites. First tergum of abdomen with dark horizontal band on transverse ridge and paired dorsolateral splotches joining band anteriorly; remaining terga mottled, some splotches forming paired dorsolateral series of markings, latter becoming succeedingly smaller on posterior terga; pleura, set off from terga by row of ventrally concave dark markings, mottled and with cream spot posteroventrally. Uropods and telson paler than more anterior part of abdomen. Antennular and antennal peduncles mottled dark brown on olive tan or light brown, rami dark olive. Third maxilliped cream suffused with olive. Chelipeds from midlength of merus distally similar in coloration to carapace, although with less extensive mottlings; tubercles mostly olive cream and fingertips orange cream to orange. Remaining pereiopods light green to olive distal to ischium. Sternal area including basal podomeres of legs bluish to greenish cream with few orange tubercles and ridges.

TYPES.—Type, UZM (♂II).

TYPE-LOCALITY.—North America, "probably neighborhood of Philadelphia, Pa." (Faxon, 1914:423).

RANGE.—The range of *C. (C.) bartonii* almost coincides with the range of the subgenus, although it does not extend so far to the west in Ohio and Indiana. In Canada it ranges from New Brunswick to Ontario, and in the United States from New England southward to northern Georgia and westward into the eastern part of Ohio, Kentucky, and Tennessee.

In Georgia it is largely restricted to the Blue Ridge and foothills and on the Appalachian Plateau, but outlier populations occur as far south as Wilkes County in the Savannah Basin, in headwaters of the Chattahoochee River in Habersham, White, and Lumpkin counties, those of the Oconee River in Hall and Clarke counties, and in those of the Etowah River in Lumpkin County. It must be more common in the headwaters of the Conasauga Basin than available specimens indicate, but so much of the upper part of this watershed is not accessible by road that few collections are available from the northward-flowing tributaries of the river.

GEORGIA SPECIMENS EXAMINED.—As indicated in the summary of the seasonal occurrence of the species in Georgia, I have examined a total of 1148 specimens from some 150 localities (Figure 29) in the following drainage systems: Chattahoochee, Conasauga, Etowah, Hiwassee, Little Tennessee, Oconee, Savannah, and Tennessee. The counties in which this crayfish has been found are: Banks, Chatham, Clarke, Dade, Dawson, Fannin, Franklin, Gilmer, Habersham, Hall, Hart, Lumpkin, Madison, Murray, Rabun, Stephens, Towns, Union, Walker, White, and Wilkes.

VARIATIONS.—The rather lengthy synonomy presented for the species suggests that this is one of the most variable crayfish species in North America, and perhaps because it is such a wide-ranging one, no detailed study of variations throughout its range has been made. Some populations appear to be so distinct that they have been accorded specific or subspecific recognition (e.g., *C. montanus*, *C. bartonii cavatus*, *C. bartonii carinirostris*), designations that have had to be relegated to synonomy when larger series of specimens from additional localities became available.

The following paragraphs and figures are devoted to an attempt to present a summary of the ranges of variation that I have observed among the Georgia specimens.

There are no features of the populations of *C. (C.) bartonii* occurring in the Little Tennessee and Savannah basins that serve to distinguish them from at least some members of the species frequenting other watersheds in Georgia. This is true largely because of the tremendous intra- and interpopulational variations that occur within the drainage systems. To be sure, specimens with rather strongly converging rostral margins and a

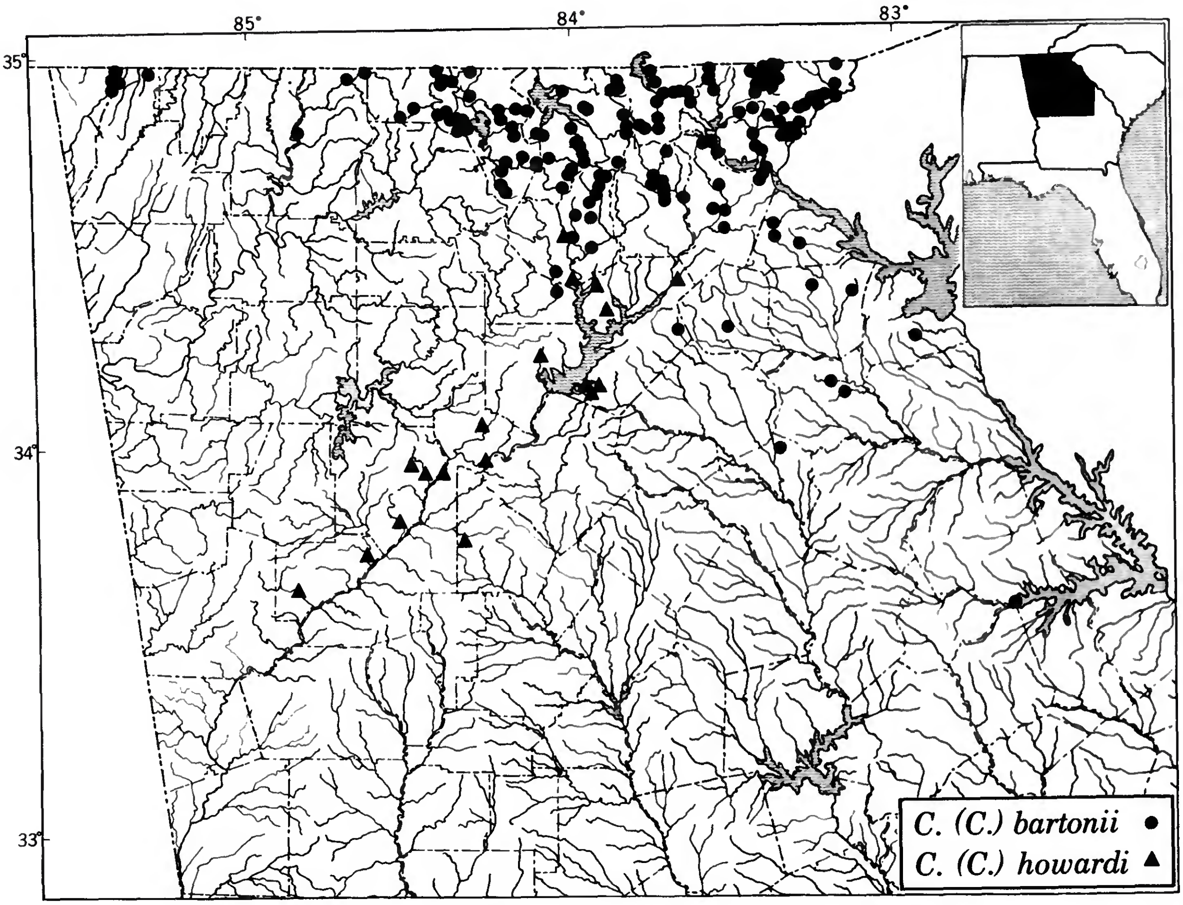


FIGURE 29.—Distribution of *Cambarus (C.) bartonii* and *C. (C.) howardi* in Georgia.

narrow acumen (Figure 30*c,f*) have not been found in the Little Tennessee Basin, but such are rare in available specimens from the Savannah River system. Although two moderately well developed rows of tubercles are present on the mesial margin of the palm in some specimens from the latter watershed in Stephens County, only one row occurs in specimens from the Little Tennessee. In view of this, Figures 30*g–k*, 33*d–f* are presented to illustrate the range of variation noted in the carapace and cheliped in the two river systems. Differences occur in the male secondary sexual characters, but no observations suggest any are typical of populations in a limited part of the two drainage basins.

The range of variations in specimens from the Etowah, Oconee (Altamaha), and the upper part of the Chattahoochee basins (Figures 30*l–o*, 32, 33*g*) does not differ markedly from that in the Little Tennessee and Savannah watersheds.

In the Hiwassee Basin (two major tributaries in Georgia: the Nottely and Toccoa), *C. (C.) bartonii* exhibits two rather striking variants. In the Toccoa, the differences between them are so marked that one might suspect that two species are represented. To point out the extremes of variation that occur there, the following remarks are oriented from downstream in Fannin County to the headwaters in Towns County.

Despite the fact that in the Toccoa watershed the two variants seem to be distinct, some individuals unite, in various combinations, the char-

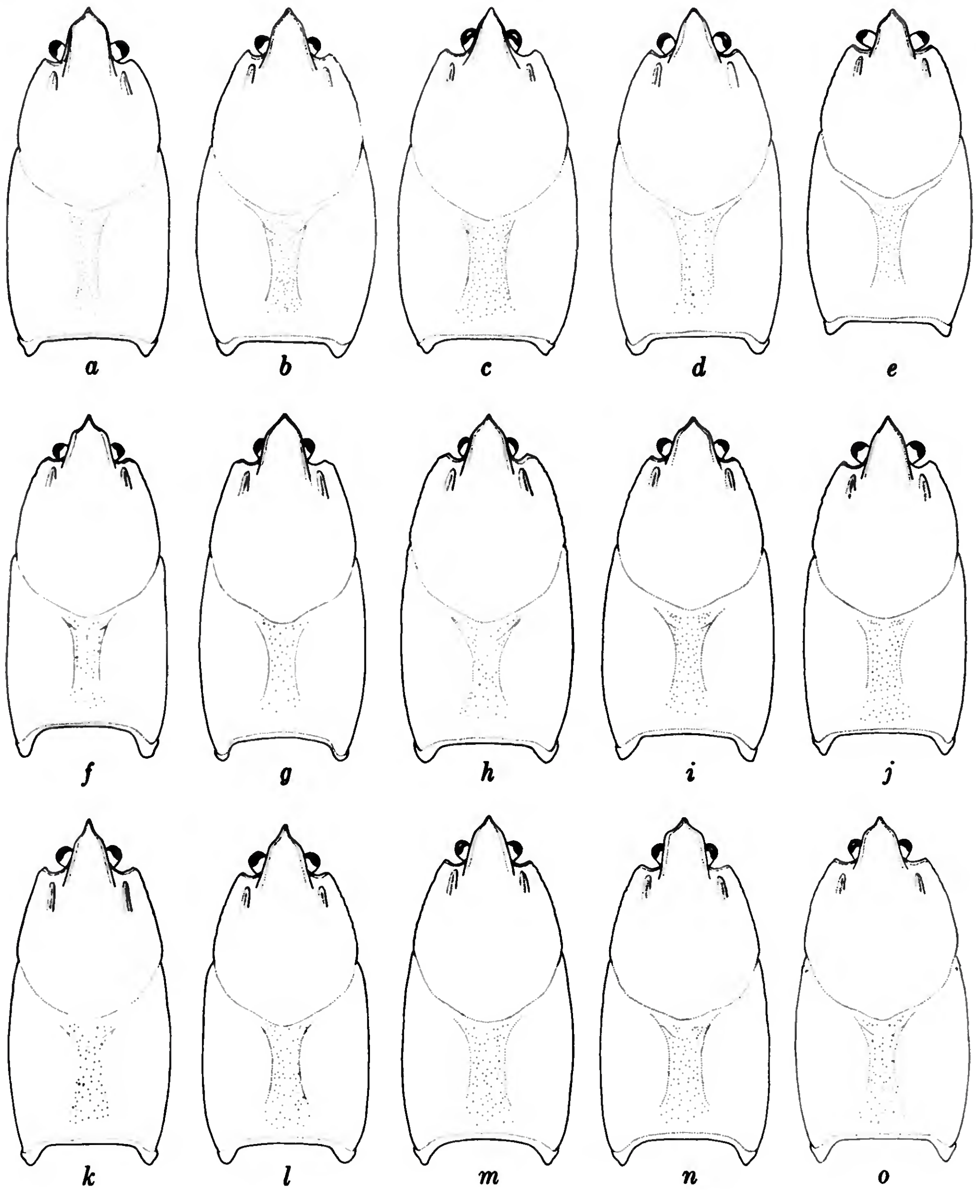


FIGURE 30.—*Cambarus (C.) bartonii*, variations in carapace (dorsal view). Tennessee Basin: *a*, Sitton's Cave near Trenton, Dade Co. Coosa Basin: *b*, Conasauga River at St Rte 286, Murray-Whitfield Co line. Hiwassee Basin: *c*, creek 5.8 mi E of Morgantown on US Hwy 76, Fannin Co; *d*, creek 7.0 mi S of Morgantown on St Rte 60, Fannin Co; *e*, spillway from Lake Suches, Fannin Co; *f*, Soapstone Creek 4.4 mi above mouth, Towns Co. Little Tennessee Basin: *g*, Little Tennessee River at Dillard, Rabun Co. Savannah Basin: *h*, creek in Warwoman's Dell State Park near Clayton, Rabun Co; *i*, creek 2.0 mi S of Clayton on US Hwy 23, Rabun Co; *j*, Toccoa Falls, Stephens Co; *k*, Little River at St Rte 80, Wilkes Co. Altamaha Basin: *l*, tributary of Oconee River 2.0 mi NW of Gillsville on St Rte 52, Hall Co. Chattahoochee Basin: *m*, Chattahoochee River at St Rte 17, White Co; *n*, *o*, Soquee River at St Rte 197, Habersham Co.

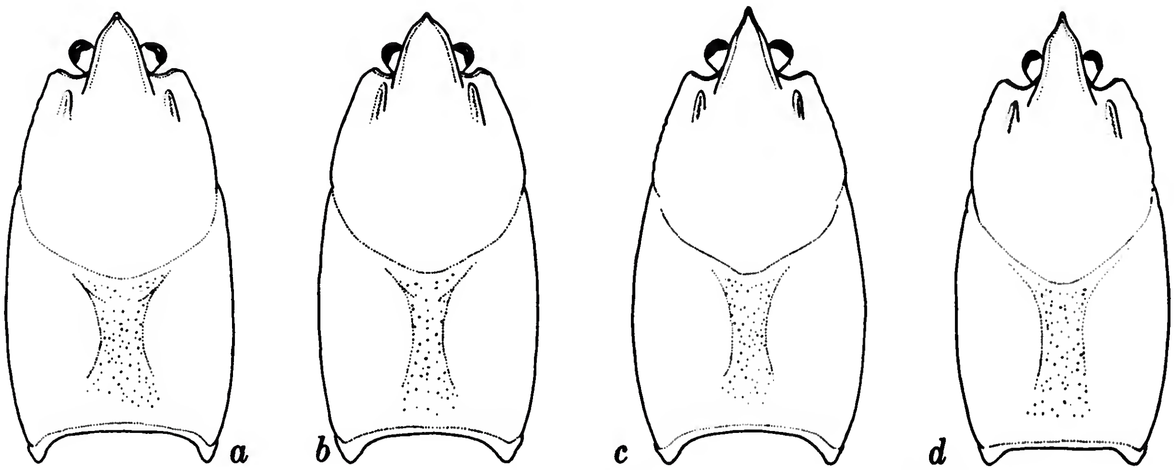


FIGURE 31.—*Cambarus (C.) bartonii* (*a, b,*) and *C. (C.) howardi* (*c, d*), variations in carapace (dorsal view). Coosa Basin: *a*, Etowah River at US Hwy 19, Lumpkin Co; *b*, creek 11.3 mi NW of Cleveland on US Hwy 129, Lumpkin Co. Chattahoochee Basin: *c*, Sope Creek at Paper Mill Rd, Cobb Co; *d*, Nickajack Creek at Camp Highlands, Cobb Co.

acteristics that, for the most part, typify them. By far the more commonly occurring variant (Figure 30*c*) may be characterized by a rostrum with strongly convergent margins flanked to the base of the acumen by subrostral ridges that are clearly evident in dorsal aspect. The areola is densely beset with punctations, and the chela is rather weakly costate laterally (frequently the costa is virtually obsolete); the mesial margin of the palm bears a row of typically seven or eight tubercles that often are not nearly so strongly protruding as those of the other variant sharing the watershed. The other, more nearly resembling the representatives of the species in the previously discussed basins, often attains a greater size and possesses a rostrum with distinctly less convergent margins, approaching, in the latter respect, that in most populations occurring in the upper Hiwassee and headwaters of the Savannah and Chattahoochee basins. The subrostral ridges are not so clearly evident dorsally; the areola appears to be narrower, frequently somewhat longer, and always bears fewer punctations than that of the other variant. The chela is strongly costate laterally, bears deeper and somewhat larger punctations, and there are never more than seven tubercles in the row along the mesial margin of the palm; these tubercles protrude from the surface rather strongly, and occasionally one or two occur immediately dorsolateral to the mesial row. The tapered rostral margins of the more commonly occurring variant resemble those of *C. (C.) howardi*, but in the former the carapace and chelipeds are never lavender to green with scarlet markings.

In the Nottely watershed, this crayfish resembles the predominant variant occurring in the Toccoa, but the rostrum is usually less tapering; the areola, although variable in width, is most often narrower and typically has fewer punctations. The chelae are, on the whole, similar in being rather weakly costate and frequently possess as many as eight tubercles along the mesial margin of the palm. In most of the first form males, the central projection of the first pleopod is strongly recurved, with the subapical notch facing the proximal end of the appendage (Figure 34*e*), although in occasional individuals, it is almost as straight as that in Figure 34*d*.

Whereas in the upper Hiwassee in Towns County there is much variation among the available specimens, on the whole, the limits do not exceed those that exist in populations frequenting the headwaters of the Chattahoochee and Savan-

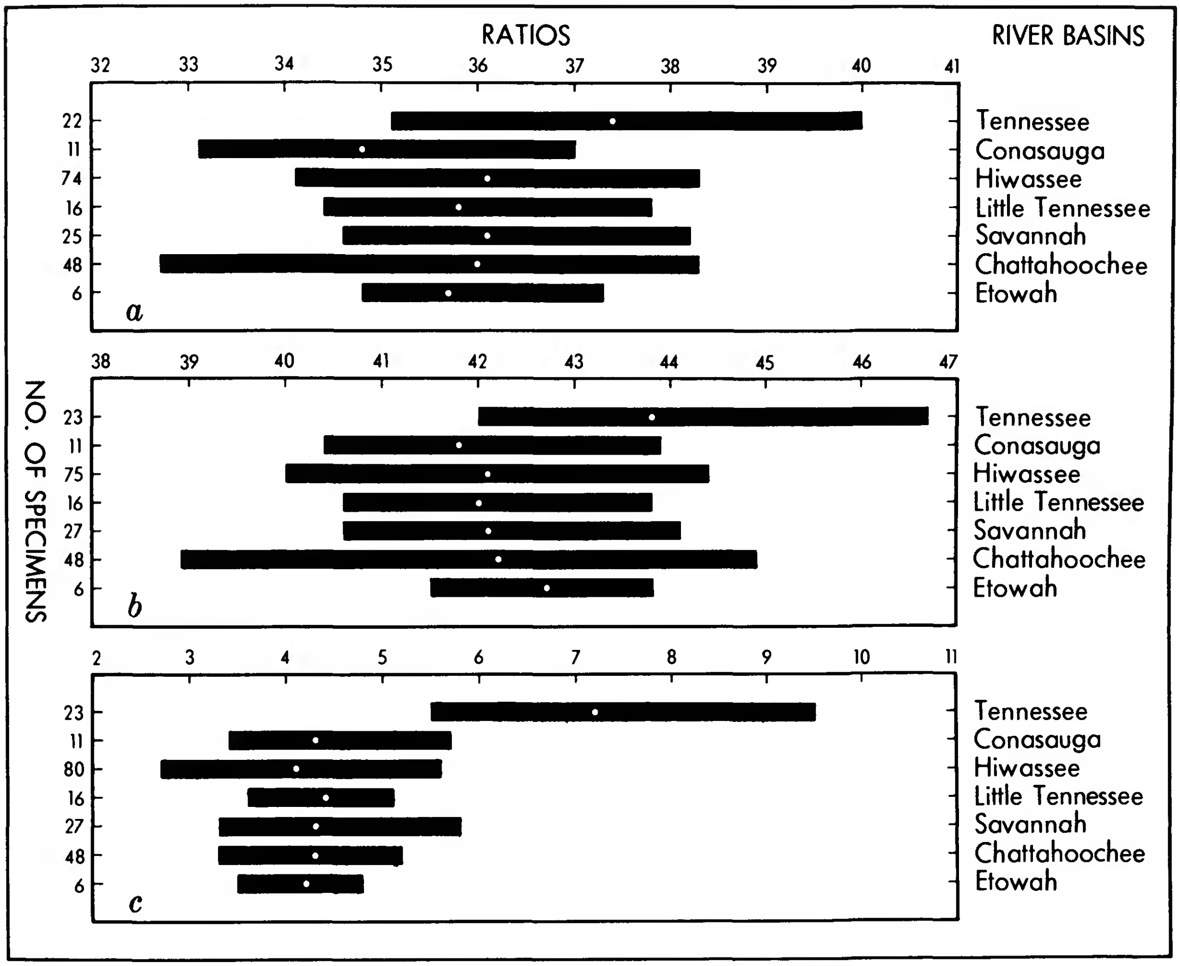


FIGURE 32.—*Cambarus (C.) bartonii*, morphometric variations in Georgia: *a*, ratio of areola length to carapace length expressed in percentages; *b*, ratio of areola length to postorbital carapace length expressed in percentages; *c*, ratio of areola length to areola width. (White spot indicates mean.)

nah basins. Figure 30*f* is illustrative of the appearance of *C. (C.) bartonii* in this part of the Hiwassee Basin. The rostral margins are usually distinctly contracted at the base of the acumen (sometimes more convergent than in that illustrated), rendering the shape of the rostrum subtrapezoidal with a small triangular acumen. The areola is moderately broad, usually with comparatively few punctations; the chela is distinctly costate laterally, and the mesial margin of the palm bears six or seven (rarely eight) tubercles.

The only specimens available from the Conasauga Basin were collected in (1) Jacks River near Flattop Mountain in the southwestern part of Fannin County, (2) near the mouth of Jacks River in the northeastern part of Murray County, (3) in a small tributary to the Conasauga River some two miles west of the crossing on State Route 2 (east of U.S. Highway 341), and (4) in the Conasauga River at State Route 286. These specimens exhibit, in various combinations, the features of the two variants in the Toccoa watershed.

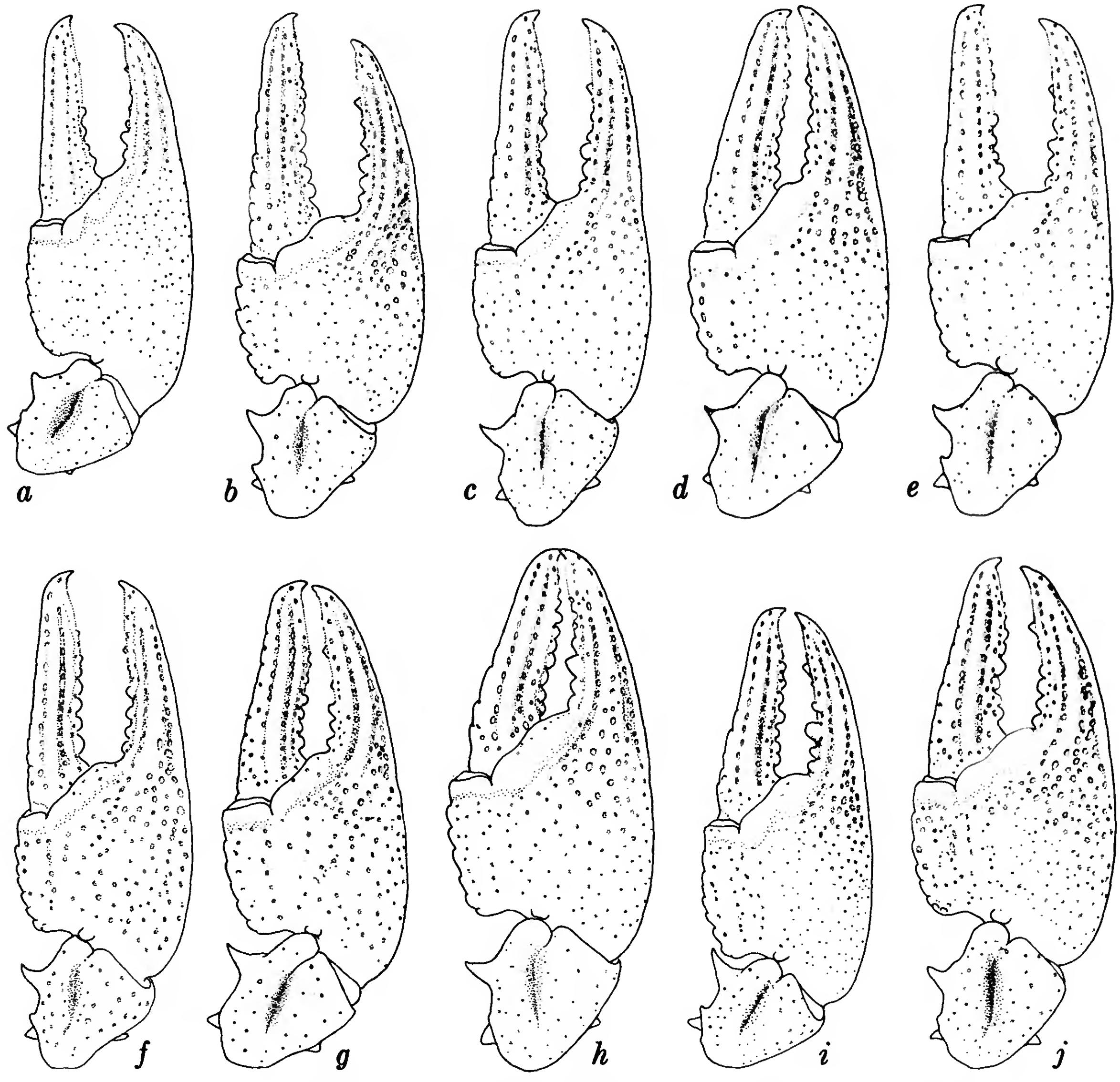


FIGURE 33.—*Cambarus (C.) bartonii* (*a–h*) and *C. (C.) howardi* (*i–j*), variations in chela of first form male. Hiwassee Basin: *a*, stream 5.8 mi E of Morgantown on US Hwy 76, Fannin Co; *b*, spillway from Lake Suches, Union Co; *c*, Soapstone Creek 4.4 mi upstream from mouth, Towns Co. Savannah Basin: *d*, 2 mi S of Clayton, Rabun Co; *e*, stream in Warwoman's Dell near Clayton, Rabun Co; *f*, Little River 200 m upstream from St Rte 80, Wilkes Co. Chattahoochee Basin: *g*, Chattahoochee River at St Rte 17, White Co. Coosa Basin: *h*, Etowah River 0.7 mi N of Landrum on St Rte 136, Dawson Co. Chattahoochee Basin: *i*, Nickajack Creek at Camp Highlands, Cobb Co; *j*, Sope Creek at Paper Mill Rd, Cobb Co.

The mesial process of the first pleopod of the first form male is flared apically, and the terminal part is directed somewhat distally in respect to the shaft of the appendage.

The populations of *C. (C.) bartonii* occurring on the Appalachian Plateau in Dade and Walker counties, in streams flowing into the Tennessee River, differ from most others in the state in two

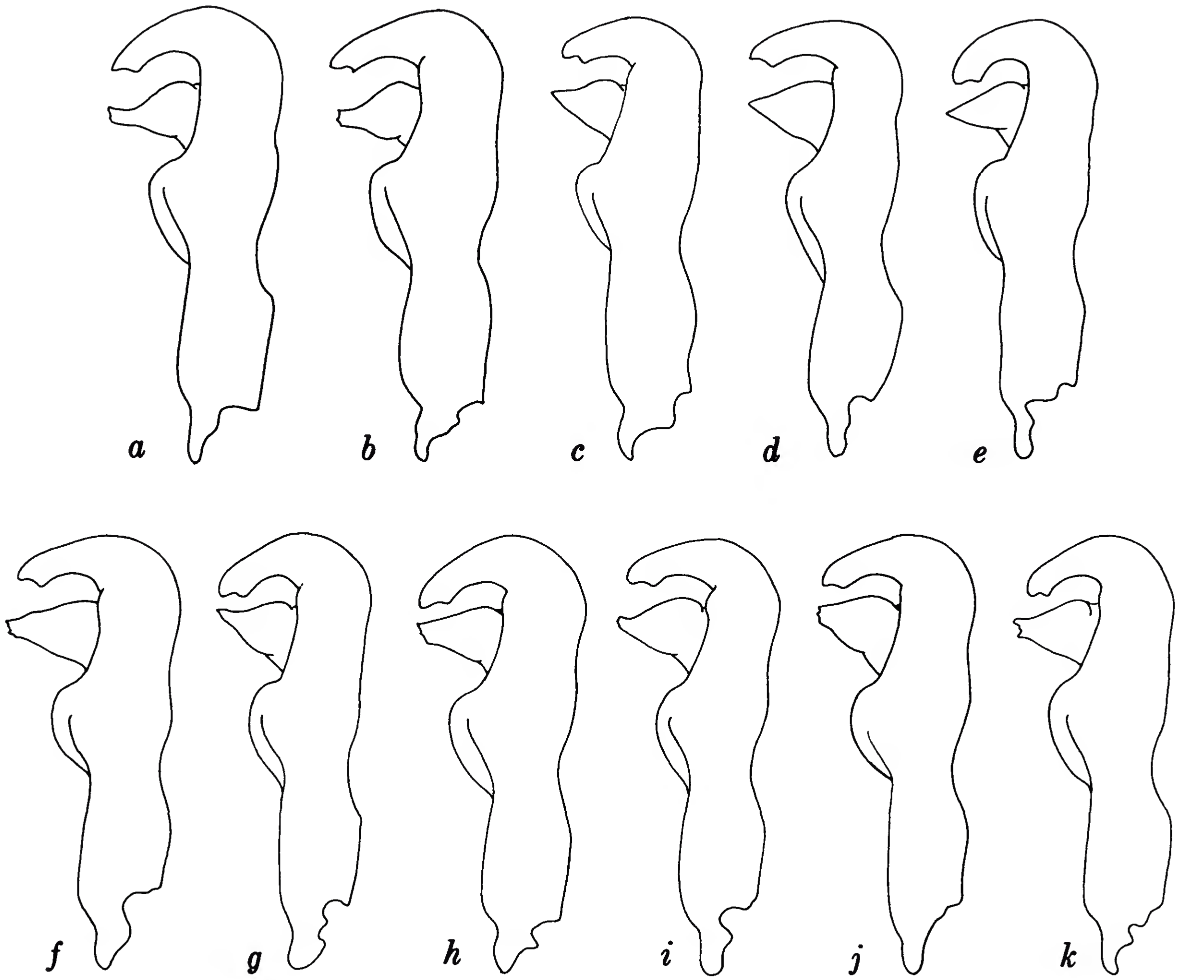


FIGURE 34.—*Cambarus (C.) bartonii* (*a–j*) and *C. (C.) howardi* (*k*), variations in first pleopod (lateral view) of first form male. Tennessee Basin: *a*, Pope Creek 2.8 mi S of Tennessee line on US Hwy 11, Dade Co. Coosa Basin: *b*, Conasauga River at St Rte 286, Murray-Whitfield Co line. Hiwassee Basin: *c*, creek 5.8 mi E of Morgantown on US Hwy 76, Fannin Co; *d*, spillway from Lake Suches, Fannin Co; *e*, tributary to Nottely Lake 15.2 mi SW of Towns Co line on US Hwy 76, Union Co; *f*, creek at E city limits of Young Harris on US Hwy 76, Towns Co; *g*, Soapstone Creek 4.4 mi above mouth, Towns Co. Savannah Basin: *h*, creek in Warwoman's Dell State Park near Clayton, Rabun Co; *i*, Little River at St Rte 80, Wilkes Co. Chattahoochee Basin: *j*, Chattahoochee River at St Rte 17, White Co; *k*, Sope Creek at Paper Mill Rd, Cobb Co.

conspicuous respects: there are two rows of tubercles along the mesial margin of the palm of the chela, and the areola is proportionately narrower than in most specimens from elsewhere, ranging from 5.6 to 7.3 times as long as broad. Rarely in other localities is it more than five times as long as broad. The shape of the broadly excavate rostrum is also somewhat distinctive (Figure 30*a*). Worthy of note is the observation that in the two specimens from Case Caverns and Sitton's Cave (I have not seen the specimens from Twin Snakes Cave reported by Cooper and Iles, 1971), the areola constitutes 40.0 and 38.9 percent of the carapace length (46.4 and 46.7 percent of the postorbital carapace length), ratios higher than those not only in the other specimens from the plateau but also of any other members of the species from the state. The corresponding ranges in other specimens on the plateau are 36.6 to 37.9 and 42.9 to 44.1 percent, respectively.

SIZE.—The largest specimen available from Georgia is a female from Dade County (Tennessee Basin), having a carapace length of 51.3 (postorbital carapace length 43.0) mm. The largest first form male is from Rabun County (Savannah Basin) with corresponding lengths of 41.9 (36.7) mm. Comparable lengths of the smallest first form male (from Fannin County, Hiwassee Basin) are 20.9 (17.4) mm. The smallest ovigerous female has corresponding lengths of 19.1 (16.8) mm.

LIFE HISTORY NOTES.—First form males have been collected during each month from March to June and August to November. No collections made in December, January, and February are available, and only eight specimens were obtained during July. It therefore seems probable that first form males occur throughout the year, but it is likely that the majority of the adult males are in the second form during the months of July and August, and revert to first form in September.

Ovigerous females, carrying eggs 2.3 to 3.1 mm in diameter, were found in April and June, and two females carrying young were collected in June and August. Judging by the stage of development of the embryos on the ovigerous females and the presence of young on the abdomen of the female carrying young in August, the egg-laying season occurs from mid-March into July. The smallest ovigerous female (see above) carried 24 eggs, and the largest (40.0 and 35.0 mm carapace and postorbital carapace lengths, respectively) bore 117 eggs. Figure 35 represents only those ovigerous females carrying a nearly complete complement of eggs. So many eggs had been dislodged from the remaining specimens in berry that they have been omitted from the graph.

While samples of populations from any one locality are too small to provide an analysis of the composition of age groups within them, there is evidence of the occurrence of no more than three such groups in a population at any time, and in

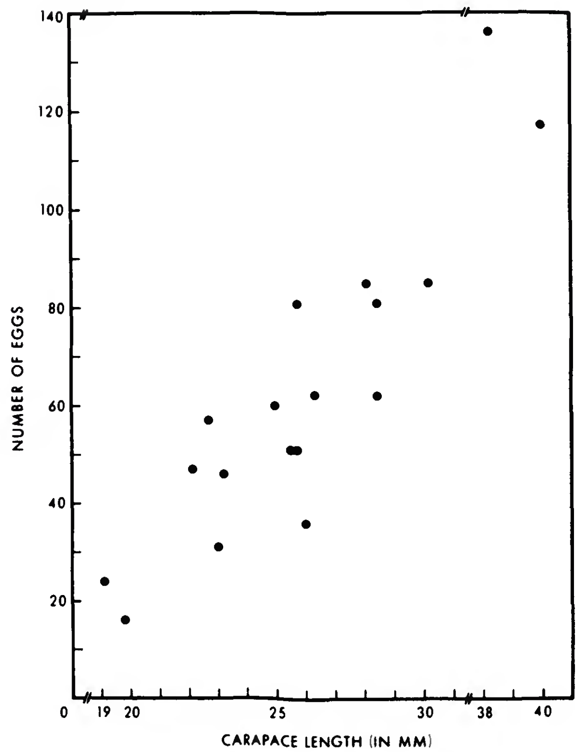


FIGURE 35.—*Cambarus (C.) bartonii*, number of eggs borne by ovigerous females.

several of the larger collections made in November, there seem to be only two, suggesting a loss of at least most of the three-year-old members of the population during the summer months.

To summarize what appears to be the generalized life cycle, the young hatching in the late spring grow until winter sets in. Undergoing no further growth until spring, they remain in the juvenile stage until the following fall when they become sexually mature, the males molting to form I at that time, and the females producing their first clutch of eggs in the spring when they are almost two years old. Following the breeding season (late fall to spring), the males molt to form II and in the fall return to form I to enter their second (and for most, their last) breeding season, dying in the summer at an age of slightly more than three years. The females, in contrast, molt in the summer, following the departure of their first brood of young, and apparently do not molt again before producing their second (and at least for most, their last) clutch of eggs the following spring. The females die at about the same age as do the males.

As in other crayfishes, a few individuals that hatch in the early spring enter the breeding population during their first fall, and rarely do there appear to be individuals living for four years. There is no evidence for a greater longevity.

Seasonal Data

Sex/stage	*J*	*F*	*M*	*A*	*M*	*J*	*J*	*A*	*S*	*O*	*N*	*D*	*?*
♂I			3	30	8	10		3	3	11	55		1
♂II			4	69	24	48	4	44	35	29	54		1
♀			5	47	34	70	4	38	56	24	75		2
♂j			4	42	15	24		13	11	6	23		1
♀j			2	40	24	27		27	22	13	30		
♀ ovig				10		22							
♀ with young								1					

Ecological Notes.—There can be little question that in Georgia *Cambarus (C.) bartonii* is primarily associated with mountainous terrain even though in a few instances it has penetrated the foothills and upper piedmont sections of the state. Within the mountains, it frequents habitats ranging from seepage areas at high elevations, cascading brooks, and torrents, to the more quietly flowing valley streams, and it is not adverse to invading at least littoral sections of impounded waters. It is common in springs and, on the Appalachian Plateau in the extreme north-western part of the State, it has been found in three caves (see discussion on "Variations").

In many streams, it is the sole crayfish inhabitant where it occupies the entire stream bed, occurring in riffles, pools, among roots along undercut banks, and in burrows dug into the clay walls. Like the majority of crayfishes, during the day individuals retreat from open water to beneath rocks, to burrows, or various types of litter accumulating either in rapidly flowing water or in quiet pools.

In streams shared with other crayfishes they are not always found in all parts of the stream bed. For example, where populations of members of the subgenera *Hiaticambarus* and/or *Puncticambarus* share the same section of the stream, the usually reduced population of *C. (C.) bartonii* is found along the marginal parts of the bed. Often the larger individuals make shallow excavations under large rocks that lie partially on the stream banks.

In seepage areas, they dig winding tunnels among the rocks, the directions taken apparently being determined by the arrangement of the subsurface rocks, pebbles, and roots of trees. The excavated materials, whether mud rich in organic matter or sand and gravel, are brought to the mouth of the burrow and dumped in a circular or semicircular hillock surrounding or partially ringing the opening. Frequently the mouth of the burrow is at the edge of a rock, and, being so situated, the hillock is semicircular. Most of the galleries of such burrows are rather shallow with one passage leading downward, presumably penetrating below the frost line.

In the nonmountainous regions, this crayfish is usually found in comparatively clear, spring-fed, rapidly flowing streams with rock litter, although in a few instances it was found among large rocks in shallow backwaters of impounded streams and occasionally among leaf litter in areas of streams in which no rocks were observed in the stream bed.

Georgia Crayfish Associates.—The following crayfishes have been collected with *Cambarus (C.) bartonii* (the number of times they have been found together is indicated in parentheses): *Cambarus (D.) latimanus* (25), *C. (H.) coosawattae* (1), *C. (H.) fasciatus* (2), *C. (H.) girardianus* (2), *C. (H.) longirostris* (2), *C. (J.) asperimanus* (3), *C. (J.) conasaugaensis* (2), *C. (J.) nodosus* (7), *C. (P.) coosae* (3), *C. (P.) georgiae* (5), *C. (P.) hiwasseensis* (16), *C. (P.) parrishi* (7), *Orconectes erichsonianus* (1), *O. spinosus* (2), *Procambarus (Pe.) raneyi* (5), *P. (Pe.) spiculifer* (9).

Cambarus (Cambarus) howardi Hobbs and Hall

Figures 25*d*, 27*d*, 29, 31*c*, *d*, 33*i–j*, 34*k*, 36, 197

Cambarus (Cambarus) species K.—Hobbs, 1969a:109, fig. 5 [not p. 145].

Cambarus (Cambarus) howardi Hobbs and Hall, 1969:281-287, figs. 1-12.—Hobbs, 1972b:110, 146, 154, fig. 95b; 1974b: 11, fig. 26.—Yarbrough, 1973:18, 21, 22, 25, 30, 31, 35, 48.—Bouchard, 1976c:14.

Cambarus howardi.—Anonymous, 1970c, photograph on cover; 1971:158, 172, 173.—Wharton, 1978:220.

Procambarus howardi.—Wharton, 1978:46 [lapsus].

The above is believed to be a complete bibliography for the species, and all except Yarbrough (1973) and Bouchard (1976c) are based on the occurrence of the species in Georgia.

Summary of Literature.—The first mention of the existence of this crayfish was that of Hobbs (1969a), who noted its range in the Chattahoochee River basin of Georgia. In discussing one of its allies (p. 145), he inadvertently substituted "K" for "L"; no reference to the species subsequently named *C. (C.) howardi* appears on that page. In the same year, Hobbs and Hall described the species from five localities in Cobb, Douglas, and Hall counties. On the cover of a report of a biological investigation of streams in the Tennessee River basin of Georgia, Anonymous (1970c) presented a photograph of this crayfish, and, in a subsequent study of the Chattahoochee River system (1971), reported its occurrence in three localities, two of which were new. Hobbs (1972b) included this species in his illustrated key to the North and Middle American crayfishes, and (1974b) in his checklist. Yarbrough (1973) reported the presence of *C. (C.) howardi* in three localities on Halawakee Creek in Lee County, Alabama, and gave brief data on its ecology and life history in the area. Bouchard (1976c) included this crayfish in his list of freshwater decapod crustaceans of Alabama.

Diagnosis.—(See first sentence of "Diagnosis" of *C. (C.) bartonii.*) Rostrum with margins converging from base to apex. Areola 3.0 to 5.0 (average 4.0) times as long as broad, comprising 35.3 to 38.5 (average 36.7) percent of entire length of carapace (41.5 to 45.8, average 43.6, percent of postorbital carapace length), and bearing 3 to 6 punctations across narrowest part. Color lavender to forest green, accented by vermilion to scarlet markings on dorsum of body and chelae.

Color Notes (Figure 27*d*).—Carapace lavender brown to forest green; rostral and postorbital ridges vermilion to scarlet; cervical groove dark greenish brown; antennal region with small white to cream spot adjacent to base of antenna, and nearby tubercles similarly colored. Abdominal terga bluish green with conspicuous rust to vermilion band on posterior margin of each; pleura green dorsally, fading to cream ventrally. Telson also bluish green anteriorly, fading in caudal half to pinkish cream, articular areas at base and those abutting marginal and submarginal spines vermilion; uropods largely pinkish tan, but proximal half of mesial ramus pale blue, distal part of basal podomere, subapical spine on mesial ramus, and transverse suture on lateral ramus vermilion. Antennular and antennal peduncles green, mottled with greenish cream, flagella orange to vermilion. Third maxilliped greenish cream, more distal podomeres darker green. Chelipeds basically bluish green from midlength of merus distally, and, except for cream tubercles on opposable margins of fingers, all others, spines, and articular knobs orange to vermilion; distal part of fingers greenish cream fading to cream. Remaining pereiopods pale green or blue with articular areas and entire or distal part of dactyl vermilion. Sternal area cream to pinkish cream.

Types.—Holotype, allotype, and morphotype, USNM 129866, 129867, 129869 (♂I, ♀, ♂II); paratypes, USNM.

Type-Locality.—Sope Creek, tributary to the Chattahoochee River at Paper Mill Road, 1.5 miles above mouth, Cobb County, Georgia.

Range.—This crayfish is confined to the Chattahoochee River basin, in which it ranges from Lumpkin and Hall counties, Georgia, to Lee County, Alabama, where it has been found in several stations on Halawakee Creek.

Georgia Specimens Examined.—I have examined 107 specimens from the following localities. *Cobb County*: (1) Nickajack Creek at Camp Highlands (Hobbs and Hall, 1969:286), 2♂I, 1♀, 11 Mar 1951, D. C. Scott, collector; (2) type-locality, 2j♂, 12 Sep 1966, E. T. Hall, Jr.; 6♂I, 6♂II, 11♀, 3j♂, 1j♀, 2 ovig ♀, 21 Apr 1968, T. A. English, Jr., ETH, HHH; 1♀, 7 Oct 1970, B. A. Caldwell, M. W. Walker; (3) Sope Creek at Barnes Mill Rd (Hobbs and Hall, 1969:286), 1♂II, 2j♂, 1j♀, 12 Sep 1966, ETH; (4) Chattahoochee River

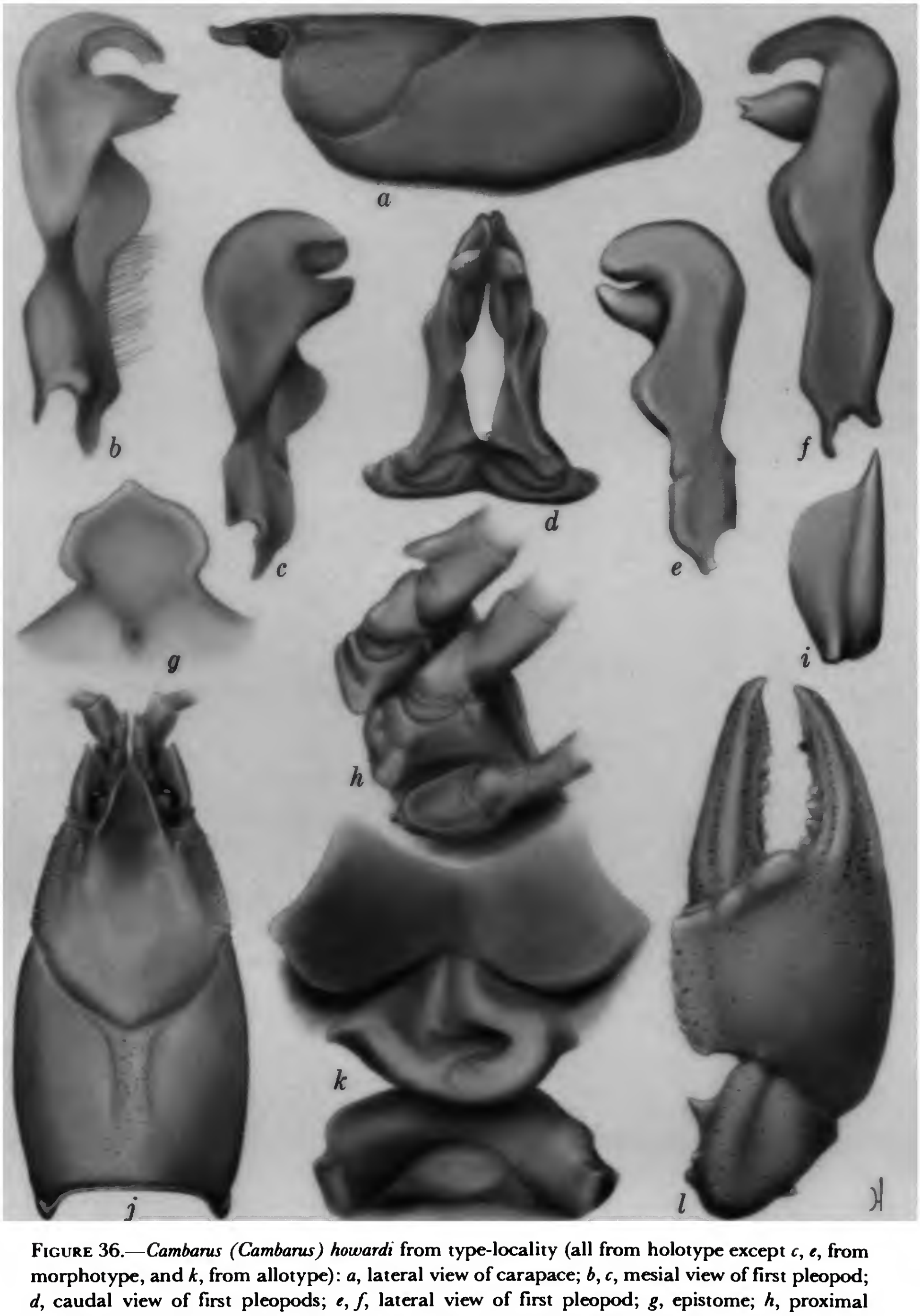


FIGURE 36.—*Cambarus (Cambarus) howardi* from type-locality (all from holotype except *c*, *e*, from morphotype, and *k*, from allotype): *a*, lateral view of carapace; *b*, *c*, mesial view of first pleopod; *d*, caudal view of first pleopods; *e*, *f*, lateral view of first pleopod; *g*, epistome; *h*, proximal podomeres of third, fourth, and fifth pereiopods; *i*, antennal scale; *j*, dorsal view of carapace; *k*, annulus ventralis; *l*, dorsal view of distal podomeres of cheliped. (From Hobbs and Hall, 1969.)

at Cobb Co water intake (Anonymous, 1971:172; also see p. 36 for physical data), 1♀, 13 Oct 1970, BAC, MWW. *De Kalb County*: (5) trib to Peachtree Creek at Lullwater Biological Field Laboratory, 1♂I, 1 ovig ♀, 23 May 1969, J. L. Boyce, HHH. *Douglas County*: (6) Sweetwater Creek at Factory Shoals Rd (Hobbs and Hall, 1969:286), 1♂I, 4♀, 2j♂, 8j♀, 3 Oct 1968, ETH; (7) Dog River at St Rte 5 (Hobbs and Hall, 1969:286), 3♀, 31 Jan 1969, R. M. Gaddis, ETH. *Forsyth County*: (8) trib to Six Mile Creek at Burruss Mill Rd, 1♂II, 24 Aug 1972, BAC, MWW. *Fulton County*: (9) Chattahoochee River at Holcomb Bridge Rd, Rte 1598, 1♂II, 24 May 1952, J. H. Martin; (10) Vickory Creek, 1.7 mi E of Alpharetta on St Rte 120, 2♀, 1j♀, 21 Apr 1968, C. R. Gilbert. *Hall County*: (11) trib to Yellow Creek (Chestatee Basin) 1 mi NW of Murraysville on St Rte 60, 1♂I, 26 Mar 1951, E. C. Raney; (12) trib to Balus Creek E of city limits of Oakwood (Hobbs and Hall, 1969:286), 1 ovig ♀, 6 May 1968, ETH; (13) Mud Creek at Rte S883, 12 mi NE of Gainesville (Anonymous, 1971:158; also see p. 23 for physical data), 1♂I, 1j♂, 15 Sep 1970, BAC, MWW; (14) Mud Creek at Ridge Rd NE of Flowery Branch, 3♂II, 5♀, ETH, RMG; 3♂II, 5♀, 19 May 1971, ETH and RMG; (15) Mud Creek at Stephens Rd NE of Flowery Branch, 1♂I, 1♂II, 2♀, 19 May 1971, ETH, RMG; (16) Squirrel Creek at Elrod Rd NW of Gainesville, 1♀, 23 Oct 1975, MWW, G. Q. Tuggle; 2♀, 1j♂, 18 Oct 1976, MWW. *Lumpkin County*: (17) Cane Branch 0.3 mi above mouth off St Rte 9E at southern edge of county, 2♂II, 5♀, 3j♂, 1j♀, 1♀ with young, 18 Jun 1975, D. J. Peters, J. E. Pugh, HHH; (18) trib to Chattahoochee River 0.3 mi W of Dahlonega on US Hwy 19, 1♂I, 1♂II, 11 Sep 1954, E. A. Lachner.

VARIATIONS.—In describing this crayfish, Hobbs and Hall (1969:286) recorded the variations that they had noted. Among others, they commented that the specimens from Douglas County possessed, in general, areolae in which the punctations are more crowded and deeper than in those specimens from the type-locality. Such areolae have since been observed in specimens from De Kalb and Hall counties. The degree of spination of the cephalic extremity of the postorbital ridges is at least in part an expression of the stage in the molting cycle of the individual—those that have encrusted exoskeletons have less acute tubercles than those in which the body surface is comparatively clean, suggesting that the tubercles often become abraded between molts. The rather distinctive chelae, especially of the first form males in specimens from the type-locality, occur also in most of the individuals from Hall County, but, as pointed out by Hobbs and Hall (1969:286), in the lots from Douglas County "... the fingers are distinctly longer and slenderer and the palm less inflated." The same is true in specimens from De Kalb County, in those from Lee County, Alabama, and in some of those from Lumpkin County. The series available from all stations except the type-locality are inadequate to evaluate the presence or absence, as well as the position, of the small tubercle on the ventral surface of the palm of the chela mentioned by Hobbs and Hall. The materials from Lumpkin County are assigned to this species with some reluctance because the specimens from Cane Creek, except for the coloration and conformation of the chelae of several, resemble, especially in the shape of the rostrum, the up-stream *Cambarus (C.) bartonii* as much as they do typical *C. (C.) howardi*. In contrast, in the specimens from the stream 0.3 mile west of Dahlonega, the rostrum tapers from the base even more strongly than in most specimens from the type-locality of the latter. Furthermore, a first form male collected from a tributary of Yellow Creek (Hall County), the adjacent major tributary to the Chestatee River downstream from Cane Creek, appears to be typical of *C. (C.) howardi* (unfortunately I have no knowledge of its color in life). These observations on the specimens from Lumpkin and adjacent part of Hall counties (Chestatee River basin) prompt the question as to whether or not the ranges of the two species overlap in the vicinity of and downstream from Dahlonega, or whether there is a gene exchange occurring between them in this area. Further observations of living specimens from this segment of the watershed must be made to determine the relationships between these closely allied crayfishes.

SIZE.—The largest specimen available is a female having a carapace length of 35.8 (postorbital carapace length 30.5) mm. (This is one of the specimens from Cane Creek, Lumpkin County, questionably assigned to the species.) Corresponding lengths of the smallest and largest first form males are 20.2 (17.0) mm and 33.1 (27.8) mm, and the smallest female carrying eggs or young, 21.2 (18.6) mm.

LIFE HISTORY NOTES.—In Georgia, first form males have been collected in January, March, April, May, September, and October. Yarbrough (1973:21) reported that in Alabama they had been found from May to October. Ovigerous females were collected in April and May, and a female with young was observed in Cane Creek, Lumpkin County, on 18 June 1975. The smaller of two of the ovigerous females retaining what appears to be a full complement of eggs (see "Size") was carrying 20 eggs having diameters of 2.2 to 2.3 mm. The other, having a carapace length of 23.8 (postorbital carapace length, 19.8) mm, carried 42 eggs with the same range of diameters.

Seasonal Data (Alabama and Georgia)

Sex/stage	*J*	*F*	*M*	*A*	*M*	*J*	*J*	*A*	*S*	*O*	*N*	*D*
♂I	1		4	6	2				1	3	2	
♂II				6	8	2		1	1			
♀	3		3	1	12	5				13		
♂j	1			3		3			5	3		
♀j			1	10		1			1	8		
♀ ovig				2	2							
♀ with young						1						

Ecological Notes.—In Georgia, this crayfish is an inhabitant of riffle areas of streams, vicariating for members of the subgenus *Hiaticambarus* in streams in the Chattahoochee River basin in which no representative of the latter occurs. They have been found among rocks of various sizes in the swiftest water. At the type-locality, Sope Creek, "some 70 feet wide and 2–3 feet in depth, flows with a cascading current over bed rock and scattered stones, the latter entrapping masses of filamentous algae" (Hobbs and Hall, 1969:285). The following physical data were obtained at this locality on 7 October 1970 (Anonymous, 1971: 29): air temperature 21.0°C; water, 18.0°; dissolved oxygen 7.8 mg/l; BOD_5, 13.6 mg/l; pH, 7.3; specific conductance, 177 μmho/cm (25°C); total phosphates as PO_4, 6.2 mg/l; nitrates (N), 0.4 mg/l; ammonia (N), 4.1 mg/l.

Mud Creek in Hall County was described by Anonymous (1971:91) as being "some 15′ wide and 6″-1′ deep. The water flowed with a swift velocity over a bed of sand littered with many stones .... The water was light brown in color." The same author provided the following data (p. 23): air temperature, 12.5°C; water, 14.0°; dissolved oxygen 8.5 mg/l; BOD_5, 1.1 mg/l; pH, 7.0; total alkalinity (as $CaCO_3$) 16 mg/l; specific conductance, 55 μmho/cm (25°C).

Other habitats for which ecological data are available were similar except at the Lullwater Laboratory in De Kalb County. There the clear spring water flowed with a sluggish current in a bed 0.3 to 0.6 m in width and three to four cm in depth. The sandy bottom had a few rocks partly embedded in the sand, and under them two specimens of this species were found along with one specimen of *C. (D.) latimanus*.

The following remarks of Hobbs and Hall (1969:287) seem apropos:

> This crayfish is an inhabitant of moderately to swiftly flowing streams and has been found only in areas where there is a rocky or rubble substrate. The type-locality is situated on the heavily polluted Sope Creek which takes its origin in the densely populated area immediately northeast of Marietta, Georgia. Almost at its source, it receives enrichment from storm sewers and an effluent from a sewage treatment plant. Six stations were established above the mouth of the creek approximately (1) 8.0, (2) 7.3, (3) 5.8, (4) 5.0, (5) 3.0, and (6) 1.5 miles above it; just above station 5 it receives water from a relatively unpolluted tributary. On 21 July 1966, the percent saturation of oxygen at these stations was 87, 40, 23, 34, [53], and 80.6, respectively. This crayfish, found only at stations 1 and 6, is believed to require an environment in which a high oxygen concentration exists, and, in view of these data, it seems possible that were it not for the turbulent area immediately above Station 6 which increases the dissolved oxygen concentration, *Cambarus howardi* would not be able to survive in the lower reaches of this stream.

The habitats in Alabama in which this crayfish have been found are markedly different from those described above. Yarbrough (1973:31) stated that "it usually occupied the deeper portions of the streams and was never collected from burrows," and in his summary (p. 48) noted that "*P. spiculifer* and *P. versutus* were found only in parts of streams with current; *C. latimanus*, *C. howardi*, and *C. halli* were always found in slack water areas of streams."

Georgia Crayfish Associates.—*Cambarus (C.) howardi* was found with *C. (D.) latimanus* in six localities and with *P. (Pe.) spiculifer* in four. In one locality, *C. (L.) acanthura* was dug from a burrow adjacent to the stream. Yarbrough (1973: 22) reported its association with *C. (D.) latimanus* and *P. (Pe.) spiculifer* in Lee County, Alabama.

Subgenus *Depressicambarus*

Subgenus *Bartonius* Ortmann, 1905a:97 [in part].
Subgenus *Cambarus* Fowler, 1912:341 [in part; not Erichson, 1846:97].
Subgenus *Depressicambarus* Hobbs, 1969a:102 [type-species: *Astacus latimanus* LeConte, 1856:402].—Bouchard, 1978: 29.

The section of this study devoted to the subgenus *Depressicambarus* was completed prior to the appearance of Bouchard's (1978) review of this species group. Of particular importance in his contribution are the discussions of relationships and phylogeny (pages 44–46). Being aware of his plan to redescribe *Cambarus (D.) latimanus*, one of the species originally and inadequately described from Georgia, the morphological account herein is limited to a diagnosis and a discussion of variations. Attention is also called to his redescription of *C. (D.) striatus*, a species around which considerable confusion has existed since soon after it was described by Hay (1902b).

DIAGNOSIS.—Eyes variable in size and pigmented. Rostrum with or without marginal spines or tubercles and margins seldom thickened. Postorbital and cervical spines present or absent. Suborbital angle acute to obsolete. Branchiostegal spines, if present, usually reduced. Areola width highly variable, obliterated to 3.1 times as long as broad and constituting 28.9 to 44.9 percent of entire length of carapace (38.0 to 50.9 percent of postorbital carapace length) and bearing 1 to 9 punctations across narrowest part. Chela broadly triangular, strongly depressed, and with mesial margin of palm comparatively short (width of palm at least 1.5 times length of mesial margin) and bearing at least 2 rows of tubercles; additional squamous tubercles usually present on mesial half of dorsal surface of palm; lateral margin of broad fixed finger strongly costate and punctate, sometimes subserrate basally; fingers never widely gaping but with well-defined longitudinal ridges dorsally, proximal opposable margin of dactyl never deeply concave; conspicuous tuft of setae rarely present at mesial base of fixed finger in adults never so prominent as in most members of *Hiaticambarus*. First form male with hook on ischium of third pereiopod very rarely opposed by tubercle on basis; first pleopod with terminal elements consisting of (1) bladelike, broad or tapering (sometimes subsetiform) central projection recurved 90 or more degrees to main shaft and occasionally forming arc of 180 degrees; subapical notch present or absent; (2) mesial process usually bulbiform, variously directed, frequently overreaching tip of central projection; contracted apical portion sometimes with 1 or more short projections; and (3) caudal knob present or absent. Female with annulus ventralis asymmetrical, cephalic area usually weakly calcified, line of junction with heavy caudal portion almost always serving as hinge for slight vertical movement of latter; first pleopod present, often reaching midlength of annulus.

RANGE.—From Kentucky to Mississippi and panhandle of Florida northeastward in the piedmont and mostly upper coastal plain to the Cape Fear and Tar drainage systems in North Carolina. In Georgia, from the upper coastal plain to the mountains in all of the major drainage systems therein except the Hiwassee and Little Tennessee.

SPECIES OCCURRING IN GEORGIA.—Bouchard (1978:44) has recognized two groups within the subgenus: the *halli* Group in which the areola is broad and densely punctate, and the rostrum of adults have subparallel margins usually supporting marginal tubercles or spines; and the *latimanus* Group in which the areola is not so broad, less densely punctate, and the rostral margins of the adults almost always lack marginal spines or tubercles. The *halli* Group: *Cambarus (D.) englishi* and *C. (D.) halli*. The *latimanus* Group: *Cambarus (D.) cymatilis*, *C. (D.) harti*, *C. (D.) latimanus*, *C. (D.) reflexus*, *C. (D.) striatus*, *C. (D.) strigosus*, and *C. (D.) truncatus*.

HABITATS.—The nine species recognized here as members of the subgenus *Depressicambarus* occupy habitats ranging from riffle areas (characteristic habitat of *C. (D.) englishi*) to usually quieter lotic waters (*C. (D.) halli*, *C. (D.) latimanus*, and *C. (D.) striatus*) and floodplain pools and burrows (latter two species). Five of the members are restricted to burrows (*C. (D.) cymatilis*, *C. (D.) harti*, *C. (D.) reflexus*, *C. (D.) strigosus* and *C. (D.) truncatus*). Both *C. (D.) latimanus* and *C. (D.) striatus* also construct burrows that do not communicate with open water, the latter often doing so in parts of the range where it encounters the former. In the southern part of its range as well as in seepage areas and lowlands elsewhere, representatives of *C. (D.) striatus* appear to have become restricted to burrows. In contrast, both this species and *C. (D.) latimanus* have occasionally been taken from cascading mountain streams.

REMARKS.—From the standpoint of distinguishing between the species, the assemblage assigned to this subgenus in Georgia is perhaps the most difficult of those occurring in the state. The most distinctive member of the group is the burrowing, blue *C. (D.) cymatilis*. In sharp contrast, the two exhibiting the broadest range of variation are *C. (D.) latimanus* and *C. (D.) striatus*, the two most widely distributed *Depressicambarus*, which occur also in Georgia. In certain parts of their ranges, not only do individuals of these two species exhibit features of one or more of the other four, but also some specimens are assignable, depending on which combination of characters are chosen, to either *C. (D.) latimanus* or *C. (D.) striatus*. Because of this, the notion has been entertained that two ecophenotypes of a single species have been accorded names! Indeed, there is some evidence for such in that, in general, the specimens of *C. (D.) striatus* collected from burrows have narrower and longer areolae than do most of those taken from streams, and the apparent replacement of *C. (D.) latimanus* in much of the Conasauga Basin by *C. (D.) striatus* could be construed to mean that selection has favored the "*striatus* facies" of the species in that part of the basin. In several localities, the crayfish taken from a stream have a broader, shorter areola (characteristic of *C. (D.) latimanus*) than do those dug from burrows in an adjoining seepage area or swamp, the latter specimens possessing a longer, narrower areola characteristic of *C. (D.) striatus*. Paradoxically, these same observations might equally well be construed as evidence that two species are involved, reflecting to a degree the environment in which they are living. Such an interpretation is enhanced by both having been collected in the same area of a stream. Furthermore, the western and northwestern parts of the range of *C. (D.) latimanus* fall far short of that of *C. (D.) striatus* which exploits stream habitats that appear to be the kind that would favor a "*latimanus* facies" were the two ecophenotypes of a single species. Obviously, I am far from certain as to the relationships between these crayfishes; however, inasmuch as names have been applied to them, I propose that they be retained even though occasional specimens are encountered that cannot with assurance be assigned to one or the other. The key and diagnosis provided below has proven to be helpful in identifying all except a very few of the Georgia specimens examined.

Baffling also is the status of the populations of *C. (D.) latimanus* occurring in the upper Savannah River Basin. For some time, I was convinced, as was Hall (1957), that the specimens collected there that possessed a broad areola with rather crowded punctations, an acuminate rostrum, strong cervical spines, and a subapical notch on the central projection of the first pleopod of the male represented a distinct assemblage deserving taxonomic recognition. Subsequent collecting in the watershed, however, has shown that not all of the individuals belonging to the complex in the upper part of the basin uniformly possess the characteristics just noted. Except for a shallow subapical notch on the central projection in the male, some exhibit the characteristics of *C. (D.) latimanus* from the adjacent Oconee Basin, and others are somewhat intermediate between the two types. A possible explanation for the existence of these wide-areolated populations in the midst of the range of the species is that a stock possessing the primitive characteristics just cited became isolated in the Savannah Basin. Before genetic isolation became established, the basin was invaded by migrants from adjacent drainage sys-

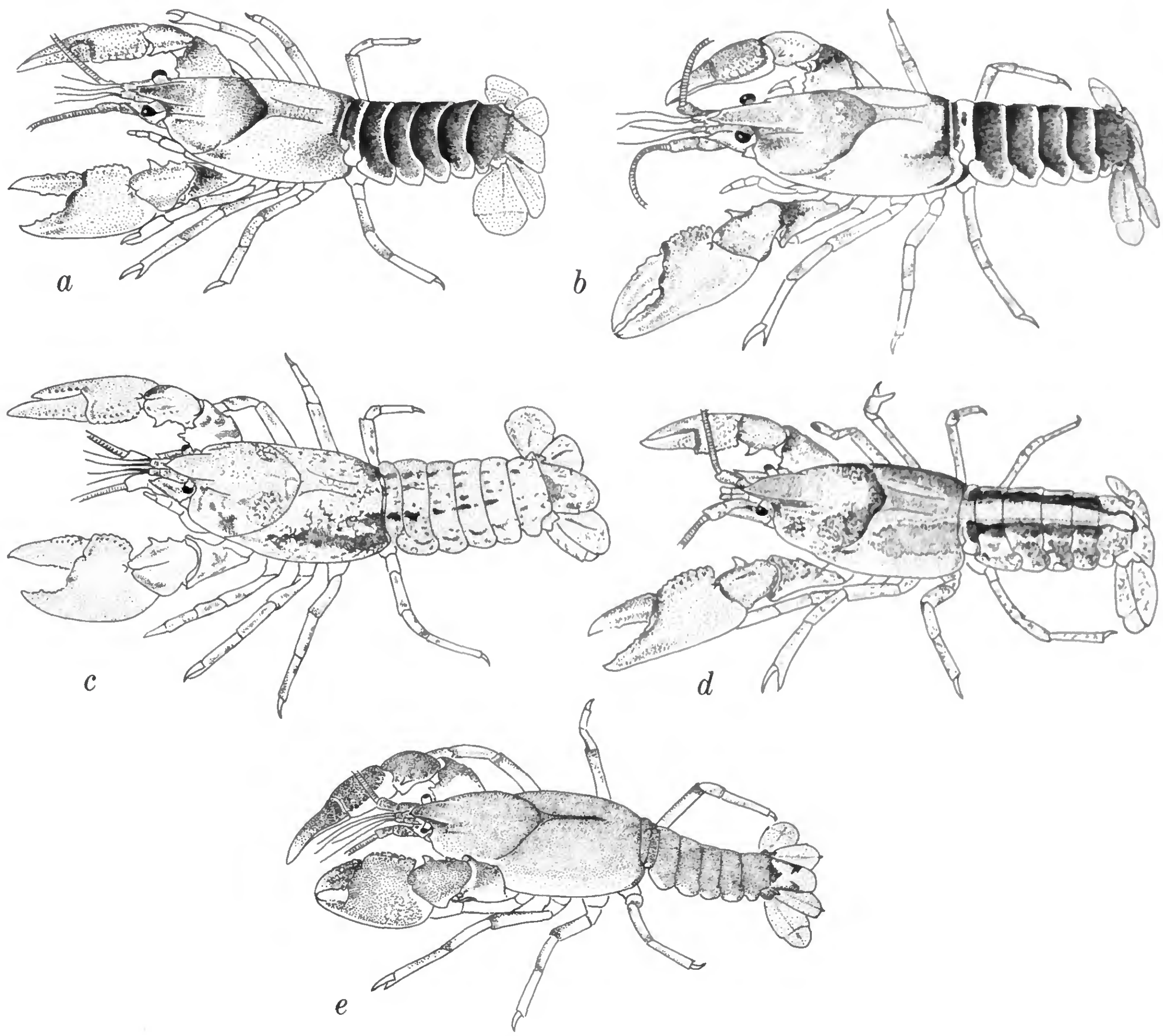


FIGURE 37.—Color patterns in members of subgenus *Depressicambarus*: *a*, *Cambarus (D.) englishi* from type-locality; *b*, *C. (D.) halli* from type-locality; *c*, *C. (D.) latimanus* from Coosawattee Basin in Gilmer Co; *d*, *C. (D.) latimanus* from North Fork of Broad River at US Hwy 123, Stephens Co; *e*, *C. (D.) cymatilis* from type-locality.

tems, primarily in the coastal plain segment of the watershed, and, as a result, the characteristics of these invaders have been passed northward where, through introgressive hybridization, occasionally recombinations result in an almost typical (Oconee-like) individual occurring among others that share, to varying degrees, the characteristics of the two extreme types. Even in the Broad River where many of the populations sampled seem to be almost uniformly of the type characterized, there appear individuals and local clusters of Oconee-like forms.

The broad, densely punctate areola of many of the *C. (D.) latimanus* in the Savannah Basin

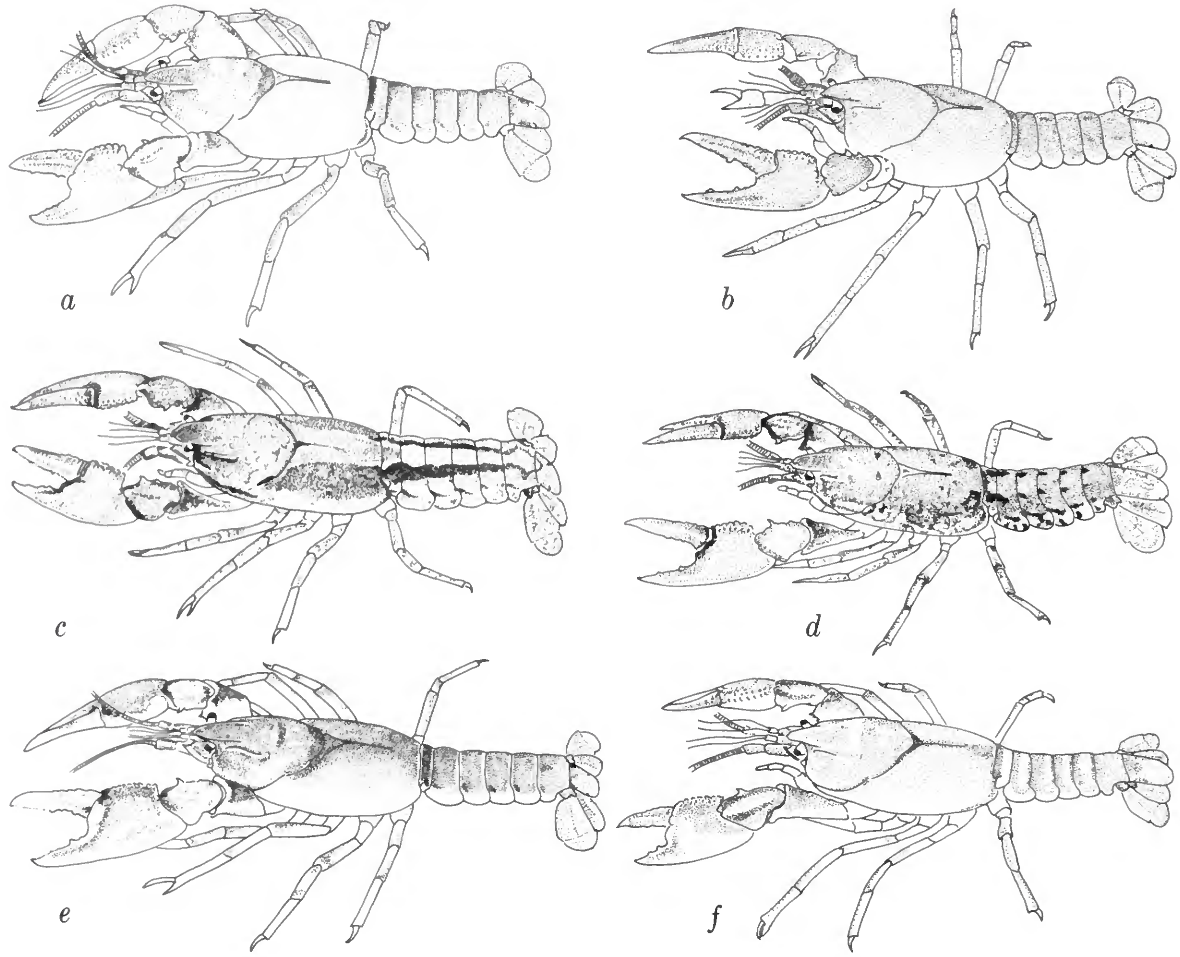


FIGURE 38.—Color patterns in members of subgenus *Depressicambarus*: *a*, *Cambarus (D.) reflexus* from Savannah River Bluff 0.5 mi NW of St Rte 119, Effingham Co; *b*, *C. (D.) harti* from type-locality; *c*, *C. (D.) striatus* from 2 mi SE of St Rte 341 on Rte 143, Walker Co; *d*, *C. (D.) striatus* from creek on Jay's Mill Rd in Chickamauga Battlefield Park, Catoosa Co; *e*, *C. (D.) strigosus* from type-locality; *f*, *C. (D.) truncatus* from 2.5 mi N of St Rte 338 on US Hwy 441, Laurens Co.

resembles markedly the areolae of *C. (D.) englishi* and *C. (D.) halli*, endemic species in the Tallapoosa watershed on the opposite side of the state. Even though the latter two are unquestionably distinct and reproductively isolated from *C. (D.) latimanus*, which shares the Tallapoosa Basin with them, some of their most distinctive features occur in the Savannah segment of the range of the latter species.

The closely allied riffle-dwelling *C. (D.) englishi* and the less ecologically selective *C. (D.) halli* so markedly resemble one another that even when alive, one must carefully examine the rostrum and first pleopod of the male to distinguish between them. So similar are they that, after recording in my field notes the possibility of two species being represented in a collection made in the Tallapoosa River, all of them were referred to *C. (D.) halli* when I returned to the laboratory. Not until weeks later, when H. H. Hobbs III was

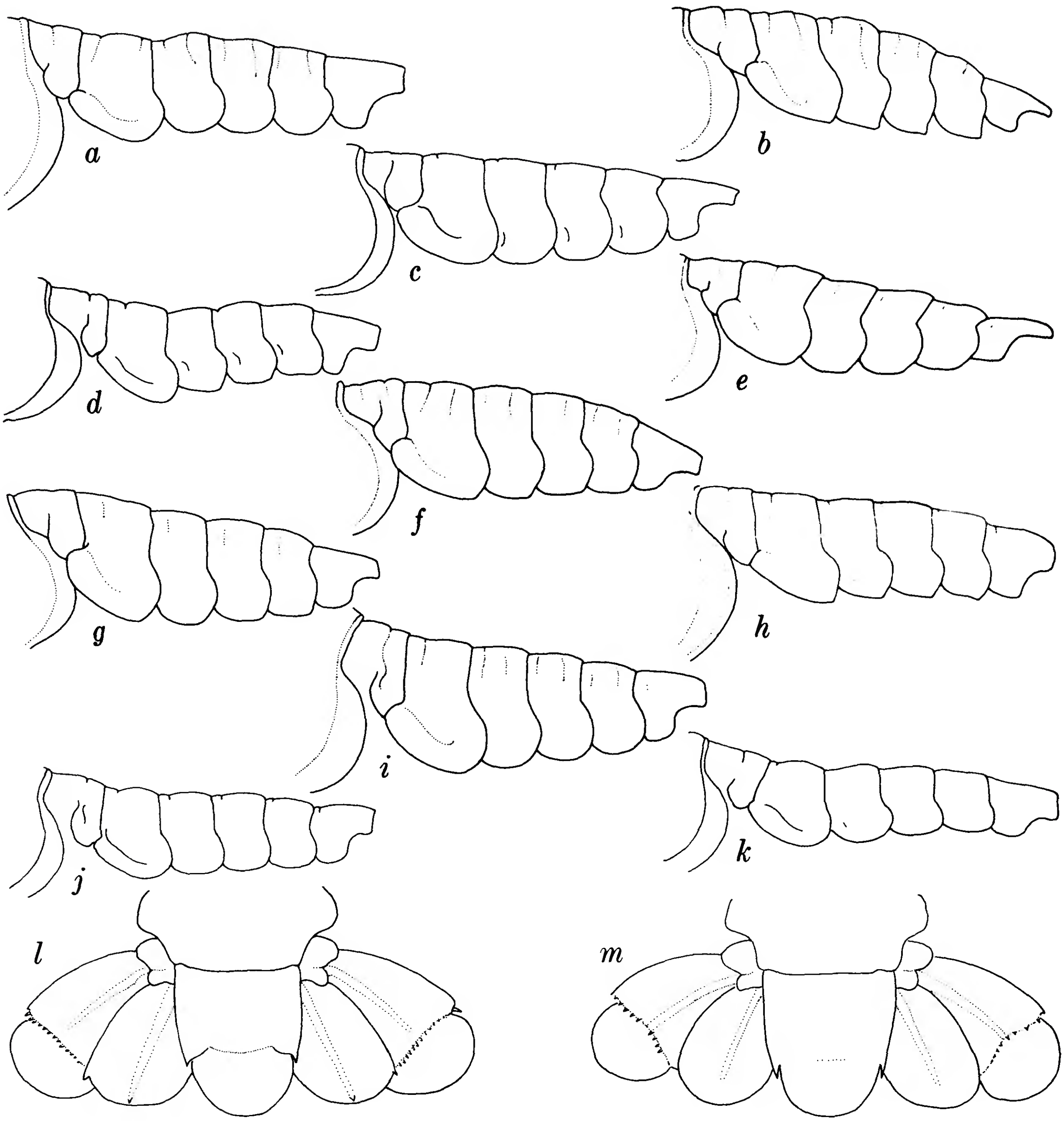


FIGURE 39.—Lateral view of abdomen (*a–k*) and dorsal view of telson and uropods (*l, m*) in male representatives of subgenus *Depressicambarus*: *a, Cambarus (D.) cymatilis* from type-locality; *b, C. (D.) englishi* from type-locality; *c, C. (D.) halli* from type-locality; *d, C. (D.) harti* from type-locality; *e, f, g, C. (D.) latimanus* from Banks, Carroll, and Madison counties, respectively; *h, C. (D.) reflexus* from Effingham Co; *i, C. (D.) striatus* from Harris Co; *j, l, C. (D.) strigosus* from type-locality; *k, m, C. (D.) truncatus* from Laurens Co.

testing a key (prepared by me) to the members of the subgenus, was it discovered that the specimens upon which the subsequent description of *C. (D.) englishi* was based were indeed different from those of *C. (D.) halli*.

An additional problem existed in distinguishing between *C. (D.) striatus* and *C. (D.) floridanus*. When I described the latter in 1941(b), I had access to limited material of what I believed to be *C. (D.) striatus* that had been collected from the type-locality, Nashville, Tennessee. These robust olive gray stream dwellers, lacking an apical notch on the central projection of the first pleopod of the first form male, were so different from the smaller brownish animals with "reddish orange chelae" that I had dug from burrows in seepage areas in the Florida panhandle that I did not hesitate to describe the latter as new. With the acquisition of numbers of specimens from the intervening area, I am now unable to find a single character on which to separate the two. In view of the foregoing remarks, those who attempt to employ the following key should not be surprised when difficulties are encountered.

Key to Georgia Members of Subgenus *Depressicambarus*

1. Areola no more than 5 times as long as broad 2
   Areola more than 5 times as long as broad 4
2. Margins of rostrum always thickened; first pleopod of first form male lacking subapical notch on central projection, mesial process with conspicuous gap between inflated portion and main shaft of appendage (endemic in Tallapoosa Basin) .... ***englishi***
   Margins of rostrum seldom thickened; first pleopod of first form male with subapical notch on central projection, mesial process lacking conspicuous gap between inflated portion and main shaft of appendage 3
3. Areola rarely (only in some individuals in Little Tallapoosa watershed) more than 4 times as long as broad and with 3 to 9 (rarely fewer than 5) punctations in narrowest part; rostrum with marginal spines or tubercles at base of acumen; abdominal terga with transverse light band on caudal margin (endemic in Tallapoosa Basin) .... ***halli***
   Areola more than 4 times as long as broad except in some populations in Savannah watershed, these with rostral margins tapering anteriorly and occasionally with weak tubercles; abdominal terga never with transverse bands, sometimes with longitudinal stripes (widespread in Georgia except south of the Altamaha and lower Ocmulgee and Flint rivers) .... ***latimanus***
4. Greatest width of abdomen of male subequal to or greater than length of areola 5
   Greatest width of abdomen of male distinctly less than length of areola 6
5. Areola usually less than 9 times as long as broad and seldom constituting as much as 37 percent of total length of carapace or 44 percent of postorbital carapace length; first pleopod of first form male usually without trace of caudal knob (widespread in Georgia except south of the Altamaha and lower Ocmulgee and Flint rivers) .... ***latimanus***
   Areola usually more than 9 times as long as broad and seldom constituting less than 37 percent of total length of carapace or 44 percent of postorbital

carapace length; first pleopod of first form male usually with caudal knob (widespread in Georgia in the northwestern and western parts of the state) .... ***striatus***

6. Suborbital angle prominent and acute; mesial ramus of uropod with distomedian spine projecting beyond distal margin (known only from Murray County) .... ***cymatilis***

   Suborbital angle never prominent, often obsolete; mesial ramus of uropod never with distomedian spine projecting beyond distal margin 7

7. Central projection of first pleopod of first form male strongly arched, forming even arc of 180 degrees, and tip extending toward base of appendage beyond margin of tumescent part of mesial process (restricted to Ogeechee and Savannah basins) .... ***reflexus***

   Central projection of first pleopod of first form male rarely strongly arched, never forming even arc of 180 degrees, tip never reaching level of tumescent part of mesial process 8

8. Base of mesial process of first pleopod of first form male with row of plumose setae extending along caudal border (known only from the Broad River basin in Elbert, Oglethorpe, and Wilkes counties) .... ***strigosus***

   Base of mesial process of first pleopod of first form male lacking plumose setae 9

9. Ventral surface of palm of chela densely punctate; mesial ramus of uropod rarely with distolateral or distomedian spines; color orange tan with darker markings (known only from the Oconee River basin) .... ***truncatus***

   Ventral surface of palm of chela sparsely punctate at most; mesial ramus of uropod with distolateral and distomedian spine; color dark blue (known only from the Flint and Chattahoochee basins in Meriwether County) .... ***harti***

The *halli* Group

Cambarus (Depressicambarus) englishi Hobbs and Hall

FIGURES 23*j*, 37*a*, 39*b*, 40, 41, 199

Cambarus (Depressicambarus) englishi Hobbs and Hall, 1972: 151–161, fig. 1.—Hobbs, 1974b:12, fig. 30.—Bouchard, 1978:30, 31, figs. 1b,h, 3c.
Cambarus englishi.—Bouchard, 1978:29, 43–45.—Wharton, 1978:46.

The only contribution to our knowledge of this crayfish that has been published since the appearance of the original description is that of Bouchard (1978), who included this species in his summary of the members of the subgenus *Depressicambarus*, citing records of its occurrence in Clay, Cleburne, and Tallapoosa counties, Alabama.

DIAGNOSIS.—Eyes moderately large. Rostrum usually with margins bearing spines or tubercles, occasionally tapering without interruption to apex. Carapace with well-developed cervical spine. Areola 4.2 to 4.9 times as long as wide and constituting 33.2 to 38.0 percent of entire length of carapace (41.3 to 46.7 percent of postorbital carapace length), with 4 to 6 punctations across narrowest part. Suborbital angle broadly rounded to obsolete. Postorbital ridge with cephalic spine or tubercle. Antennal scale about 2.8 times as long as broad, widest at about midlength. Palm of chela with 5 to 8 tubercles in mesialmost row. First pleopod of first form male with central

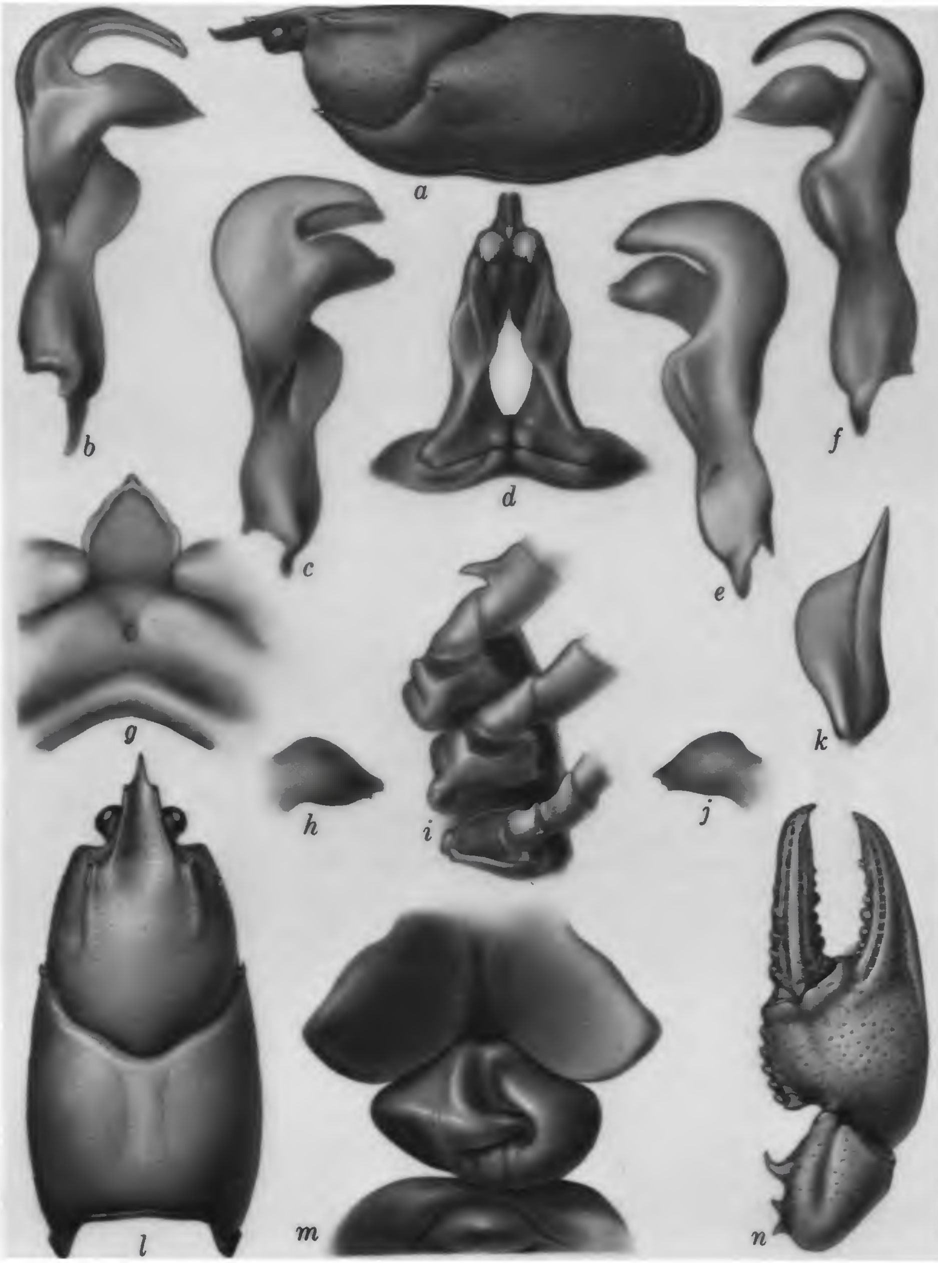


FIGURE 40.—*Cambarus (Depressicambarus) englishi* (all from holotype except *b*, *f*, from paratopotypic male, form I, *c*, *e*, from morphotype, and *m*, from allotype): *a*, lateral view of carapace; *b*, *c*, mesial view of first pleopod; *d*, caudal view of first pleopods; *e*, *f*, lateral view of first pleopod; *g*, epistome; *h*, mesial view of left mesial process; *i*, basal podomeres of third, fourth, and fifth pereiopods; *j*, mesial view of right mesial process; *k*, antennal scale; *l*, dorsal view of carapace; *m*, annulus ventralis; *n*, dorsal view of distal podomeres of cheliped. (From Hobbs and Hall, 1972, fig. 1.)

projection, long, narrow, tapering, gently curved, lacking subapical notch, and directed at angle of approximately 110 degrees to main shaft of appendage, its tip not reaching proximally to level of mesial process; latter with conspicuous gap between bulbiform portion and shaft of appendage, distal extremity with 1 to 3 acute or subacute apices; caudal knob absent. Carapace brown to olive; abdominal terga blackish, with transverse light band posteriorly. Female with first pleopod present.

COLOR NOTES (Figure 37*a*).—

Cephalic portion of carapace brownish olive dorsally with cream-tan markings over origins of gastric muscles; hepatic area greenish blue, fading ventrally to bluish cream; rostral margins, postorbital and suborbital ridges orange; tubercles in hepatic area and cephalic margin ventral to orbit cream. Thoracic area with areola straw-brown, dorsal portions of branchiostegites orange tan fading ventrally to bluish cream and studded with small pale tubercles; caudal ridge on carapace pinkish cream with narrow, almost black band immediately cephalic to ridge; band, except on dorsolateral area of branchiostegite, fading rapidly anteriorly, there more gradually. Dorsal surface of first abdominal segment mostly pinkish cream with one broad or two narrow blackish transverse bands cephalically; remaining abdominal terga and pleura blackish with narrow pinkish cream transverse band along caudal margin of each, band continuing on ventral margin of pleura and expanding on cephalic side of latter. Telson and uropods blackish dorsally and pale bluish green bordered in tan ventrally. Chela olive green dorsally with orange to cream-orange tubercles, lateral costa, and distal portions of fingers; latter with yellowish orange (corneous) tips. Carpus brownish olive dorsally with orange-cream tubercles and spines; dorsodistal part of merus dark olive with orange-cream spines. All podomeres fading ventrally to pinkish or bluish cream. Remaining pereiopods with podomeres distal to ischium pale olive dorsally, carpus darkest with other podomeres fading gradually toward proximal and distal ends of appendages; all podomeres fading ventrally (Hobbs and Hall, 1972:157–158).

TYPES.—Holotype, allotype, and morphotype, USNM 131700, 131701, 132519 (♂I, ♀, ♂II); paratypes, USNM.

TYPE-LOCALITY.—Tallapoosa River, 1 mile north of Tallapoosa, in riffle area a few hundred yards upstream from bridge on State Route 100, Haralson County, Georgia.

RANGE.—Endemic in the Tallapoosa Basin, where known from two subjacent localities in Georgia and from Clay, Cleburne, and Tallapoosa counties, Alabama (Bouchard, 1978:31). Its entire range lies in the Piedmont Province.

GEORGIA SPECIMENS EXAMINED.—I have examined 41 specimens that have been collected in two localities on the Tallapoosa River. *Haralson County*: (1) 2.5 mi W of Tallapoosa, 1j♂, 2j♀, 3 Sep 1969, Max W. Walker, E. T. Hall, Jr., collectors; (2) type-locality, 1♂I, 1♀, 3j♂, 4j♀, 3 Sep 1969, R. F. Holbrook, ETH; 4♂I, 6♀, 5j♂, 3j♀, 13 Oct 1969, ETH, HHH; 1♀, 25 Jul 1971, ETH, T. A. English, Jr.; 4♂I, 1♂II, 1♀, 1j♂, 3j♀, 23 Sep 1971, ETH, TAE.

VARIATIONS.—

Among the more conspicuous variations occurring in *C. (D.) englishi* is the presence or absence of marginal tubercles or spines on the rostrum. All of the young individuals, as well as some of the largest, have well-developed spines, but in several adults there is not a trace of a tubercle and scarcely any interruption of the margins between the basal portion of the rostrum and the acumen. The areola varies from 4.2 to 4.9 times as long as wide and comprises from 33.2 to 38.0 (average 35.4) percent of the total length of the carapace; only two specimens, however, have areolae constituting less than 34 percent and two others as much as 37 percent.

The row of tubercles on the mesial surface of the palm of the chela varies from five to eight, with seven the usual number; only one individual has eight on one chela and another has five on one member of the pair. The tubercle on the ventral surface of the palm, at the base of the dactyl, may be simple, essentially bifid, or absent, and there are one to three proximal to it. The number of tubercles along the fixed finger and dactyl ranges from five to eight and seven to eight, respectively. The two spines on the mesial surface of the carpus are present in all except one specimen in which the proximal one is lacking, and, in one individual, there are two additional small tubercles. The ventral surface of the carpus always has the two tubercles as described for the holotype, and an occasional third tubercle is present as in the allotype. The dorsal surface of the merus of all of the specimens except one, in which there are three, bears two spiniform tubercles; the ventromesial row consists of seven to nine tubercles and the ventrolateral of two to seven.

The mesial process of the first pleopod of the first form male may be somewhat more inflated that those illustrated [Figure 40*b,d,f,h,j*], but the distal extremities do not exceed the limits indicated in the figure. The cephalic portion of the annulus ventralis is consistently membranous, but in all except three of the females, the tongue is directed dextrally (Hobbs and Hall, 1972:159–160).

SIZE.—The largest specimen available is a female having a carapace length of 39.2 (postorbital carapace length, 31.9) mm. The largest and smallest first form males have corresponding

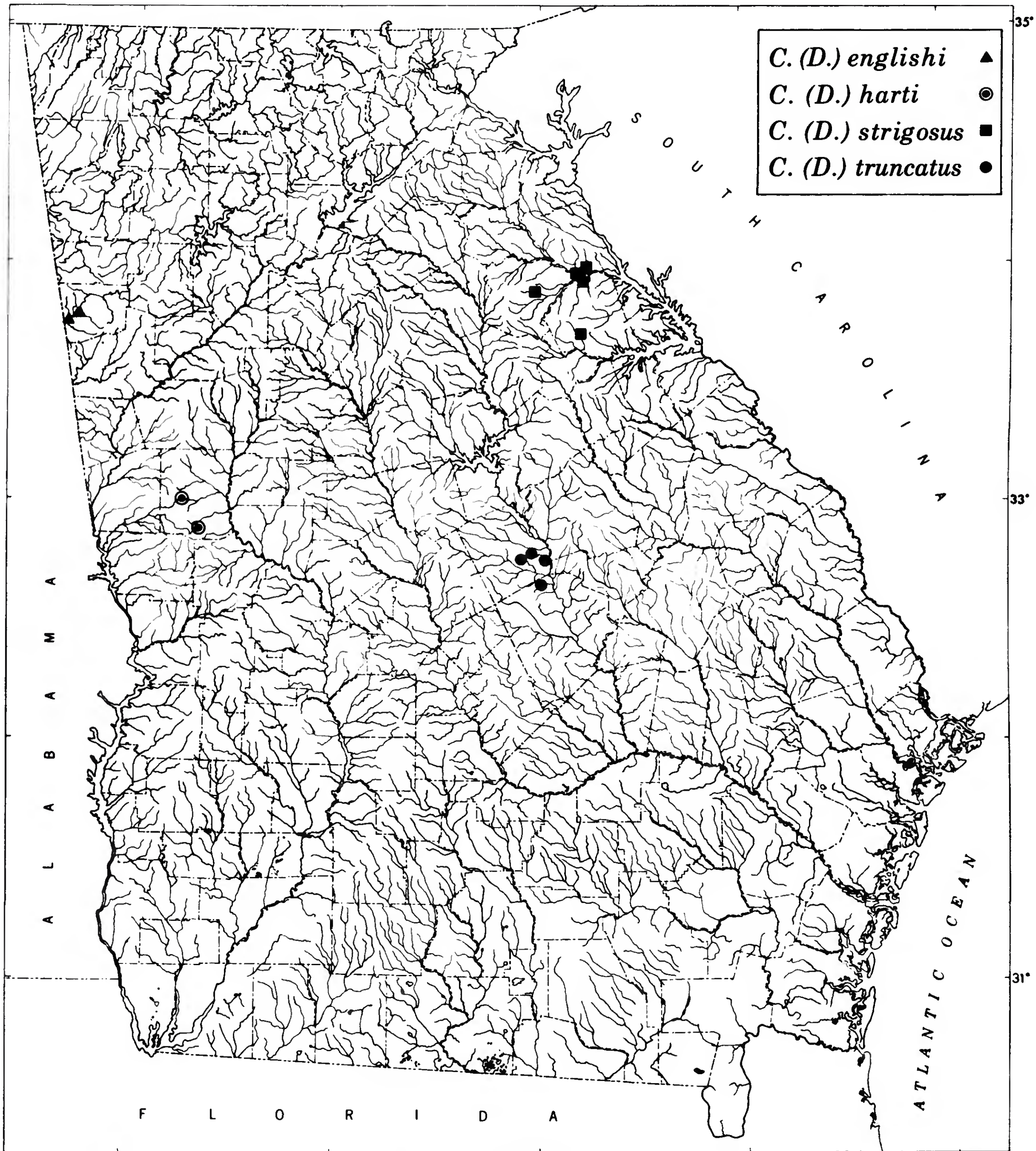


FIGURE 41.—Distribution of *Cambarus (D.) englishi*, *C. (D.) harti*, *C. (D.) strigosus*, and *C. (D.) truncatus* in Georgia.

lengths of 36.4 (30.3) and 29.1 (23.3) mm. No females carrying eggs or young have been obtained.

LIFE HISTORY NOTES.—

First form males have been collected in September and October, and inasmuch as those that were taken on 23 September 1971 were encrusted, it may be concluded that they had not molted for a number of months, which suggests, in turn, that the breeding season extends through the summer months. Seemingly paradoxically, among the specimens collected in September and October 1969, all of the adult males had recently molted to first form! Only one second form male, the morphotype, has been obtained, and that specimen, taken on 23 September 1971, was also encrusted (Hobbs and Hall, 1972:161).

ECOLOGICAL NOTES.—In the only two localities in which this crayfish was collected from Georgia, it was found in a riffle area, where the water was one to two feet deep and flowing with a moderate current over a bed of large rocks partially embedded in sand, supporting a dense growth of *Podostemum ceratophyllum*. Except following rains when the water is reddish orange, it is clear. As pointed out in the original description, four crayfishes frequent the river at the type-locality. Dominating the riffle area is *C. (D.) englishi*, and whereas *C. (D.) halli* is there in small numbers, it is far more abundant in the litter and along the banks where there are exposed mats of roots. Far less abundant are *Procambarus (Pe.) spiculifer* and *C. (D.) latimanus*, both of which are found more often below the riffle area.

An appreciation of the apparent restriction of *C. (D.) englishi* to the riffle at the type-locality was realized when T. A. English, Jr., and I attempted to collect there on 30 April 1971 when the stream was flooded and the water so swift that we were unable to wade out into the riffle area. Using a seine along the bank, we netted only eight crayfishes, five adults and one juvenile of *C. (D.) halli* and one juvenile each of *Procambarus (Pe.) spiculifer* and *C. (D.) latimanus*. On a previous visit to the same locality by E. T. Hall, Jr., and me, at which time collections were also made in the riffle areas, 36 specimens were obtained of which 19 were *C. (D.) englishi*, 12 *C. (D.) halli*, four *P. (Pe.) spiculifer*, and one *C. (D.) latimanus*. Thus, unlike observations on other members of the subgenus *Depressicambarus*, there is no evidence that *C. (D.) englishi* occurs anywhere except in riffles.

GEORGIA CRAYFISH ASSOCIATES.—*Cambarus (D.) englishi* has been collected with the following crayfishes (the number of times they have been found together is indicated in parentheses): *C. (D.) halli* (4), *C. (D.) latimanus* (1), and *Procambarus (Pe.) spiculifer* (4).

Cambarus (Depressicambarus) halli Hobbs

FIGURES 23*i*, 37*b*, 39*c*, 42, 43, 200

Cambarus extraneus.—Anonymous, 1967i, tab. 3*.
Cambarus halli Hobbs, 1968a:269*–273*, figs. 12–22; 1968b: K-16*.—Anonymous, 1968:11*[photograph]; 1970b: (219, 220, 222–225)*.—Hart and Hart, 1971: [not 107]; 1974:90*, 134*, [not 31].—Bouchard, 1978:29, 43, 45–46.—Wharton, 1978: 46*, 220*.
Cambarus (Depressicambarus) halli.—Hobbs, 1969a:(102, 104, 136, 138, 154)*, figs. 8, 18e; 1972b:113*, 146*, figs. 92d, 97b, 99b; 1974b:13*, fig. 29.—Hobbs and Hall, 1969:293; 1972:151*, 159*, 160*.—Bouchard, 1972:33; 1978:30, 33–34*, figs. 1a,e,f, 3f*.

The above references constitute a complete bibliography for the species; those pages on which Georgia representatives are included are marked with an asterisk.

SUMMARY OF LITERATURE.—The first published record of this crayfish (Anonymous, 1967i) was based on the erroneous identification of specimens from three localities in the Tallapoosa Basin, two in Haralson County, Georgia, and one in Cleburne County, Alabama. The only recorded data not accompanying the original description of the species are the photograph (Anonymous, 1968) and new locality records (Anonymous, 1970b, and Hart and Hart, 1974). Hart and Hart (1971) mistakenly cited this crayfish along with *Procambarus (Pe.) spiculifer* as hosts of *Ankylocythere tallapoosa*, a new entocytherid ostracod described by them. In their monograph (1974:31), they listed the hosts in the same locality as *C. (D.) latimanus* and *C. (D.) halli*. Actually the hosts were *C. (D.) latimanus* and *P. (Pe.) spiculifer*. In their Paulding County station (pages 90 and 134), they reported *C. (D.) halli* as host to *Entocythere internotalus* Crawford (1959) and *Uncinocythere simondsi*. The remaining citations include remarks on its relationships to *Cambarus (J.) unestami* Hobbs and Hall (1969), to *C. (D.) englishi*, and to other members of the subgenus (Hobbs, 1969a). The latter reference also includes keys and a summary of the distribution of this crayfish as does Hobbs (1972b). The distribution is also summarized in Hobbs (1974b). The most recent account of the species is that of Bouchard (1978), who included a diagnosis, statement of the range, and commented on its relationships. All confirmed previous records for the State are included under "Georgia Specimens Examined."

DIAGNOSIS.—Eyes moderately large. Rostrum with marginal spines or tubercles, rarely abraded in larger animals. Carapace with well-developed cervical spine. Areola 3.0 to 5.0 times as long as wide and constituting 30.0 to 33.7 percent of entire length of carapace (38.0 to 41.9 percent of postorbital carapace length) with 3 to 9 punctations across narrowest part. Suborbital angle broadly rounded to obsolete. Postorbital ridge with cephalic spine or tubercle. Antennal scale about 2.5 times as long as broad, widest at about midlength. Palm of chela with 5 to 7 tubercles in mesialmost row. First pleopod of first form male with central projection moderately long and wide, strongly arched, bearing distinct subapical notch, and directed at angle of approximately 125 degrees to main shaft of appendage, its tip reaching proximally to level of mesial process; latter with very narrow gap between bulbiform portion and shaft of appendage, distal extremity usually with single rounded to subacute apex; caudal knob absent. Carapace brown to olive; abdominal terga with transverse light bands. Female with first pleopod present.

COLOR NOTES. (Figure 37*b*).—

Cephalic portion of carapace dark brown with cream tubercles laterally. Margins of rostrum and postorbital ridges red. Branchiostegites tan, areola dark olive brown. Abdomen dark olive with narrow transverse pinkish yellow band on caudal margin of each tergum; pleura with cream margins. Chela olive with basal articular tubercle and those at base of dactyl red; tubercles on mesial surface of palm orange; fingers dark green basally fading rapidly to cream; tubercles on mesial surface of dactyl orange. Entire ventral surface of animal greenish cream (Hobbs, 1968a:273).

The color of this crayfish is so markedly similar to that of *C. (D.) englishi* that if consistent differences exist, they have not been recognized.

TYPES.—Holotype, allotype, and morphotype, USNM 129288, 129289, and 129290 (♂I, ♀, ♂II); paratypes, USNM.

TYPE-LOCALITY.—Small tributary of the Tallapoosa River, 1.3 miles south of the river on U.S. Highway 27, Haralson County, Georgia.

RANGE.—Endemic in the Tallapoosa Basin, where known from Paulding County, Georgia, to Lee and Tallapoosa counties, Alabama.

GEORGIA SPECIMENS EXAMINED.—I have examined 136 specimens all from the Tallapoosa Basin. *Carroll County*: (1) Little Tallapoosa River 3.1 mi NW of Carrollton (Anonymous, 1970b:222), 1j♂, 2j♀, 4 Sep 1969, M. W. Walker, R. F. Holbrook, collectors; (2) Little Tallapoosa River at St Rte 100, 2.5 mi S of Bowden (Anonymous, 1970b:225), 1♂II, 2j♂, 1j♀, 3 Sep 1969, RFH, E. T. Hall, Jr.; (3) Little Tallapoosa River 3.7 mi SE of Bowden (Anonymous, 1970b:224) off Rte S838, 1j♀, 4 Sep 1969, MWW, RFH; (4) Buffalo Creek at Rte S838, 6 mi SE of Bowden and 5.6 mi SW of Carrollton (Anonymous, 1970b:223), 2♀, 2j♂, 4j♀, 4 Sep 1969, MWW, RFH. *Haralson County*: (5) type-locality (Anonymous, 1970b: 219), 1♂I, 3♂II, 4j♂, 2j♀, 18 Apr 1966, ETH, HHH; 1♀, 2j♂, 1969, ETH, R. M. Gaddis; 1♂I, 1j♂, 2j♀, 2 ovig ♀, 26 Apr 1968, John Ross, HHH; (6) Tallapoosa River at St Rte 100, first riffle upstream from bridge, 1♀, 9j♂, 14j♀, 3 Sep 1969, ETH, RFH; 4♂I, 4♀, 5j♂, 13 Oct 1969, ETH, HHH; 2♂I, 1♂II, 2♀, 1j♀, 30 Apr 1971, T. A. English, Jr., HHH; 1j♂, 2j♀, 25 Jul 1971, TAE, ETH; 1♂I, 1j♂, 2j♀, 23 Sep 1971, ETH, TAE; (7) Tallapoosa River at US Hwy 27, 3♂I, 4♂II, 3♀, 1j♂, 5j♀, 18 Apr 1966, ETH, HHH; (8) trib of Tallapoosa River, 0.7 mi S of river on US Hwy 27, 1♂I, 2j♂, 7j♀, 26 Apr 1968, JR, HHH; (9) Tallapoosa River at RR bridge, 2.5 mi W of Tallapoosa (Anonymous, 1970b:219), 4j♂, 3j♀, 13 Sep 1969, ETH, MWW; (10) Walker Creek, 3.8 mi SW of Buchanan on St Rte 120, 1j♂, 23 Apr 1968, C. R. Gilbert; (11) Beach Creek 4.5 mi E of junction of St Rte 100 on Rte 120, 3j♀, 30 Apr 1971, TAE, HHH; (12) Tallapoosa River 1.1 mi N of Draketown on unnumbered road, 1♀, 23 Apr 1968, CRG; (13) Beach Creek at unnumbered road, last bridge before creek joins Tallapoosa River (Anonymous, 1967i, tab. 3), 1j♂, 12 Dec 1966, Donald Schultz; (14) Tallapoosa River at US Hwy 78 (Anonymous, 1967i, tab. 3), 1j♂, 2j♀, 12 Dec 1966, DS. *Paulding County*: (15) Tallapoosa River at St Rte 101 (Hart and Hart, 1974:90), 2♀, 5j♂, 2j♀, 18 Apr 1966, ETH, HHH.

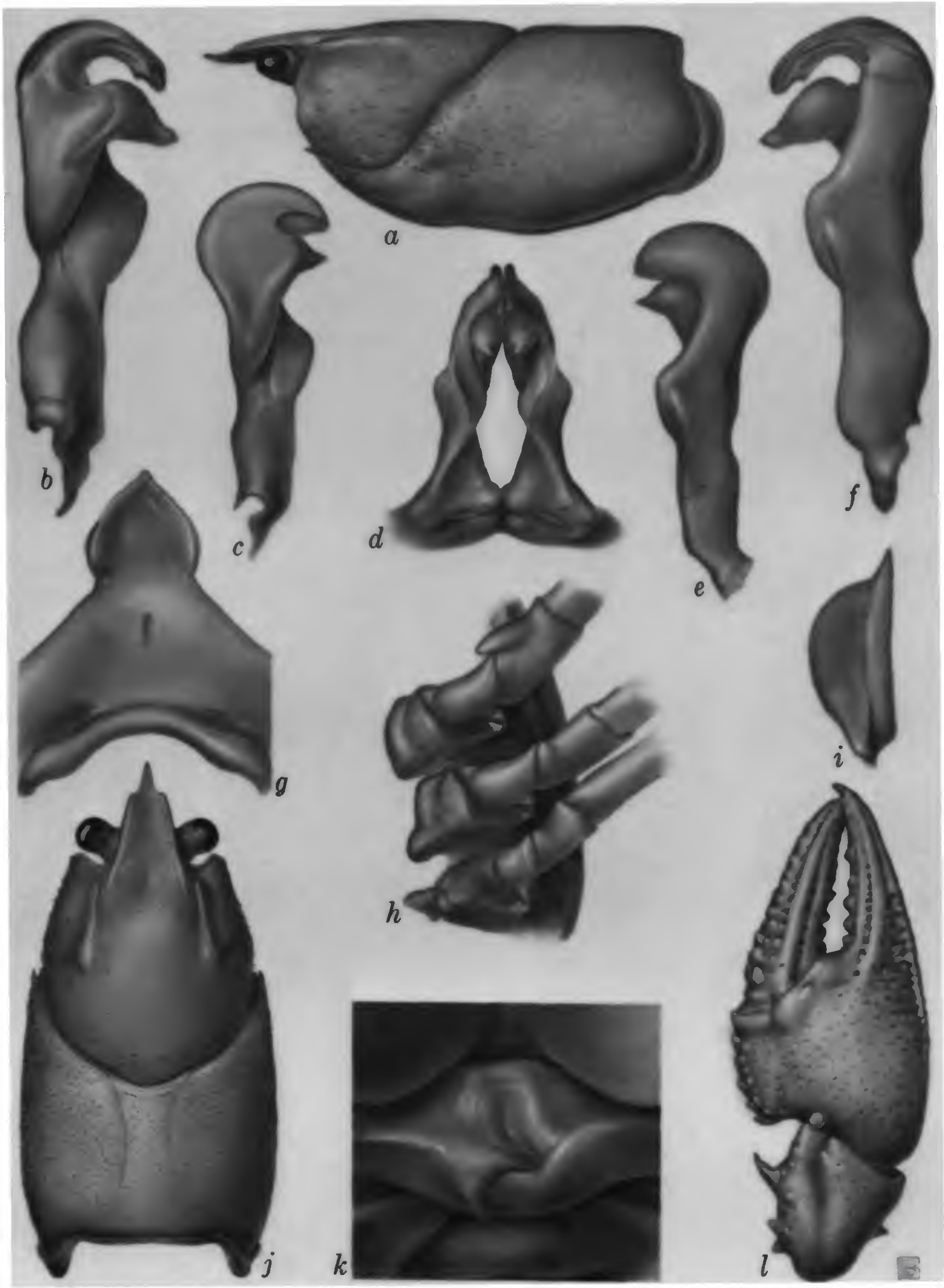


FIGURE 42.—*Cambarus (Depressicambarus) halli* (all from holotype except *c*, *e*, from morphotype, *d*, from paratypic male, form I, from Tallapoosa River at US Hwy 27, and *k*, from allotype): *a*, lateral view of carapace; *b*, *c*, mesial view of first pleopod; *d*, caudal view of first pleopods; *e*, *f*, lateral view of first pleopod; *g*, epistome; *h*, proximal podomeres of third, fourth, and fifth pereiopods; *i*, antennal scale; *j*, dorsal view of carapace; *k*, annulus ventralis; *l*, dorsal view of distal podomeres of cheliped.

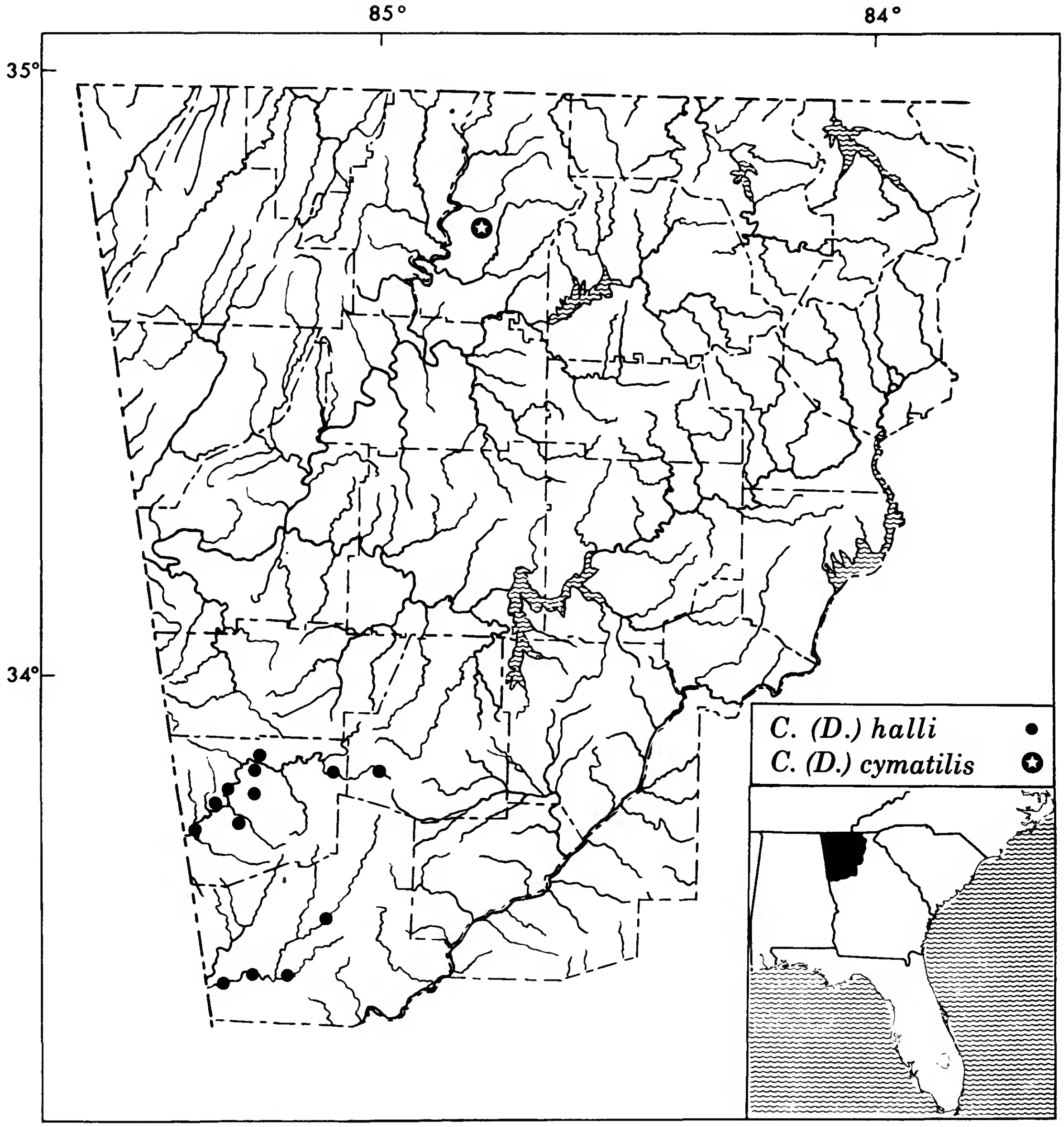


FIGURE 43.—Distribution of *Cambarus (Depressicambarus) cymatilis* and *C. (D.) halli* in Georgia.

VARIATIONS.—The only regionally restricted variation observed is the narrower areola in specimens from the Little Tallapoosa watershed. Whereas in the Tallapoosa Basin in Haralson and Paulding counties, it ranges from 2.9 to 4.0 times as long as broad, in the Little Tallapoosa in Carroll County, it ranges from 4.0 to 5.0. Partially reflecting the narrower areola of the latter, the punctations within it are fewer, with only three extending across the narrowest part; in contrast, in the Tallapoosa specimens the punctations are crowded, four to nine present in the most constricted part. Although the following variations have been observed in specimens from Georgia, none is characteristic of populations occupying a limited part of the range in the state. The rostrum varies considerably in length, and, to some degree, in the relative thickness of the margins; usually, however, the latter are narrow and only slightly swollen. In an occasional individual that is in a late intermolt stage, the marginal spines or tubercles are abraded, and the margins are almost smooth from base to apex of acumen. The chelipeds exhibit few variations worthy of note: except in regenerated appendages, the mesialmost row of tubercles on the palm ranges from five to seven (usually six), and the ventral rows on the merus consist of six to nine in the mesial one and two to four in the lateral.

Size.—The largest Georgia specimen available is an ovigerous female having a carapace length of 37.0 (postorbital carapace length 29.5) mm. The corresponding lengths of the largest and smallest first form males are 35.0 (28.4) and 30.0 (23.3) mm; those of the smallest ovigerous female are 33.5 (26.7) mm.

Life History Notes.—First form males have been collected in April, September, and October in Georgia (also in November in Alabama), and males having recently molted to first form were found on 18 April 1966. In the latter collection there was an encrusted first form male as well as an encrusted, late premolt (soft) second form male. Adults of the species have not been obtained from December to March, and few adults (1♂II, 6♀ from Alabama) have been taken from May to August. In April, two ovigerous females were collected in Georgia and five in Alabama. Data on five of the ovigerous females follow.

Carapace and postorbital carapace lengths (mm)	*Number of eggs*	*Diameter of eggs (mm)*
21.4 (16.2)	94	2.2-2.3
25.5 (20.5)	132	2.1-2.3
33.6 (26.6)	171	2.4-2.5
*34.9 (27.4)	166	2.3-2.4
*36.9 (29.9)	182	2.3-2.5

The two specimens marked with an asterisk were preserved together in a container on the bottom of which were 17 additional eggs that were lost by one or both females.

Seasonal Data (Alabama and Georgia)

Sex/stage	*J*	*F*	*M*	*A*	*M*	*J*	*J*	*A*	*S*	*O*	*N*	*D*	*?*
♂I				16					1	8	3		
♂II				14	1				1	1			
♀				17	2	2	1	1	3	10	12		1
♂j				28		2	2		19	9	5	2	2
♀j				35		3	2		27	7	3	3	
♀ ovig				7									

Ecological Notes.—*Cambarus (D). halli* occurs only in lotic habitats and is most frequently found in debris or among exposed mats of roots of shoreline plants along undercut banks. It does not shun riffle areas, but in sharing a stream with *C. (D.) englishi*, it is far more abundant in quieter water than in the riffle proper (see "Ecological Notes" for the latter). On the basis of shallow water collections available, *C. (D.) halli* appears to be the most abundant of the five species occurring in the upper Tallapoosa Basin. Both *C. (D.) latimanus* and *Procambarus (Pe.) spiculifer* have been collected in this basin in Georgia, and a juvenile female of *C. (D.) striatus* was dug from a burrow in a swampy area along Little River in Haralson County.

Georgia Crayfish Associates.—*Cambarus (D.) halli* has been collected with the following crayfishes (the number of times they have been found together is indicated in parentheses): *C. (D.) englishi* (4), *C. (D.) latimanus* (3), and *Procambarus (Pe.) spiculifer* (8).

The *latimanus* Group

Cambarus (Depressicambarus) cymatilis Hobbs

Figures 23*h*, 37*e*, 39*a*, 43, 44, 198

Cambarus (Depressicambarus) cymatilis Hobbs, 1970:241, 250-259, figs. 3, 4; 1972b:112, 146, figs. 97a, 99a; 1974b:12, 89, fig. 37; 1976:545.—Bouchard, 1972:34, 35; 1978:30-31, figs. 1c, j, m, 3b.

Cambarus cymatilis.—Bouchard, 1972:56, 91, 106; 1978:29, 44-46.

These citations constitute a complete bibliography for the species and, excluding references to its occurrence in Tennessee by Bouchard (1972, 1978), are based on Georgia materials.

SUMMARY OF LITERATURE.—Except for its inclusion in keys, a few illustrations and discussions of certain anatomical features, the only new data presented for this species are those of Bouchard (1978), who pointed out several additional characters of the cheliped, added Bradley County, Tennessee, to its range, and discussed its affinities with other members of the subgenus, assigning it to his "*latimanus* group."

DIAGNOSIS.—Eyes small. Rostrum without marginal spines, tubercles, or carina. Cervical spines or tubercles lacking. Areola very narrow or obliterated and constituting 41.7 to 44.8 percent of total length of carapace (48.2 to 50.9 percent of postorbital carapace length) and never with more than 1 punctation in narrowest part. Suborbital angle conspicuous and acute. Postorbital ridge terminating cephalically without spines or tubercles. Antennal scale 2.4 to more than 3 times as long as wide, broadest distal to midlength. Palm of chela with 5 to 7 tubercles in mesialmost row. First pleopod of first form male with short central projection recurved at 110 to 120 degrees to shaft of appendage, and provided with prominent subapical notch; mesial process inflated, subconical, and extending caudally much beyond tip of central projection; caudal knob absent. Mesial ramus of uropod with distomedian spine far overreaching margin of ramus (similar to Figure 86*b*). Color blue; abdominal terga without stripes or bands. Female with first pleopod present.

COLOR NOTES (Figure 37*e*).—

Dorsal surface of carapace and abdomen dark cobalt blue, fading rapidly on lateral surfaces of hepatic area, branchiostegites, and pleura through pale blue to cream with a faint bluish suffusion. Cephalic section of telson mottled with blue laterally and dark blue triangular area medially, caudal section pale bluish gray. Uropod also pale bluish gray with median longitudinal dark blue line in each ramus, lateral ramus with additional dark blue line along proximal margin of transverse suture. Dorsal surface of peduncle of antenna and lateral margin of antennal scale dark blue. Cheliped dark blue dorsally from distal third of merus almost to ends of fingers, [costa on propodus cream] and ventral surface pale gray to bluish cream [virtually all tubercles cream to white]; tips of fingers corneous (yellow [to pinkish] orange). Dorsal portions of remaining pereiopods from merus to propodus mottled with dark blue, otherwise cream to pale grayish blue. Sternal area mostly cream to white with isolated blue patches (Hobbs, 1970:257).

TYPES.—Holotype, allotype, and morphotype, USNM 129860, 129861, 129862 (♂I, ♀, ♂II); paratypes, USNM.

TYPE-LOCALITY.—Near the western city limits of Chatsworth, Murray County, Georgia, in lawn and rose garden of Mr. Charles S. Dunn off Chestnut Street.

RANGE.—Previously known only from the immediate vicinity of Chatsworth, Murray County, Georgia. Dr. Bouchard has kindly informed me that D. A. Etnier had found 2♂I, and 1 ovigerous ♀ in a seepage area along Mill Creek upstream from State Route 74, Bradley County, Tennessee, on 21 April 1977.

GEORGIA SPECIMENS EXAMINED.—I have examined a total of 15 specimens that have been collected in three localities. *Murray County*: (1) type-locality, 2♂I, 2♀, 1j♀, 1 ovig ♀, 24 Apr 1968, C. S. Dunn, E. T., Hall, Jr., HHH, collectors; 2♂I, 2♀, 4 Apr 1973, CSD; (2) 214 Fourth Avenue, Chatsworth, 2♂II, 25 Apr 1968, ETH, HHH; (3) field adjacent to Holly Creek approximately 1 mi NE of Chatsworth, 1♂I, 2♀, 25 Apr 1968, ETH, HHH.

VARIATIONS.—As was pointed out in the original description, there are few variations the limits of which were not included in the descriptions of the three primary types. The rostral margins may be angular at the base of the short acumen, or they may be so gently curved as to obscure any demarcation of the base of the latter. The areola, always narrow, is reduced to a line in some individuals, and its length seems to increase proportionately with increase in carapace length (Hobbs, 1970:258, fig. 4). The mesial half of the dorsal surface of the palm of the chela may or may not bear tubercles lateral to those comprising the two mesial rows; the mesialmost consisting of five to seven tubercles (in one specimen, an eighth tubercle is eccentrically situated), and the adjacent one of three to seven. On the ventral surface of the chela, there are typically one tubercle on

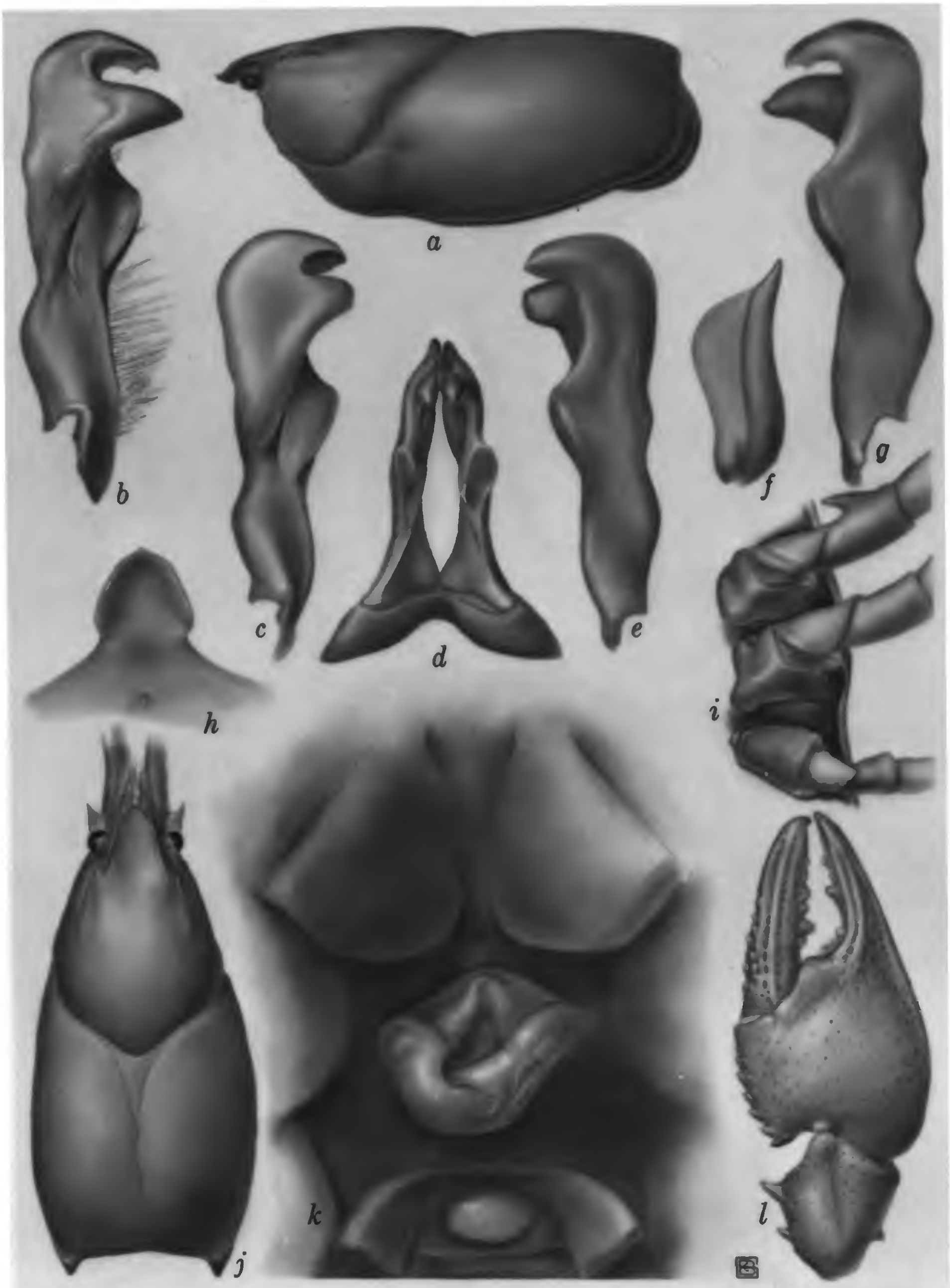


FIGURE 44.—*Cambarus* (*D.*) *cymatilis* (all from holotype except *c*, *e*, from morphotype, and *k*, from allotype): *a*, lateral view of carapace; *b*, *c*, mesial view of first pleopod; *d*, caudal view of first pleopods; *e*, *g*, lateral view of first pleopod; *f*, antennal scale; *h*, epistome; *i*, basal podomeres of third, fourth, and fifth pereiopods; *j*, dorsal view of carapace; *k*, annulus ventralis; *l*, dorsal view of distal podomeres of cheliped. (From Hobbs, 1970, fig. 3.)

the thickened ridge opposite the base of the dactyl and another slightly proximomesial to it; frequently there are two such tubercles in each position. The mesial surface of the carpus of the cheliped always bears one large subacute tubercle, and two or three additional smaller ones may or may not be situated proximal to it. The ventrolateral and ventromesial rows of tubercles on the merus of the cheliped range from three to five and seven to ten, respectively; that on the ischium ranges from two to four.

SIZE.—The largest specimen available is the allotypic female, which has a carapace length of 39.7 (postorbital carapace length 35.0) mm. The largest and smallest first form males have corresponding lengths of 34.5 (30.9) and 30.7 (26.9) mm, respectively. The only female I have examined that carried eggs or young is the ovigerous allotype.

LIFE HISTORY NOTES.—All of the available specimens were collected in April. These include both first form males and an ovigerous female bearing seven eggs measuring 1.9 to 2.0 mm in diameter.

ECOLOGICAL NOTES.—On the basis of our knowledge of the habits of *Cambarus* (*D.*) *cymatilis* it must be classified as a primary burrower. Although considerable field work has been conducted in the vicinity of Chatsworth, this crayfish has never been found in open bodies of water. All have been dug from burrows. Its existence first came to my attention on my third or fourth visit to Chatsworth seeking a first form male of *Cambarus* (*L.*) *acanthura* (described below). After previous failures, my companion, E. T. Hall, Jr., suggested that I call the local forester for advice as to where I might locate a burrowing crayfish. It was approaching 6:00 P.M. when I reached Mr. Dunn at his home and asked where in the area he might have seen the holes or chimneys of burrowing crayfishes. He immediately told me that he was sorry that I had not called a day or so earlier for he had seen his cat playing with a crayfish on his lawn. With that information, I immediately asked when it would be convenient for me to stop by his house to look for others. Assured that I would not be interrupting his dinner, within a few minutes I had my hands in the mouth of a burrow that had been constructed against the foundation of his house. The water table was approximately 15 cm below the surface, and in this burrow the crayfish was cornered within a third of a meter. Much to my surprise, it was a first form male of an undescribed species. Without having wrought too much damage to his lawn and rose garden, by 7:00 P.M. we had managed to obtain six specimens of this blue species and a single one of *Cambarus* (*D.*) *striatus*. On the advice of Mr. Dunn, the following morning we collected in the other two localities, where five additional specimens were taken from burrows.

After having caught the 11 specimens, we realized that the males had been taken from comparatively simple as opposed to highly branching burrows. Such burrows, where the water table was only a few centimeters below the surface, consisted of a vertical passage with one or two short secondary tunnels, none of which was more than 0.5 meter deep. In marked contrast, the burrows of the females were highly branched, with two or more openings to the surface and with one or more long horizontal passageways; one such dissected gallery extended almost three meters from the center of the maze to an opening guarded at the surface by a low pile of sandy clay. Near Holly Creek, the water table was slightly more than a meter below the surface, and the burrows were not so complex as they were where the water table was shallow. In opening a burrow there, I had enlarged the passage leading to the surface sufficiently so that my fingers were about 0.5 meter below the surface. When I lifted my arm from the hole to discard a handful of sandy clay, the crayfish moved up the passageway to that level where it blocked the passage spreading its chelae wide apart with fingers gaping. Each time I attempted to seize the animal, it turned so that for a few minutes there was a definite "standoff." When the crayfish was caught, it was discovered to be a female. On the basis of very limited observations, even in the laboratory the females seem to be more aggressive than do the males.

GEORGIA CRAYFISH ASSOCIATES.—*Cambarus* (*D.*)

cymatilis has been collected in burrows near those of *C.* (*D.*) *striatus* once and near those of *C.* (*L.*) *acanthura* twice.

Cambarus (*Depressicambarus*) *harti*, new species

FIGURES 23*e*, 38*b*, 39*d*, 41, 45, 201

Cambarus sp.—Hart and Hart, 1974:21 (see "Georgia Specimens Examined").

DIAGNOSIS.—Eyes small. Rostrum without marginal spines or tubercles and lacking median carina. Cervical spines reduced to small, rounded tubercles. Areola 17 to 46 times as long as broad, constituting 38.2 to 40.3 (average 39.4) percent of entire length of carapace (44.2 to 45.8, average 44.8, percent of postorbital carapace length), and never with more than 2 punctations in narrowest part. Suborbital angle usually obsolete, at most broadly obtuse. Postorbital ridge terminating cephalically without spine or tubercle. Antennal scale about 3 times as long as wide, widest at about midlength, mesial margin sloping strongly. Palm of chela with 5 to 7 tubercles in mesialmost row; opposable margin of fixed finger with row of 4 or 5 tubercles (see exception under "Variations") in addition to distal one situated on lower level. Mesial ramus of uropod with premarginal distomedian spine and distolateral marginal spine. First pleopod of first form male with short, rather strongly arched central projection, its tip directed proximocaudally and flanked by adjacent subapical notch; mesial process inflated but with tapering, acute, upturned apical portion; caudal knob clearly evident. Color blue, prominent tubercles on chelipeds pinkish cream to white. Female with first pleopod present.

HOLOTYPIC MALE, FORM I.—Body subcylindrical (Figure 45*a*, *l*). Abdomen distinctly narrower than cephalothorax (8.9 and 12.1 mm); maximum width of carapace greater than depth at caudodorsal margin of cervical groove (12.1 and 9.8 mm, respectively). Areola 46 times as long as broad with 1 punctation in narrowest part; length 38.7 percent of total length of carapace (44.4 percent of postorbital carapace length). Rostrum with gently convergent thickened margins to base of anterior third, where turning more abruptly mesially along sides of rather large acumen, latter almost reaching distal end of penultimate podomere of antennular peduncle; dorsal surface of rostrum concave with few punctations other than usual submarginal row, those at level of posterior part of orbit forming transverse grooves. Subrostral ridges rather weak but evident in dorsal aspect to base of acumen. Postorbital ridges only moderately strong, truncate cephalically and swollen caudally. Suborbital angle broadly rounded, therefore obsolete; branchiostegal spine represented by rudimentary subangular prominence. Cervical tubercle only slightly larger than others nearby. Carapace punctate dorsally, granulate to tuberculate laterally. Abdomen shorter than carapace (20.4 and 23.8 mm), pleura rather short and rounded ventrally and caudoventrally (Figure 39*d*). Cephalic section of telson with 2 strong spines in each caudolateral corner. Proximal podomere of uropod with spine on each lobe; mesial ramus with submedian ridge terminating in short premarginal spine.

Cephalomedian lobe of epistome (Figure 45*g*) subrhomboidal with short cephalomedial projection and scalloped cephalolateral margins lacking distinct fovea; slitlike pits on cephalolateral margins of strongly arched epistomal zygoma rather inconspicuous. Ventral surface of proximal podomere of antennular peduncle with small acute spine near distal margin. Antennal peduncle without spines; flagellum reaching third abdominal tergum; antennal scale (Figure 45*i*) approximately 3 times as long as broad, widest at about midlength, mesial border injured but rather steeply inclined, distal spine reaching ultimate podomere of antennular peduncle. Ventral surface of ischium of third maxilliped with mesial half bearing irregular rows of long stiff setae and with submarginal lateral row of much smaller ones; distolateral angle subacute.

Left chela (Figure 45*j*) (right chela probably regenerated) 1.9 times as long as broad and mesial margin of palm occupying about one-third of its length. Mesial surface of palm with 2 well-defined rows of tubercles, mesialmost of 7 and adjacent

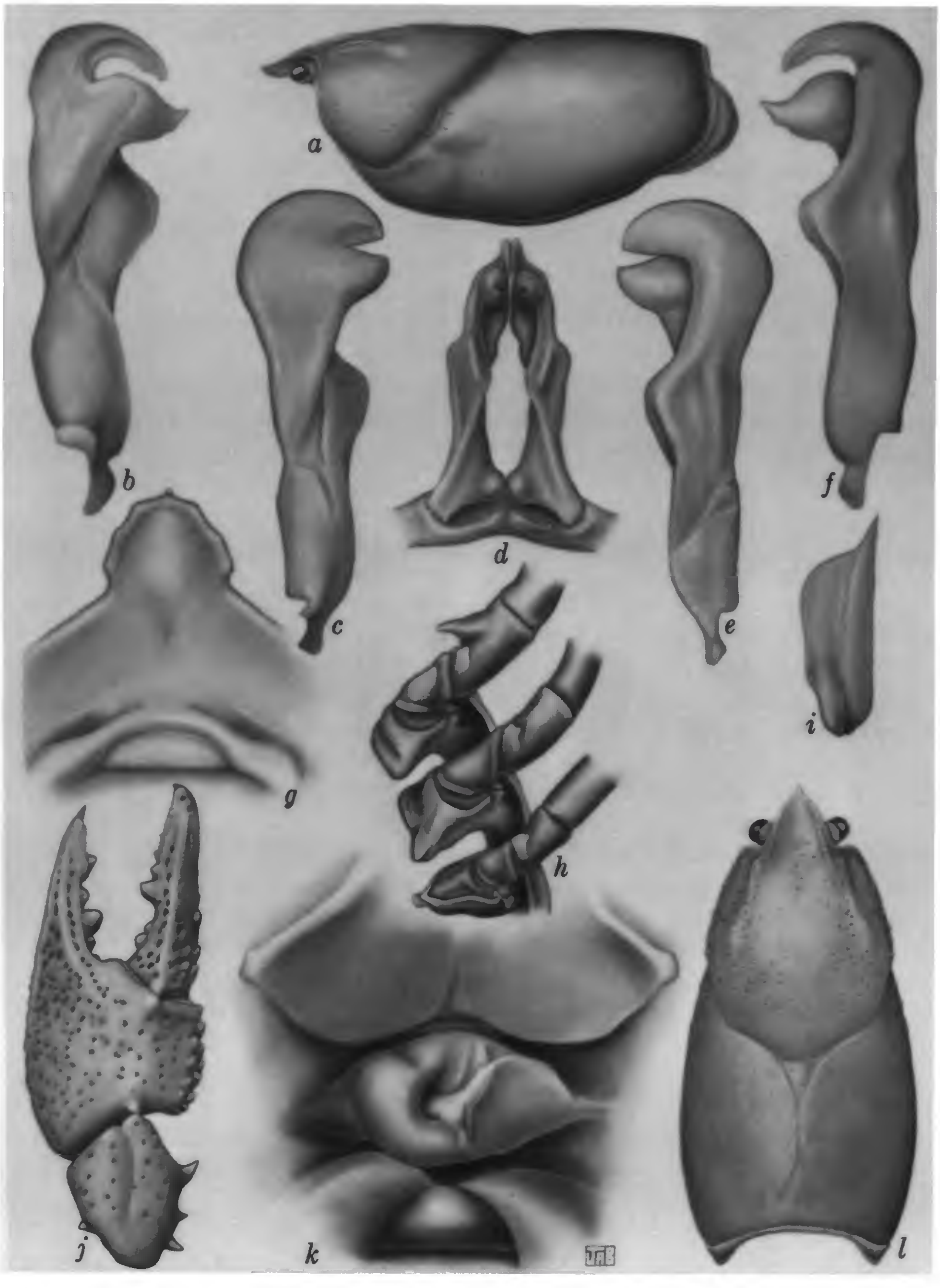


FIGURE 45.—*Cambarus (Depressicambarus) harti* (all from holotype except *c*, *e*, *i*, from morphotype, and *k*, from allotype): *a*, lateral view of carapace; *b*, *c*, mesial view of first pleopod; *d*, caudal view of first pleopods; *e*, *f*, lateral view of first pleopod; *g*, epistome; *h*, ventral view of basal podomeres of third, fourth, and fifth pereiopods; *i*, antennal scale; *j*, dorsal view of distal podomeres of cheliped; *k*, annulus ventralis; *l*, dorsal view of carapace.

one of 5; 2 additional much smaller tubercles present dorsolaterally, remainder of dorsal surface punctate, those punctations adjacent to strong lateral costa and on basal part of fixed finger larger and deeper than others; ventral surface of palm mostly punctate but with 2 prominent tubercles proximal to marginal thickening opposite base of dactyl and 2 low large ones on thickening. Both fingers of chela with well-defined submedian longitudinal ridges dorsally and ventrally; opposable margin of fixed finger with row of 4 tubercles, third from base much larger than others, and single large one on lower level at base of distal third of finger; single row of minute denticles extending from third tubercle to corneous tip of finger, row interrupted by fourth tubercle. Dactyl (strongly resembling that of members of *Fallicambarus*) with opposable margin bearing row of 7 tubercles, third from base much larger than others; row of minute denticles interspersed between third and more distal tubercles and continuing to corneous tip of finger; mesial surface of dactyl with cluster of tubercles proximally giving way to single row of deep setiferous punctations extending to corneous tip of finger.

Carpus of cheliped with dorsal surface bearing deep longitudinal groove and scattered punctations on both sides; mesial surface with large spikelike tubercle, similar smaller one proximally, and much smaller one dorsal to and between them; ventral surface with large median tubercle on distal margin and smaller one proximomesial to it. Merus with 2 prominent premarginal tubercles dorsally, ventrolateral row of 3 tubercles and ventromesial one of 9; podomere otherwise polished and/or punctate. Ventromesial margin of ischium with 1 small tubercle.

Ischium of third pereiopod with simple acute hook extending proximally over basioischial articulation (Figure 45*h*), not opposed by tubercle on basis. Coxa of fourth pereiopod with obliquely disposed low caudomesial boss; that of fifth pereiopod lacking boss but with ventral membrane bearing scattered setae.

First pleopod (Figure 45*b,d,f*) reaching coxa of third pereiopod. (See "Diagnosis" for description.)

ALLOTYPIC FEMALE.—Differing from holotype, other than in secondary sexual characters, as follows: areola only 20 times as long as broad with 2 punctations in narrowest part; dorsomesial surface of palm with several small tubercles lateral to 2 rows on mesial surface, ventral surface of left with only 1 tubercle on ridge at base of dactyl and single one proximal to ridge; right chela with only 3 tubercles on opposable margin of fixed finger, second from base largest; corresponding margin of dactyl with row of 6 tubercles; carpus of left cheliped with proximal tubercles on mesial surface very small; ventral surface of merus of right cheliped with 4 tubercles in lateral row and 9 in mesial, left with 4 and 8, respectively; ischium of cheliped lacking tubercles on mesial surface. (See "Measurements.")

Annulus ventralis (Figure 45*k*) deeply embedded in sternum, capable of hingelike motion cephalic to midlength, subovate, broader than long, greatest width about 1.7 times length along median line; cephalomedian part less sclerotized than asymmetrical caudal and lateral parts, with broad caudally flaring trough (supporting dextrally curving low ridge) flanked by low, rounded ridges; caudodextral wall much inflated and rising ventrally above remainder of annulus just posterior to midlength; sinistrocaudal wall somewhat flattened and sloping gradually; sinus originating at caudodextral extremity of cephalomedian trough and, curving around dextrally directed tongue, proceeding gently sinistrocaudally slightly beyond median line before turning caudally in arc, and ending on midcaudal wall. Postannular plate strongly arched cephalically, approximately 2.2 times as broad as median length, and about three-fifths as wide as annulus. First pleopod reaching midlength of annulus when abdomen flexed.

MORPHOTYPIC MALE, FORM II.—Differing from holotype in following respects: rostrum reaching end of penultimate podomere of antennule; branchiostegal spine in form of minute tubercle; cephalic lobe of epistome with paired, slightly asymmetrically arranged, anterolateral prominences; antennal scale with anteromesial border less strongly inclined; mesial margin of palm of right chela with row of 5 tubercles, that of left with 6, more dorsally situated row consisting of 4 on both, several situated dorsolateral to rows; ventral surface of left chela with only 1 tubercle on thickening at base of dactyl, and both right and left with only 1 proximal to it; opposable margin of fixed finger with 5 tubercles on left chela; corresponding margin of dactyl with 6 tubercles on both; dorsomesial tubercle on carpus absent; ventrolateral row of setae on carpus reduced to 2 and ventromesial row to 8; mesial surface of ischium of cheliped devoid of tubercles, hook on ischium of third pereiopod represented by large, low tubercle, and boss on coxa of fourth considerably reduced. (See "Measurements.")

First pleopod (Figure 45*c,e*) reaching third pereiopod when abdomen flexed; central projection contiguous with mesial process basally, both with acute tips, and disposed as in holotype; no trace of subapical notch on central projection; caudal knob not discernible.

COLOR NOTES (Figure 38*b*).—Carapace almost uniformly dark cobalt blue fading slightly ventrally to brighter blue; anteroventral margin from antennal region to cervical groove with narrow cream stripe. Abdomen also dark blue but with paired tan splotches dorsolaterally on third through sixth terga; all pleura pale bluish gray toward borders. Anterior section of telson dark blue basally, with paired sublateral dark blue stripes and similarly colored spots at caudolateral angles, otherwise light blue; uropods pale blue with keels and articulation between proximal and distal parts of lateral ramus darker blue. Antennular and antennal peduncles as well as flagella dark blue. Cheliped dark blue dorsally distal to ischium, major tubercles on merus and carpus white tipped; tubercles on ventral surface of palm at base of dactyl pink; those on opposable margins of fingers entirely white; finger tips and costa cream to pinkish cream. Third maxilliped and remaining pereiopods (distal to ischium) light blue. Ventral surface of body pinkish cream.

TYPES.—The holotypic male, form I, allotype, and morphotypic male, form II (numbers 148348, 148349, and 148350, respectively), are deposited in the National Museum of Natural History,

Measurements (mm)

	Holotype	*Allotype*	*Morphotype*
Carapace			
Height	9.8	11.5	9.1
Width	12.1	13.3	11.4
Entire length	23.8	26.6	22.5
Postorbital length	20.7	23.1	19.7
Areola			
Width	0.2	0.5	0.4
Length	9.2	10.2	8.9
Rostrum			
Width	3.6	4.3	3.6
Length	4.5	4.8	4.0
Chela			
Length of mesial margin of palm	5.4	5.6	4.2
Width of palm	8.5	8.7	7.4
Length of lateral margin	16.5	16.8	13.6
Length of dactyl	10.2	10.5	8.8
Abdomen			
Width	8.9	10.2	8.2
Length	20.4	24.1	19.5

Smithsonian Institution, together with the paratypes, comprising 1♂I, 1♂II, 8♀, 2j♂, and 1j♀.

TYPE-LOCALITY.—Seepage and wooded area adjacent to the National Fish Hatchery at Warm Springs, Meriwether County, Georgia. There shrubs form the understory of a shaded habitat in which *Cornus florida*, *Liriodendron tulipifera*, *Acer* sp., and *Quercus* sp. are conspicuous elements of the flora. The crayfish were dug from complex burrows in a soil rich in humus matted with roots of trees and shrubs. (See "Ecological Notes.")

RANGE.—Known from only two localities in the piedmont section of the Chattahoochee and Flint river basins in Meriwether County, Georgia.

GEORGIA SPECIMENS EXAMINED.—I have examined a total of 16 specimens from the following localities. *Meriwether County*: (1) burrows along trib of Flatshoal Creek, 7.2 mi E of Troup Co line on St Rte 109 and 0.9 mi S on unpaved road (Hart and Hart, 1974:21), 1♂II, 2♀, 1j♂, 20 Apr 1966, E. T. Hall, Jr., HHH, collectors; (2) type-locality, 1♂I, 1♂II, 2♀, 1j♂, 22 Apr 1977, C. E. Carter, J. H. Chandler, Jr., J. E. Pugh, HHH; 1♂I, 5♀, 1j♀, 2-10 May 1977, JHC.

VARIATIONS.—Among the many variations noted in the 16 available specimens of this crayfish are the following: The rostrum is occasionally so broad basally that the rather sudden convergence of the margins at the base of the acumen, described above, is far less pronounced. The suborbital angle, although usually obsolete, is sometimes broadly obtuse. The cephalic lobe of the epistome may have two pairs of subacute prominences, one pair situated posterolaterally and the other anterolaterally, and in some individuals only the latter pair is present. The caudolateral angle of the cephalic section of the telson rarely lacks the more mesial, movable spine. The proximal podomere of the antennule may or may not possess a spine distoventrally, or, if present, may be very small or rather conspicuous. The lamellar part of the antennal scale is often very irregular, marked by rather deep excisions, perhaps resulting from injury. Excluding variations in regenerated chelipeds, the mesial margin of the chela always has two prominent rows of tubercles, the more mesial one consisting of from five to seven, and the other of three to five; in addition, occasionally two other rows of five or six tubercles may be present lateral to the latter mentioned row; the ventral surface of the palm possesses one or two tubercles on the ridge abutting the base of the dactyl and one or two situated proximolateral to it or them; the opposable margin of the fixed finger bears a row of four or five tubercles (third from base largest) but in one of the larger females there are six, one situated distal to the large ventral tubercle; the opposable margin of the dactyl bears a row of five to seven tubercles, of which the third or fourth from base is largest; the proximomesial tubercle on the carpus ranges from well developed to vestigial and is occasionally absent; the ventrolateral row of tubercles on the merus varies from two to five and the ventromesial row from seven to 10; the mesial margin of the ischium may lack or possess one or two very small tubercles. The asymmetrical annulus may be entirely sclerotized and virtually inflexible, or the cephalomedian part may be more membranous and serve as a hinge for a slight deflection (dorsally) of the thickened caudal part. The asymmetry is sometimes reversed from that described for the allotype, and the tongue accordingly directed sinistrally. The surface of the postannular sclerite may be gently rounded or so strongly elevated (ventrally) as to appear tuberculiform.

Size.—The largest specimen available is a female, which has a carapace length of 33.2 (postorbital carapace length 29.2) mm. Corresponding lengths of the two first form males are 23.8 (20.7) and 24.4 (21.4) mm.

Life History Notes.—Collections have been made only during April and May, and first form males were found in both months. Neither ovigerous females nor ones bearing young have been obtained.

Ecological Notes.—*Cambarus (D.) harti* is a primary burrower and has been collected from complex tunnels in a seepage area and in the floodplain of a stream where the water table ranged from the surface of the ground to scarcely more than 50 cm. Each burrow had two to four openings marked by well-defined chimneys, some of which were 10 to 15 cm in height. In the seepage area, there were several often anastomosing horizontal galleries in addition to one or two vertical ones, but where the water table was lower, there were few, if any, horizontal passageways; instead, there were two or three sloping ones from the surface that joined in a single, deep subvertical tunnel, penetrating the water to a depth of at least one meter. Only one crayfish was found in each burrow. The soil in both localities was sandy but rich in organic matter, and roots of the surrounding vegetation provided considerable support for the burrows and greatly hindered tracing the passageways and locating the crayfish. None of the animals could be induced to come to the surface of the water in the burrow, and Mr. Chandler, who sought them at night with the aid of a flashlight, saw none at the mouths of the burrows.

Relationships.—This crayfish is a member of the *latimanus* Group (Bouchard, 1978:44) and appears to have its closest affinities with *C. (D.) cymatilis* and *C. (D.) striatus*. The strong similarity to the former is apparent in features of the rostrum, the narrow, comparatively small abdomen, the conformation of the chela, particularly in the few tubercles on the opposable margin of the fixed finger, the slender hook on the ischium of the third pereiopod of the first form male, and in the structure of the first pleopod, the central projection of which has a well-defined subapical notch (rarely present in *C. (D.) striatus*). In lacking an acute suborbital angle, it resembles most individuals of *C. (D.) striatus*, and the presence of a caudal knob on the first pleopod is also shared with some representatives of the latter species. It may be distinguished readily from *C. (D.) cymatilis* by the premarginal spine on the mesial ramus of the uropod that in the latter projects well beyond the margin. It differs from all specimens of *C. (D.) striatus* that I have examined in its blue coloration and in possessing a row of usually no more than five tubercles (only one exception known) on the opposable margin of the fixed finger of the chela.

GEORGIA CRAYFISH ASSOCIATES.—*Cambarus (D.) latimanus* was found in streams adjacent to the area where *C. (D.) harti* was found in both localities, and *P. (O.) a. acutus* was also present in the creek adjacent to the type-locality.

ETYMOLOGY.—This crayfish is named for my friend and fellow student of entocytherid ostracods, C. W. Hart, Jr., who for more than two decades has assisted me in collecting crayfishes and who has donated many specimens of crayfishes and ostracods to the Smithsonian Institution.

Cambarus (Depressicambarus) latimanus (LeConte)

FIGURES 23*f*, 37*c,d*, 39*e–g*, 46–51, 202

Astacus latimanus LeConte, 1856:402*.—Hagen, 1870:9*, 10*, 79*.

Cambarus latimanus.—Hagen, 1870:78, 80, 82–84*, 98*, 100*, 105–107*, pl. I: figs. 43–46; pl. III: fig. 162.—Cope and Packard, 1881:881*, 882.—Faxon, 1884:144*; 1885a:(63, 69, 159, 167, 173),* pl. II: fig. 3; 1914:395*, 425*.—Underwood, 1886:370*.—Packard, 1888:40*, 41*.—Harris, 1903a:(59, 106, 138, 143, 152)*.—Goodnight, 1941: 72*.—Hobbs, 1942b:14, 20, 21, 158–161*; 1952b:172*; 1958a:74; 1959:897*; 1968a:272*; 1968b:K-16*, fig. 32*j*; 1969b:343.—Hall, 1957:(3–34, 51–53)*, pls. 1, 2, 5, map 1.—Hobbs and Hart, 1959:148*, 151, 159–161, 164, 172*, 185, 186*, 187.—Anonymous, 1967e, tab. 3*; 1969a:C-31*; 1969b:30–33*, 35–38*; 1969c:(61, 65, 66, 72, 74, 77, 82, 85)*; 1970b:(168, 172, 191, 211, 226)*; 1971:(159, 170, 179, 197)*; 1972b:10*; 1972d:81*, 85*, 99*; 1972f:169*, 178*, 179*.—Holt, 1968a:(302, 305, 310, 312)*; 1968b: 26*, 32*.—Boyce, 1969:(1, 6, 7, 73, 74, 76, 83, 85, 88, 89, 90, 92–101, figs. 31–32)*.—Sullivan and Heard, 1969: 307*.—Hobbs and Hall, 1969:286*; 1974:(199, 202, 205, 206)*.—Hart and Hart, 1971:107*, 108*; 1974:(21, 31, 32, 61, 73, 79, 88, 90, 131, 134, 136)*.—Holsinger and Peck, 1971:30*.—Bouchard, 1978:27–29*, 39, 43–44, 46, 47.—Wharton, 1978:(37, 46, 220)*.

Cambarus obesus var. *latimanus*.—Packard, 1880:222.

Cambarus Jordani Faxon, 1884:119–120*, 145* ["Holotype", MCZ 3561 (♂II). Type-locality, Etowah River, Rome, Floyd Co., Georgia.]; 1885a:59, (83, 84, 160, 167, 173, 178)*, pl. 3: fig. 3.—Underwood, 1886:370*.

Cambarus jordani.—Hay, 1899b:959*, 963; 1902a:436–437.—Ortmann, 1902:277; 1931:97*–99, 103*, 104.—Steele, 1902:7.—Harris, 1903a:(59, 106, 144, 152)*.—Faxon, 1914:423*.—Creaser, 1931a:6.—Hobbs, 1956c:115, 120*; 1969a:104*.—Hall, 1959:221.—Anonymous, 1967a, tab. 6*; 1967i, tab. 3*.—Bouchard, 1978:27, 29*.

Cambarus latimus.—Steele, 1902:7 [erroneous spelling].

Cambarus (Bartonius) jordani.—Ortmann, 1905a:118 [by implication], 120, 121*, 130.

Cambarus (Bartonius) latimanus.—Ortmann, 1905a:120, 122*.

Cambarus (Cambarus) latimanus.—Fowler, 1912:341 [by implication].—Ortmann, 1931:124*, 125*.

Cambarus (Cambarus) jordani.—Fowler, 1912:341 [by implication].

Cambarus (Cambarus) extraneus.—Ortmann, 1931:97*, 98*, 104.

Cambarus sp.—Hobbs and Walton, 1960a:18*.—Holsinger and Peck, 1971:30*.—Hart and Hart, 1974:88*, 134*.

Cambarus (Depressicambarus) latimanus.—Hobbs, 1969a:104, 138*, figs. 1f, 8*, 13g, 14g, 18f; 1972b:114*, 146*, figs. 8b, 89o, 90e, 92b, 100b; 1974b:13*, fig. 33.—Hobbs and Hall, 1972:159*.—Holt, 1973a:246, 248*.—Bouchard, 1978:30, 34–37*, fig. 1 l.

Cambarus species F.—Hobbs, 1969a:(104, 136–138, fig. 8).*.

Cambarus (Depressicambarus) jordani.—Hobbs, 1969a:104* [by implication]; 1972b:114*, 146*, figs. 97d, 99d; 1974b:13*, fig. 32.—Hobbs and Hall, 1972:160*, 161.

Cambarus halli.—Hart and Hart, 1971:107*.

Cambarus (Depressicambarus) sp.—Hart and Hart, 1974:(21, 61, 73, 79, 88, 134)*.

Cambarus (Depressicambarus) sp. nov.—Anonymous, 1975a: 142*, 143*, 147.*

The synonomy presented here is believed to be complete only for Georgia.

SUMMARY OF LITERATURE PERTAINING TO GEORGIA.—The earliest record of the occurrence of this crayfish in Georgia was that of LeConte (1856: 402), who described it from "Georgia superiore." In his monograph of the Astacidae, Hagen (1870:

84) cited two specific localities: Athens (Clarke County) and Milledgeville (Baldwin County), and a third locality, Roswell (Fulton County), was added by Faxon (1885a:69). The description of *Cambarus jordani* Faxon (1884:119) was based on a juvenile male, and, as pointed out by Bouchard (1978:29) and below, this crayfish differs in no important respect from *C. (D.) latimanus*. Although the latter was reported to occur in several localities in neighboring states, no additional records or information on it in Georgia were reported for more than 60 years. Between 1950 and 1960, Hobbs (1952b:172) added one locality, Wesleyan College at Rivoli, Bibb County, and he and Hart (1959:186) cited this crayfish from 0.75 mile east of Fort Gaines in Clay County. They indicated that in the lower Flint-Chattahoochee-Apalachicola system, *C. (D.) latimanus*

> ... appears to be confined to the small sand-bottomed tributaries ... flowing in deep shaded ravines. Here they are found in the debris littering the stream beds and in burrows excavated in the banks of the stream. Many of the complex, highly branching burrows have openings above the water level in addition to those in the stream.

They also noted that first form males had been collected in April. Until recently the most outstanding contribution to our knowledge of this species is that of Hall (1957), who summarized previous published data, adding new information on its range and habits. Except for differences in interpretations of the limits of variation (involving the recognition of subspecies), his account of the species in Georgia is still apropos.

During the next decade several additional localities were added: (Anonymous, 1969a, b, c), Hobbs (1968a), Holt (1968a, b), and Sullivan and Heard (1969). Boyce (1969) also conducted a comparative ecological study of *C. (D.) latimanus* and *P. (Pe.) spiculifer* in the Yellow River with emphasis on respiration and tolerance to low oxygen concentrations. He found no significant difference in the respiration rate in the mature males of the two (p. 59), and both occur throughout the basin upstream from the Annistown Bridge.

Until recently I was convinced that the recognition by Hall (1957) of two subspecies of *C. (D.) latimanus* was tenable (Hobbs, 1969a) and referred to that segment of the species occupying the Savannah River Basin as "*Cambarus* species F." Larger series from additional localities have shown that the populations in the basin are highly variable in most respects and should not be recognized as distinct.

Within the current decade, an additional 38 localities were cited for this crayfish: Anonymous (1971, 1972b, d, f), Hobbs and Hall (1972), and Hart and Hart (1974). On the basis of my erroneous identifications of a female and juvenile male, Holsinger and Peck (1971:30) reported this species from Byers and Hurricane caves in Dade County. Both specimens should be referred to *C. striatus*.

Despite the comparatively large list of references cited in the above synonomy, our understanding of this crayfish is still limited. The contributions of Holt and of Hart and Hart are primarily concerned with the commensal branchiobdellids and entocytherids, respectively, providing no data other than localities where this crayfish serves as host to one or more of these animals. As indicated above, among the most valuable contributions was that of Hall (1957). The anonymous references consist of reports of water quality surveys, and in them, not only are there a number of new localities cited, but also the physical and chemical data provided for the stations investigated broaden our appreciation of the habitats exploited by *Cambarus (D.) latimanus*. In his review of the subgenus *Depressicambarus*, Bouchard (1978) presented a detailed description and illustrations of topotypes; a discussion of its range and variations precede a brief statement of size and notes on its life history. The remaining references—the early ones largely repetitious—are concerned with relationships or the distribution of the species.

Diagnosis.—Eyes of moderate size. Rostrum with or without marginal spines and almost always lacking median carina. Carapace usually with cervical spine or tubercle. Areola 3.4 to 10.0 (average 6.3) times as long as broad, constituting 30.1 to 37.1 (average 34.3) percent of entire length

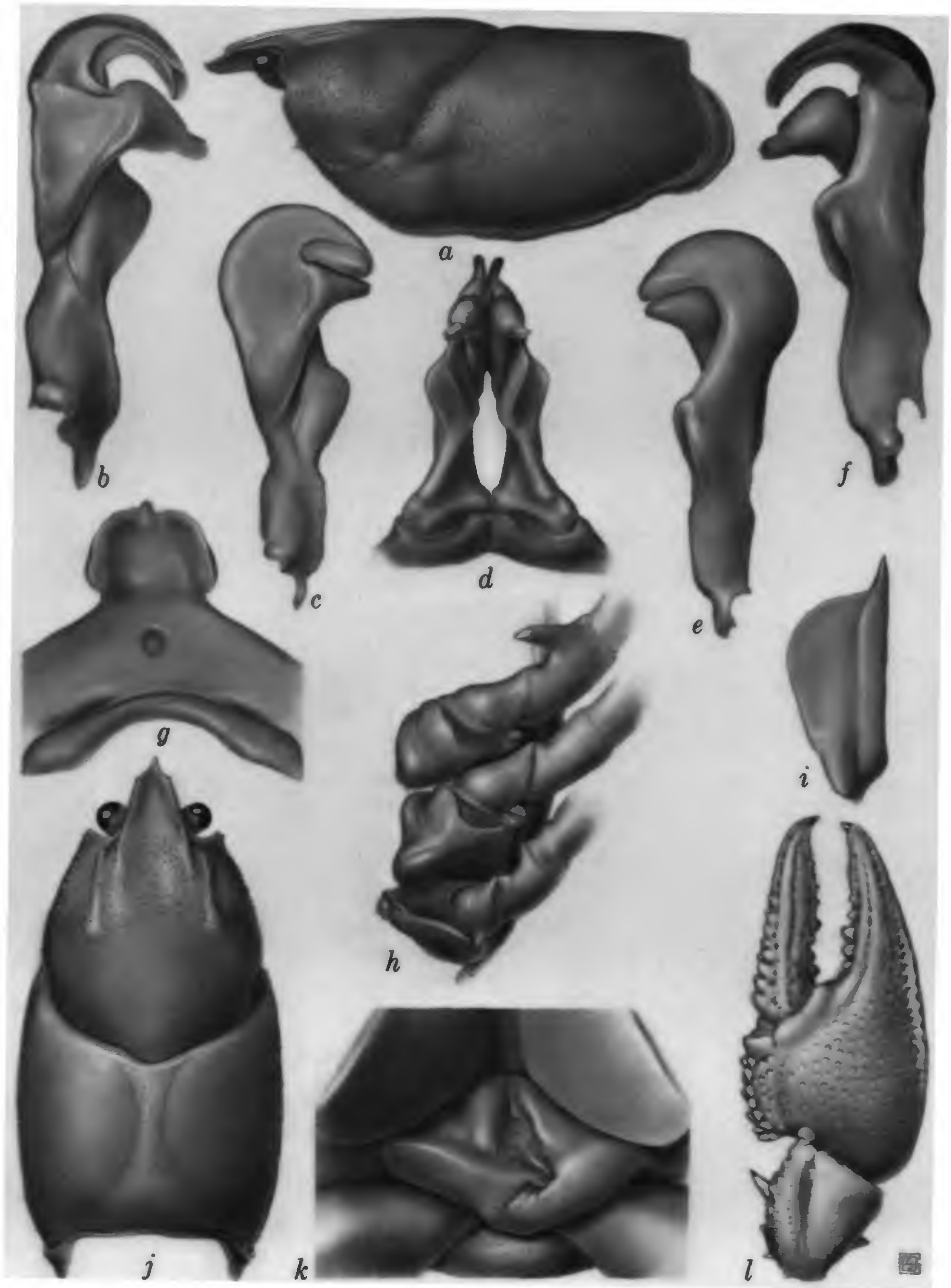


FIGURE 46.—*Cambarus (Depressicambarus) latimanus* from Athens, Clarke County, Georgia (all from male, form I, except *c*, *e*, from male, form II, and *k*, from female): *a*, lateral view of carapace; *b*, *c*, mesial view of first pleopod; *d*, caudal view of first pleopods; *e*, *f*, lateral view of first pleopod; *g*, epistome; *h*, basal podomeres of third, fourth, and fifth pereiopods; *i*, antennal scale; *j*, dorsal view of carapace; *k*, annulus ventralis; *l*, dorsal view of distal podomeres of cheliped.

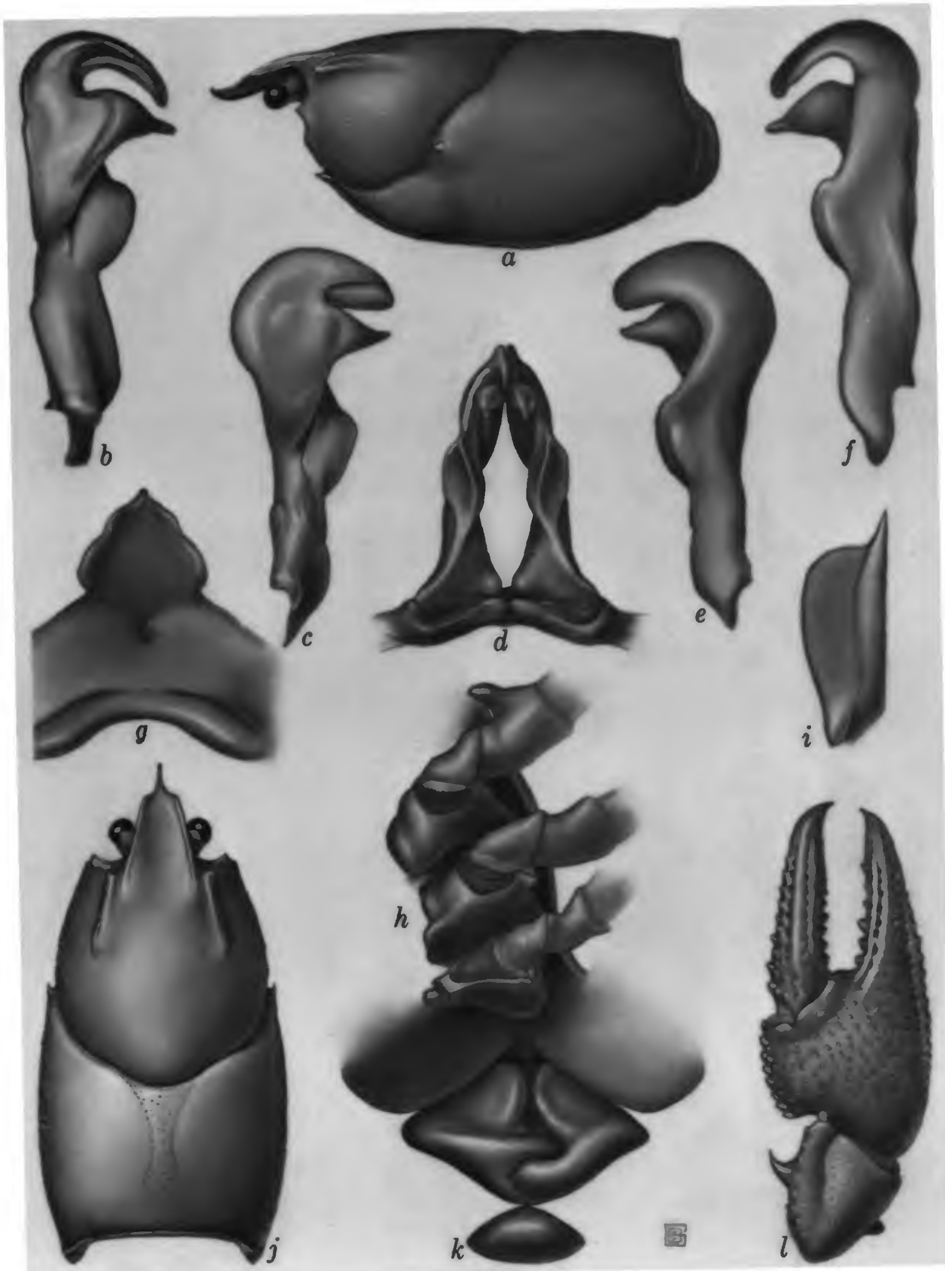


FIGURE 47.—*Cambarus (D.) latimanus* from tributary to Ohatchee Creek 4.3 mi W of jct of US Hwy 431 and St Rte 62, Calhoun Co, Alabama (all from male, form I, except *c*, *e*, from male, form II, and *k*, from female; these specimens are rather typical of adult individuals formerly referred to *Cambarus jordani* Faxon): *a*, lateral view of carapace; *b*, *c*, mesial view of first pleopod; *d*, caudal view of first pleopods; *e*,*f*, lateral view of first pleopod; *g*, epistome; *h*, basal podomeres of third, fourth, and fifth pereiopods; *i*, antennal scale; *j*, dorsal view of carapace; *k*, annulus ventralis; *l*, dorsal view of distal podomeres of cheliped.

of carapace, and 38.2 to 44.9 (average 41.4) percent of postorbital carapace length, with 2 to 6 punctations across narrowest part. Suborbital angle obtuse to obsolete (rarely subacute). Postorbital ridge terminating cephalically in spine, more frequently in tubercle, or merging almost imperceptibly with cephalic area of carapace. Antennal scale approximately 2.5 times as long as broad, broadest distal to midlength. Palm of chela with 5 to 9 (usually 7) tubercles in mesialmost row, squamous tubercles scattered over at least mesial half of dorsal surface of palm, frequently over entire surface. First pleopod of first form male with moderately long to short terminal elements; central projection very variable, strongly arched or bent at angle only slightly greater than 90 degrees, usually tapering and with or without subapical notch; mesial process likewise markedly variable, usually inflated, truncate or tapering distally, occasionally overreaching distal extremity of central projection; caudal knob rarely present even as vestige. Color olive gray to orange tan; abdominal terga frequently with longitudinal stripes. Female with first pleopod present.

Color Notes (Figure 37*c,d*).—(Two phases: 1, dark olive and greenish gray; 2, brownish olive and orange tan; latter described here). Cephalic region of carapace olive with lighter olive tan dorsomedian area sharply delimited laterally by darker olive dorsolateral area; latter continuing caudally on branchiostegite to caudal margin of carapace; margins of rostrum and postorbital ridges pale tan; hepatic region with reticulate pattern of dark brown on olive; mottled pattern of similar colors overlying mandibular adductor region and continuing mesially in band along cephalic side of cervical groove, flanking caudal margin of submedian pale shield in caudomedian gastric region; thoracic region pale tan dorsally with irregular dark brown splotches on dorsolateral part of branchiostegites, latter somewhat concentrated in paired longitudinal bands; lateral surface of carapace fading to pale tan ventrally. Ground color of abdomen dark olive; terga with paired dorsolateral very dark brown spots, latter conspicuous on first three terga, becoming progressively smaller and less obvious on caudal ones; pleura with similarly colored ventrally convex markings at bases and with ventral portions pale tan to cream; caudolateral margin of sixth abdominal pleuron dark brown. Telson and uropods somewhat mottled, former frequently with lateral margins of cephalic section dark brown. Cheliped distal to midlength of merus with dorsal surface very dark olive and bearing tan to cream spines, tubercles, and knobs; lateral costa of propodus also light in color. Remaining pereiopods with dark olive mottlings on cream background proximally and on olive tan distal to midlength of merus.

Occasional individuals occur from almost all parts of the range in Georgia in which the dark spots of the carapace and abdomen are sufficiently large to fuse, forming broad longitudinal stripes extending from the cervical groove caudally almost to the base of the telson (Figure 37*d*). This striped pattern has been observed more frequently in the Savannah Basin than elsewhere. Other specimens have been collected that are virtually concolorous; usually, these are individuals that were found on a light sandy substrate and adapted to a light background.

Boyce (1969:83) also noted two color patterns indicating that both occur in males and females.

Types.—Syntypes, MCZ 3378 (♂I dry), ANSP 329 (♀).

Type-Locality.—Athens, Clarke County, Georgia (by subsequent restriction, see below). LeConte (1856:402) listed a single source, "Georgia superiore," for the specimens that were available to him. A no more precise locality was suggested until 1914 when Faxon (p. 395), in mentioning a collection of 19 specimens from Athens, stated: "These are essentially paratypes, and are of interest as fixing the type locality, Athens, Ga. which was not specified in LeConte's original description of the species nor on the labels accompanying the type specimens in Cambridge and Philadelphia." In the same publication (p. 425) he cited the type-locality as "Athens, Clarke Co., Georgia."

Range.—Piedmont and coastal plain from the Tar and Cape Fear basins in North Carolina southward to the Altamaha and Apalachicola basins in Georgia and Florida, westward to the Coosa Basin in Alabama.

In Georgia (Figure 48), it occurs in most of the counties upstream from and along the southern flank of the fall line. Only in Bulloch, Effingham, and Jenkins counties (along the Ogeechee and Savannah rivers), Pulaski County (along the Ocmulgee River), and Clay, Quitman, Randolph, and Stewart counties (along the Chattahoochee River) is it known to invade far into the coastal plain. In the Chattahoochee drainage system, its range, although apparently interrupted in southwestern Georgia, extends southward into the Florida panhandle (Hobbs, 1942b:159). Considerable field work in northwestern Georgia failed to reveal its presence in the Tennessee Basin except in tributaries of the Hiwassee River. Most surprising was my failure to find it in so much of the Conasauga drainage system, particularly in view of the occurrence of an apparently large population in Minnewauga Creek, a tributary stream in Polk County, Tennessee, that was sampled by R. W. Bouchard.

GEORGIA SPECIMENS EXAMINED.—I have examined 2424 specimens from approximately 400 localities (Figure 48).

VARIATIONS.—*Cambarus (D.) latimanus* is one of the most variable crayfishes in the state. Almost every characteristic that has been evaluated has a broader range of variability than has been noted in other species; furthermore, few of the variations can be correlated with a restricted part of the range within the state. The unusual lack of stability is clearly evidenced in the illustrations of the first pleopods of the first form male (Figures 49, 50). Most noticeable perhaps are the differences existing in the central projection. A long, strongly recurved element lacking a subapical notch seems to be typical of those populations occurring in the Hiwassee drainage system and in the Coosawattee segment of the Coosa Basin, but, elsewhere in the latter, the projection is less strongly recurved and not infrequently possesses a subterminal notch that is usually shallow. Similar to the appendage characteristic of populations in the Hiwassee and Coosawattee basins are those of members of the species occurring in the Flint, Chattahoochee, Ocmulgee, and Oconee drainage systems and of some individuals in the Tallapoosa. Generally, in rather marked contrast, the corresponding pleopods of individuals in the Ogeechee and Savannah basins possess a shorter central projection that is not so strongly recurved (the tip rarely reaching proximally beyond the level of the distal margin of the base of the mesial process) and almost invariably provided with a distinct subapical notch. The extreme variation of this type of central projection occurs in the Broad River in Banks and Madison counties, but downstream, in particular, and elsewhere in tributaries of the Savannah and Ogeechee, the subapical notch is less distinct and the element is longer. Throughout most of the range of the species within the state, the caudal knob is not recognizable; however, it is moderately prominent in four individuals from one locality each in Bartow (Figure 49*h*), Pickens (Figure 49*i*), Polk (Figure 49*j*) and Douglas (Figure 49*s*) counties (Coosa and Chattahoochee basins). The most heavily ornamented mesial process occurs in individuals in the Chattahoochee Basin.

Among the most conspicuous variations noted are those of the rostrum. In most populations, the smaller juvenile members possess marginal spines that, as the individual increases in size, seem progressively, with each molt, to become more atrophied until in the adult there is little or no trace of their earlier presence. In some isolated individuals this juvenile trait is retained in the form of marginal tubercles that may or may not be acute. In some populations, virtually all of the members have such tubercles or at least distinct angles at the base of the acumen (Figures 47*a,j*, 51*a,c,e*); this is the variant that was described by Faxon (1884:119) as *Cambarus Jordani*. In a few localities in Georgia, for example, 5.5 miles northeast of Molena on U.S. Highway 18, Pike County, and 6.5 miles south of the Chattahoochee River on U.S. Highway 219, and in several localities in the Oconee Basin, no marginal spines or tubercles occur on the rostra of even the smallest individuals (see Hall, 1957:18 and Hobbs, 1958a:74).

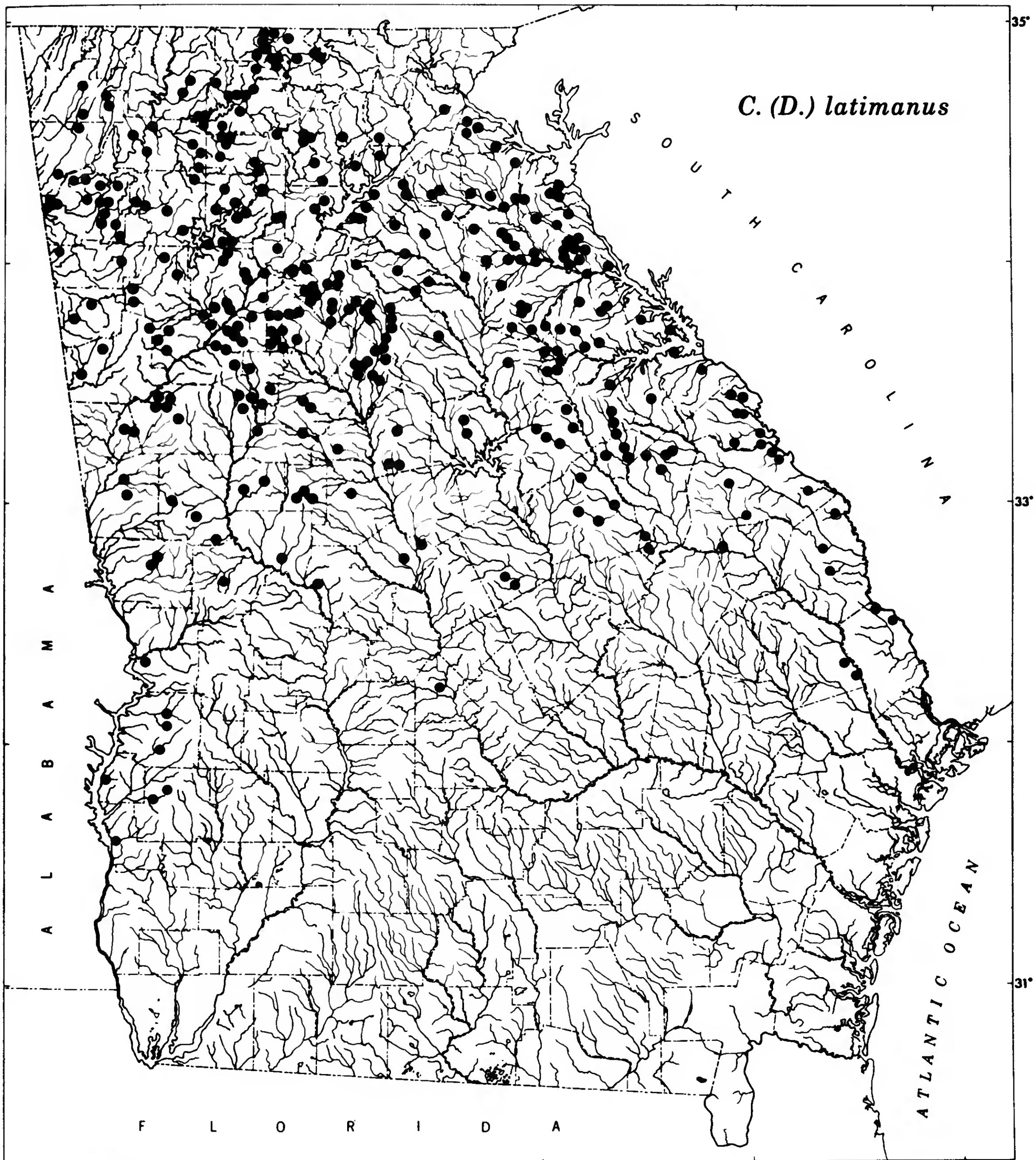


FIGURE 48.—Distribution of *Cambarus (D.) latimanus* in Georgia.

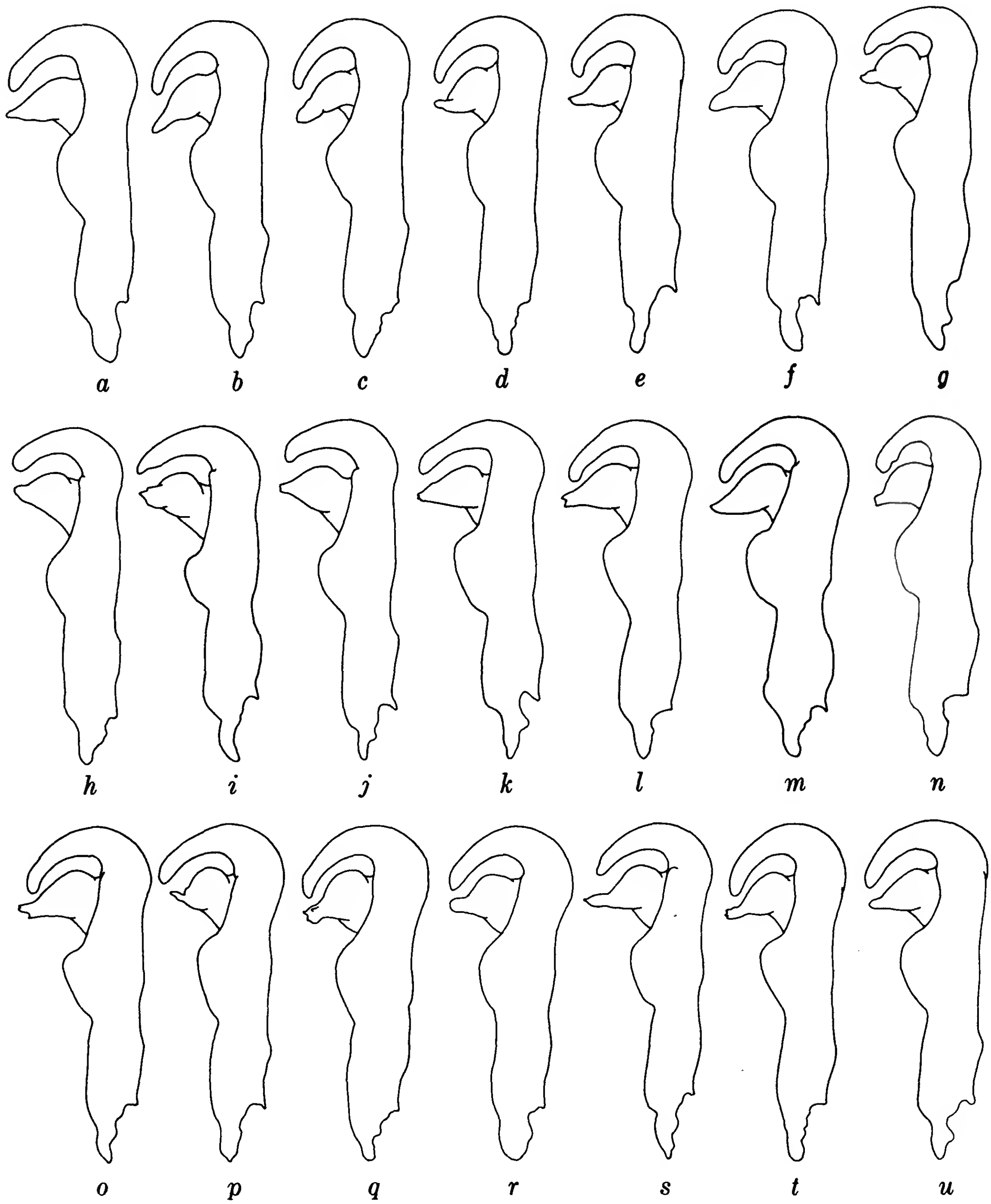


FIGURE 49.—*Cambarus (D.) latimanus*, lateral view of left first pleopod of male, form I. Hiwassee Basin: *a*, *b*, Fannin Co. Coosa Basin: *c–e*, Gilmer Co; *f*, Chattooga Co; *g*, Cherokee Co; *h*, Bartow Co; *i*, Pickens Co; *j*, Polk Co. Tallapoosa Basin: *k*, *l*, Paulding Co; *m*, *n*, Carroll Co. Chattahoochee Basin: *o*, Fulton Co; *p*, Decatur Co; *q*, *r*, De Kalb Co; *s*, *t*, Douglas Co; *u*, Stewart Co.

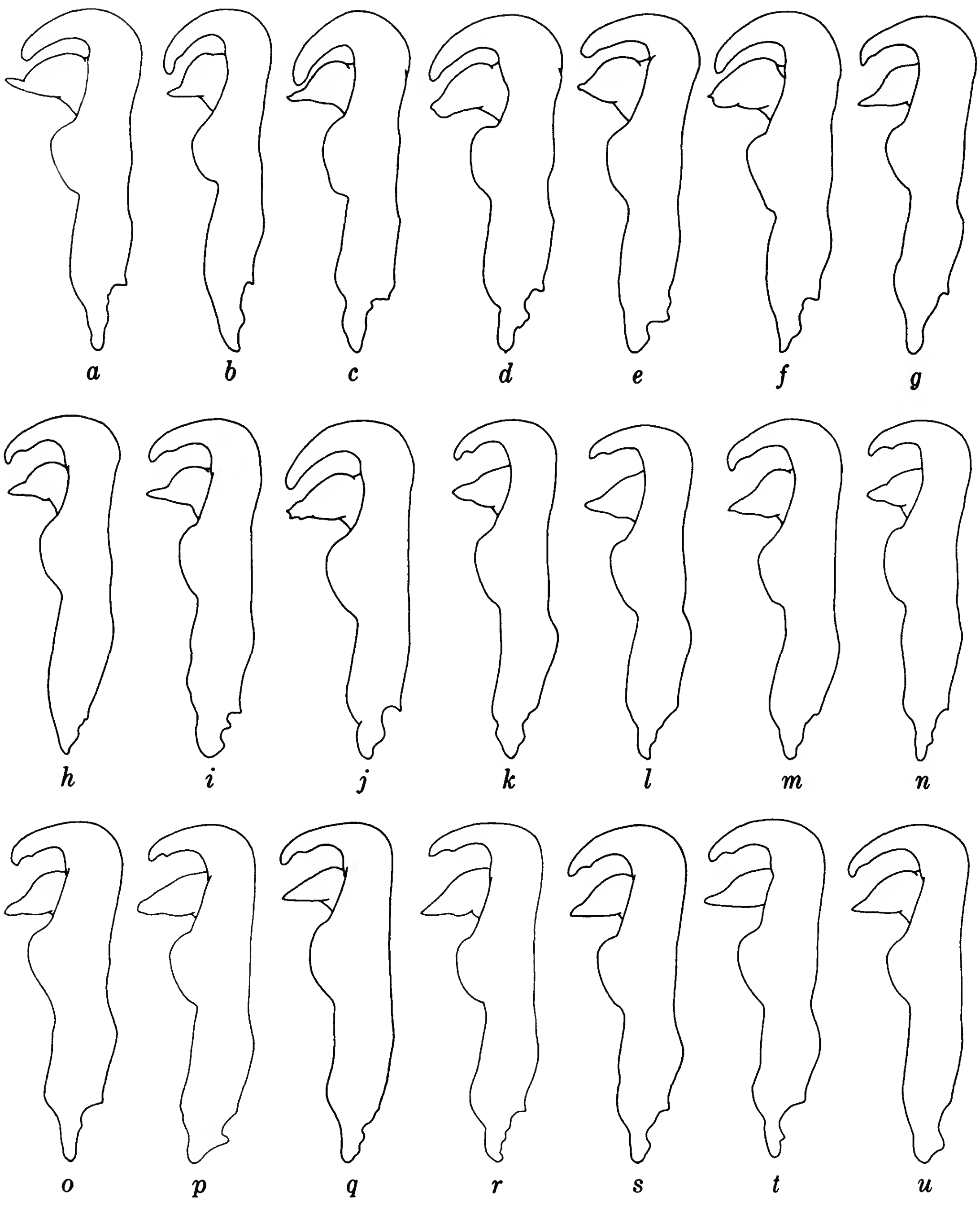


FIGURE 50.—*Cambarus (D.) latimanus*, lateral view of left first pleopod of male, form I. Flint Basin: *a*, Fulton Co; *b*, Talbot Co. Ocmulgee Basin: *c*, *d*, Bibb Co; *e*, Walton Co. Altamaha Basin: *f*, Clarke Co. Ogeechee Basin: *g*, Warren Co; *h*, Hancock Co; *i*, Jenkins Co. Savannah Basin: *j*, *n–p*, Madison Co; *k*, *l*, Banks Co; *m*, Hart Co; *q*, *r*, Elbert Co; *s*, Greene Co; *t*, Taliaferro Co; *u*, Richmond Co.

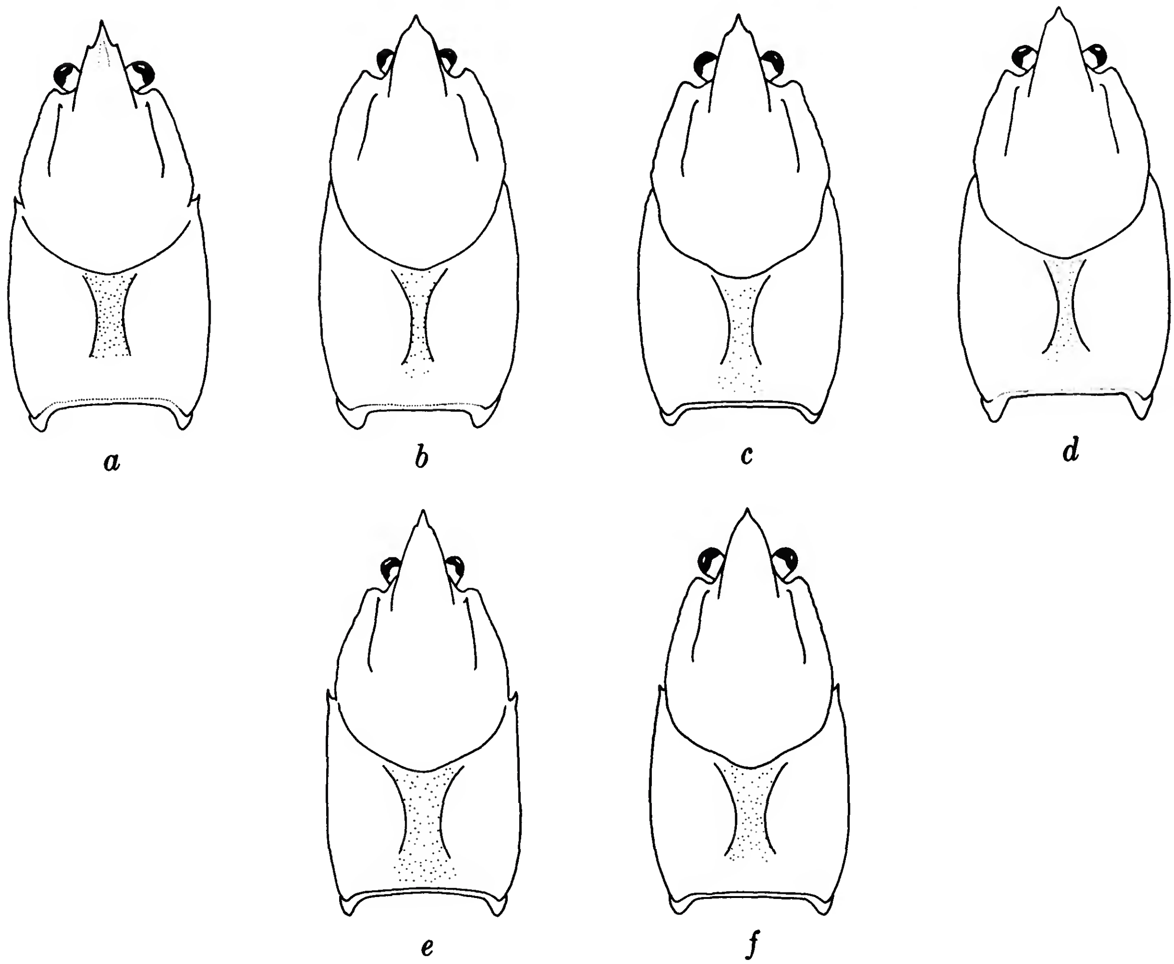


FIGURE 51.—*Cambarus (D.) latimanus*, dorsal view of carapace of male, form I. Coosa Basin: *a*, Lumpkin Co. Tallapoosa Basin: *b*, Carroll Co. Chattahoochee Basin: *c*, Carroll Co. Oconee Basin: *d*, Clarke Co. Savannah Basin: *e*, Stephens Co; *f*, Madison Co.

Occasionally there is a weak median carina on the rostrum, but typically the upper surface is shallowly to moderately deeply concave.

Cervical spines are frequently present, particularly well developed in small individuals, and often accompanying them are spines on the postorbital ridges. Such spines are conspicuous in many adult specimens from the Broad River and adjacent smaller tributaries to the Savannah. Elsewhere they are less well developed in adults, sometimes reduced to tubercles, and in occasional individuals, there is not a trace of either cervical or postorbital spines. The suborbital angle is usually broadly obtuse to obsolete, but infrequently it is subacute.

Some populations in the streams just mentioned possess an areola that is decidedly broad, the width constituting as much as one-third the total length, and the narrowest observed in crayfishes frequenting these tributaries of the Savannah is 8.8 times as broad as long; the average there is 4.7 as compared with 7.2 elsewhere in Georgia, where the ratio of length to width of the areola ranges from 4.1 to 10.0 although seldom greater than 9.4.

While the spines and tubercles on the chelipeds do not exhibit marked variation, there are differences in the actual numbers and in their size. As indicated in the "Diagnosis," for example, the number of tubercles in the mesialmost row on the palm varies from five to nine; similarly the adjacent row consists of four to eight.

Finally, variations in color patterns are noted in "Color Notes."

Size.—The largest specimen available from Georgia is a female from the Chattahoochee River drainage in Fulton County, which has a carapace length of 52.9 (postorbital carapace length 44.7) mm. The smallest and largest first form males have corresponding lengths of 29.5 (24.6) and 40.9 (35.0) mm, respectively.

Life History Notes.—As indicated in the accompanying summary of specimens examined, first form males have been found from September to June except during February when no collections have been made. I have no records of ovigerous females or of those carrying young anywhere within its range; however, Bouchard (1978: 37) reported that he had collected three ovigerous females in Alabama and North Carolina during April. The paucity of such females in collections almost certainly reflects inadequate sampling of burrows in the banks of streams. On the basis of size distribution in several populations represented in collections, most consist of three generations, although a few individuals may attain an age such that a fourth generation appears to be present in small numbers. Despite the suggestion that in the Yellow River (Ocmulgee-Altamaha Basin) the young are produced primarily in the fall (Boyce, 1969:94), its life history is probably markedly similar to that of *Cambarus (H.) longulus* (see Smart, 1962).

Seasonal Data

Sex/stage	*J*	*F*	*M*	*A*	*M*	*J*	*J*	*A*	*S*	*O*	*N*	*D*	*?*
♂I	2		4	27	9	6			4	10	4	1	2
♂II	1		24	107	52	40	12	26	26	30	11	1	13
♀	14		40	162	51	63	17	32	31	30	23	2	12
♂j	3		50	362	84	56	16	38	35	54	13		4
♀j	1		46	421	114	67	19	44	21	51	26	1	9

Ecological Notes.—Matching the marked anatomical variability of this crayfish is its apparently broad ecological tolerance. It has been found in all of the major physiographic provinces of the state except on the Appalachian Plateau but is most abundant in the Piedmont Province, where it occurs in a variety of streams and in burrows. Within this province, it is encountered most frequently in small to moderately large creeks but it does not shun the marginal zones of the larger rivers, where it lives among exposed roots and in burrows along the banks. Streams with clay beds seem to support larger populations than do those composed largely of sand, silt, or bedrock, but the substrate seems not to affect its presence or absence. In the smaller streams, the adults and subadults occur in greatest numbers in rock-littered pools and massive collections of debris, but they are also found at least in the marginal sections of riffle areas. Even in segments of streams where adequate cover exists in the form of debris or rocks scattered over the stream bed, many if not most of the larger members of the population seem to seek shelter in complex burrows in the stream banks. Excavations of a number of such galleries have been attempted, and while there is little uniformity in them, usually there occurs a maze of frequently anastomosing flooded passageways leading into the bank from one or more openings on a level just below the mean water level; several branches may extend above the water and at least one descends 0.3 meter or more. One of those that extends upward sometimes has one or more openings 0.3 to 1 meter above the surface of the water. Needless to comment, this crayfish has not been taken in numbers from such burrows; however, many individuals with their chelae extended have been observed at the opening just beneath the surface of the water. The young crayfish frequent accumulations of tree litter in pools or eddies, or, where aquatic vegetation is present, they seek cover among the matted plants or in the debris caught among roots and stems.

Whether or not the water is clear seems to have little influence on the presence of this crayfish, and there is evidence that it is resistant in the Atlanta area to at least moderate pollution (Anonymous, 1969c). Hobbs and Hall (1974) summarized available information on the tolerance of this crayfish to certain pollutants and deficiencies that are briefly noted in the following paragraph.

According to Hale (1969), the mean minimal tolerance to oxygen by this crayfish is 0.26 mg/l (his *Cambarus diogenes diogenes* proved to be *Cambarus* (*D.*) *latimanus*) and Boyce (1969) found that it died at concentrations ranging from 0.75 to 1.40 mg/l. In a stream in Gordon County, the oxygen concentration was 7.2 to 7.6 mg/l, *C.* (*D.*) *latimanus* occurring abundantly, but in an otherwise similar tributary in which the concentration was 0.3 to 1.5 mg/l, no crayfish were found (Anonymous, 1971). The only data on its tolerance to lowered pH are those obtained in a segment of a stream in Barrow County subjected to an effluent containing H_2SO_4. In three stations the pH value ranged from 3.1 to 3.7, 4.3 to 5.6, and 6.2 to 7.2. Only in the latter was *C.* (*D.*) *latimanus* present (Anonymous, 1971).

On a few occasions, I have dug individuals from shallow, branching burrows in seepage areas. There the burrows lacked chimneys or the latter were poorly fashioned. In the flood plains of rivers and larger creeks, specimens have been taken from isolated pools, and that individuals wander over the surface of the ground during the evening or night is confirmed by their having been caught along the Alcovy River floodplain in Newton County off U.S. Highway 278 in traps set for small mammals by C. H. Wharton. These traps consist of cans opened at one end and buried with the open end flush with the ground.

Boyce (1969) stated that in the Yellow River (Ocmulgee-Altamaha Basin) this crayfish is a detritus feeder and facultative predator and that it becomes relatively inactive during December, January, and February.

Georgia Crayfish Associates.—Further evidence of the broad ecological tolerance of this crayfish is the observation that the number of its associates exceeds that of any other crayfish in the state (the number of times they have been found together is indicated in parentheses): *Cambarus (C.) bartonii* (25), *C. (C.) howardi* (4), *C. (D.) englishi* (1), *C. (D.) halli* (3), *C. (D.) harti* (2), *C. (D.) reflexus* (4), *C. (D.) striatus* (20), *C. (D.) strigosus* (1), *C. (H.) coosawattae* (5), *C. (H.) fasciatus* (11), *C. (H.) girardianus* (2), *C. (H.) speciosus* (4), *C. (J.) conasaugaensis* (13), *C. (L.) acanthura* (10), *C. (L.) diogenes diogenes* (4), *C. (P.) coosae* (28), *C. (P.) scotti* (6), *Faxonella clypeata* (4), *Orconectes erichsonianus* (9), *O. spinosus* (4), *Procambarus (D.) devexus* (2), *P. (L.) barbatus* (1), *P. (O.) acutus acutus* (6), *P. (O.) enoplosternum* (4), *P. (O.) pubescens* (41), *P. (Pe.) gibbus* (2), *P. (Pe.) petersi* (9), *P. (Pe.) raneyi* (35), *P. (Pe.) spiculifer* (127), *P. (Pe.) versutus* (1), *P. (S.) howellae* (1), *P. (S.) paeninsulanus* (1), and *P. (S.) troglodytes* (3).

Cambarus (Depressicambarus) reflexus, new species

Figures 23*c*, 38*a*, 39*h*, 52, 53, 203

Cambarus (*Depressicambarus*) sp.—Hobbs III, Thorp, and Anderson, 1976:2, 5, 11, 20–21.

The single reference to this crayfish consists of a diagnosis, color notes, a statement of its occurrence in Burke and Effingham counties, Georgia, and Allendale and Barnwell counties, South Carolina, and ecological and life history notes; the diagnosis and life history notes were made available to the authors from an early draft of this report.

Diagnosis.—Eyes small. Rostrum without marginal spines or tubercles and lacking median carina. Carapace with cervical tubercles only slightly larger than others nearby. Areola linear to 31 times as long as broad, constituting, in adults, 40.4 to 43.9 (average 41.7) percent of entire length of carapace (45.3 to 49.1, average 46.8, percent of postorbital carapace length), and never with more than 1 punctation in narrowest part. Suborbital angle broadly obtuse to obsolete. Postorbital ridge terminating cephalically without spine or tubercle. Antennal scale about 3 times as long as broad, widest at or slightly distal to midlength. Palm of chela with 6 or 7 (rarely 8) tubercles in mesialmost row. First pleopod of first form male with short, strongly arched central projection, its tip directed proximally, flanked by adjacent subapical notch; mesial process inflated but with slender apical portion; caudal knob well defined. Mesial ramus of uropod with spine at end of median ridge not reaching distal margin of ramus. Color reddish-orange tan or blue; abdominal terga without stripes or bands. Female with first pleopod present.

HOLOTYPIC MALE, FORM I.—Body subovate, compressed (Figure 52*a,j*). Abdomen narrower than cephalothorax (13.3 and 19.1 mm); maximum width of carapace greater than depth at caudodorsal margin of cervical groove (about 19, injury prevents accurate measurements, and 17.3 mm, respectively). Areola 41 times as long as broad with 1 punctation in narrowest part; length 43.9 percent of total length of carapace (49.1 percent of postorbital carapace length). Rostrum with convergent, slightly thickened margins, contracted suddenly at base of short triangular acumen, latter reaching midlength of penultimate podomere of antennular peduncle; dorsal surface of rostrum deeply concave with comparatively few punctations, more prominent ones caudally situated. Subrostral ridge weak and evident in dorsal aspect only along basal portion of rostrum. Postorbital ridge rather weak, truncate cephalically and prominently swollen caudally. Suborbital angle very broadly obtuse and little prominent; branchiostegal spine small and tuberculiform. Cervical spines represented by 2 small tubercles no larger than those in hepatic region. Carapace punctate dorsally and granulate to tuberculate laterally, tubercles most prominent in anteroventral branchiostegal region and in hepatic region. Abdomen shorter than carapace (34.1 and 37.4 mm), pleura short, truncate ventrally and angular caudoventrally (Figure 39*h*). Cephalic section of telson with 2 spines in each caudolateral corner. Proximal podomere of uropod lacking spines; mesial ramus of uropod with well-defined submedian ridge terminating in short premarginal spine.

Cephalomedian lobe of epistome (Figure 52*g*) subtrapezoidal, narrow, and with prominent anteromedian projection; margins slightly thickened basally and elevated ventrally; main body with conspicuous submedian fovea; epistomal zygoma strongly arched. Ventral surface of proximal podomere of antennular peduncle with small subacute premarginal tubercle. Antennal peduncle without spines; flagellum reaching base of telson; antennal scale (Figure 52*i*) 2.8 times as long as broad, widest near midlength, mesial border forming broad arc rather suddenly curved across base of distal fifth, distal spine almost reaching base of ultimate podomere of antennular peduncle. Mesial half of ventral surface of ischium of third maxilliped studded with irregular rows of long stiff setae and with submarginal lateral row of much smaller ones; distolateral angle acute.

Right chela (Figure 52*l*) 2.3 times as long as broad, mesial margin of palm occupying about one-third of its length. Mesial surface of palm with 2 well-defined rows of tubercles, mesialmost of 8 (left with 7) and adjacent one of 7; 2 additional tubercles present adjacent to rows ventrally, and dorsomesial half of palm with number of squamous tubercles decreasing in size laterally; lateral half of dorsal surface of propodus punctate, those flanking costa and on basal half of finger large and deep; ventral surface of median portion of palm tuberculate and 2 large tubercles present on marginal thickening opposite base of dactyl. Both fingers of chela with well-defined submedian longitudinal ridges dorsally and ventrally; opposable margin of fixed finger with row of 10 tubercles (left with 12), fourth from base largest, extending along almost entire length of finger; additional tubercle present on lower level slightly proximal to base of distal fourth of finger; opposable margin of dactyl with row of 12 tubercles (first and fourth from base larger than others) along proximal four-fifths of finger; narrow row of minute denticles between and distal to tubercles along distal half of both fingers; mesial surface of dactyl with cluster of large tubercles in basal fourth produced in single row, decreasing in size distally, to base of distal sixth of finger; punctations continuing distally.

Carpus of cheliped with distinct oblique furrow dorsally, flanked by setiferous punctations; mesial surface with 1 moderately large tubercle near base of distal fourth and several very small ones proximal to it; ventral surface punctate and bear-

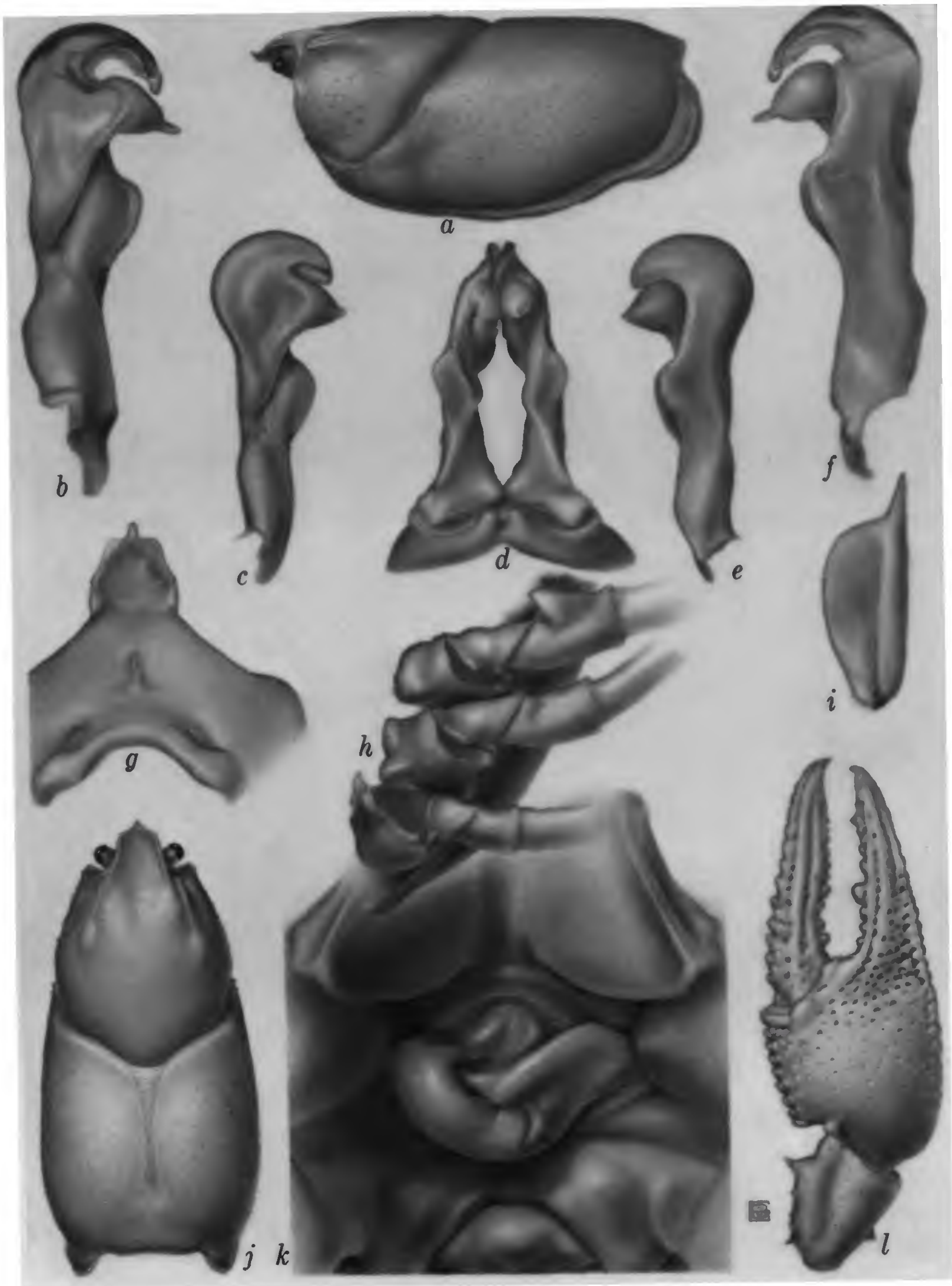


FIGURE 52.—*Cambarus* (*Depressicambarus*) *reflexus* (all from holotype except *c*, *e*, from morphotype and *k*, from allotype): *a*, lateral view of carapace; *b*, *c*, mesial view of first pleopod; *d*, caudal view of first pleopods; *e*, *f*, lateral view of first pleopod; *g*, epistome; *h*, basal podomeres of third, fourth, and fifth pereiopods; *i*, antennal scale; *j*, dorsal view of carapace; *k*, annulus ventralis; *l*, dorsal view of distal podomeres of cheliped. (Injuries on carapace in *a* and *j* omitted from illustrations.)

ing usual 2 large marginal tubercles distally. Merus with 2 premarginal tubercles dorsally, ventrolateral row of 5 tubercles and ventromesial one of 10 (left with 11); podomere otherwise polished and/or sparsely punctate. Ventromesial margin of ischium with row of 3 (left with 2) small tubercles.

Ischium of third pereiopod with simple hook extending proximally over basioischial articulation (Figure 52*h*), hook not opposed by tubercle on basis. Coxa of fourth pereiopod with obliquely vertically disposed caudomesial boss; that of fifth pereiopod lacking boss but with ventral membrane bearing scattered setae.

First pleopod (Figure 52*b,d,f*) reaching coxa of third pereiopod; central projection short, strongly recurved with tip directed proximally and bearing subapical notch; mesial process inflated, bent caudally at slightly more than 90 degrees, and with apical region suddenly and conspicuously slenderer than bulbous proximal part; caudal knob prominent.

ALLOTYPIC FEMALE.—Differing from holotype in following respects: rostrum almost reaching distal margin of penultimate podomere of antennular peduncle; suborbital angle very weak; both lobes of basal podomere of right uropod with spine; spine on antennal scale reaching base of ultimate podomere of antennular peduncle; right chela 1.9 times as long as broad; mesial surface of palm with 2 rows of 6 tubercles each; opposable margin of fixed finger with row of 7 (6 on left) tubercles, that of dactyl with 11 (10 on left); carpus with 1 or 2 major tubercles on mesial surface; merus with ventrolateral row of 5 (4 on left) and ventromesial row of 9 (10); mesial margin of ischium with 4 (3). (See "Measurements.")

Annulus ventralis (Figure 52*k*) about 1.5 times as long as broad, strongly asymmetrical, and with small cephalic region distinctly less calcified than caudal, permitting hinge action across junction of 2 areas; cephalic semimembranous area with submedian trough, caudal portion of latter curved dextrally and disappearing with tongue beneath high dextral wall; sinus originating there, and, following elongate tilted S-shaped curve, ending on caudal wall sinistral to median line. Heavy caudodextral wall strongly convex ventrally as well as caudally; sinistral wall less inflated and concave. Postannular sclerite 2.6 times as broad as long, its width subequal to length of annulus and about two-thirds as wide, otherwise unremarkable. First pleopod reaching midlength of annulus when abdomen flexed.

MORPHOTYPIC MALE, FORM II.—Differing from holotype in following respects: areola reduced to line along midlength with no punctations in narrowest part; pleura of abdominal segments rounded caudoventrally; antennal scale broadest distal to midlength; cephalic lobe of epistome without cephalomedian projection, and slightly broader; ischium of third maxilliped truncate distolaterally; right chela (left regenerated) with mesial surface of palm bearing 6 tubercles in mesialmost row and 5 in flanking row; opposable margin of fixed finger with row of only 7 tubercles, that of dactyl with 9. Hook on ischium of third pereiopod much reduced, not reaching basioischial articulation; boss on coxa of fourth pereiopod also much reduced. (See "Measurements.")

First pleopod (Figure 52*c,e*) differing from that of holotype chiefly in noncorneous texture and expanded central projection being contiguous with mesial process throughout most of its length, in less attenuate distal portion of mesial process, and in lacking caudal knob.

COLOR NOTES (Figure 38*a*).—Ground color of dorsum and hepatic region of carapace reddish-orange tan; margins of rostrum and postorbital ridges lacking tan suffusion; tubercles in hepatic region very pale orange, and branchiostegites pinkish cream laterally; no distinct markings on carapace although dark reddish brown in small areas at junction of branchiocardiac and cervical grooves. Abdomen with cephalic section of tergum of first segment almost black and caudal section very dark but diluted with red; terga of following segments progressively lighter although little different in color from fifth and sixth, all with narrow red band across caudal margin; sixth tergum with dark marking resembling bat with spread wings cephalically. First abdominal pleuron pink and caudal three-fourths of succeeding ones pale pink with small white spot; cephalic fourth of each pinkish cream, fifth and sixth with oblique brownish stripe extending caudoventrally from articular knob. Telson and uropods pinkish tan with brown edging on lateral margins and with similarly colored submedian ridges. Antennular and antennal peduncles dark reddish brown to olive with pinkish cream articular membranes; flagella tan to brown with dark bluish brown bands; antennal scale bright pink with lateral longitudinal brown stripe. Cheliped with basal podomeres and ventral surface of distal ones pink; dorsal part of distal half of merus dark brown with pink tubercles and with distal margin almost black; entire dorsum of carpus similar to coloration of distal half of that of merus; chela orange with brown suffusion, latter intense on dactyl; distal portions of fingers and lateral costa of propodus pinkish orange; tubercles on entire chela pinkish cream to orange. Remaining pereiopods pink basally and ventrally; distal podomeres of dorsum of merus through dactyl suffused with blue, rendering them light to dark lavender, darkest on distal portions of merus and carpus.

Some of the specimens examined were darker, more suffused with brown, but the basic reddish brown to orange coloration seems to be typical of the species, except in one locality in Burke County. In burrows along Newberry Creek at River Road, all of the specimens collected were almost entirely blue, the cobalt blue dorsum of the carapace fading ventrally on the branchiostegites through turquoise to pale powder blue ventrally. The pattern on the abdomen does not differ conspicuously from that described above but the colors are blue and cream. The cream tubercles on the dark blue background of the chelipeds provide a most striking contrast.

TYPES.—The holotypic male, form I, allotypic female, and morphotypic male, form II (numbers 148116, 148117, and 148118, respectively), are deposited in the National Museum of Natural History, Smithsonian Institution, together with the paratypes comprising 2♂I, 4♂II, 9♀, 8j♂, 6j♀, 1 ovigerous ♀, and 1♀ with young. Specimens from localities 2, 3, 8, 9, and 12 (see "Specimens Examined") are excluded from the type series.

Measurements (mm)

	Holotype	*Allotype*	*Morphotype*
Carapace			
Height	17.3	15.1	13.0
Width	19.1	19.4	16.1
Entire length	37.4	37.3	31.2
Postorbital length	33.4	33.4	28.2
Areola			
Width	0.4	0.5	linear
Length	16.4	15.6	13.0
Rostrum			
Width	5.3	5.3	4.6
Length	5.0	5.6	4.8
Chela			
Length of mesial margin of palm	10.0	8.4	7.8
Width of palm	14.1	13.9	11.9
Length of lateral margin	32.1	27.1	23.3
Length of dactyl	20.4	18.3	15.6
Abdomen			
Width	13.3	13.7	11.6
Length	34.1	35.5	30.0

TYPE-LOCALITY.—Savannah River floodplain at U.S. Highway 301, Allendale County, South Carolina. There the holotype was dug from a complex burrow near one of the bridge pilings and not far removed from a small sand-bottomed stream.

RANGE.—Coastal plain of the Savannah and Ogeechee basins in Georgia and South Carolina.

SPECIMENS EXAMINED.—I have examined a total of 41 specimens from the following localities in Georgia and 4 specimens from South Carolina. GEORGIA. *Burke County*: (1) burrows along Rosemary Creek, about 7 mi S of Waynesboro, 1♀ with young, 29 Aug 1941, HHH, collector; (2) burrows at Brinson's Mill (on Rosemary Creek) about 8 mi S of Waynesboro, 1j♀, 14 Apr 1944, HHH; (3) burrows along Newberry Creek at River Rd, 1.6 mi SE of St Rte 80, 2♀, 1j♂, 1 ovig ♀, 17 Apr 1977, C. E. Carter, C. W. Hart, Jr., J. E. Pugh, HHH. *Effingham County*: (4) Savannah River Bluff, 6.8 mi ENE of Kildare, 2♂II, 1j♀, 1 Jan 1971, G. K. Williamson; 1♂II, 3♀, 2j♂, 30 Jan 1971, GKW; (5) Savannah River Bluff, 6.7 mi NW of Clyo off Rte S953, 1j♂, 1j♀, 2 Sep 1972, GKW, W. Seyle; 1♂I, 1♀, 2j♂, 9 Sep 1972, WS, R. Daniel; (6) Savannah River Bluff, 0.2 mi NW of St Rte 119, 1♀, date ?, GKW, WS; (7) Savannah River Bluff, 0.5 mi NW of St Rte 119, 1♂II, 1♀, 1j♂, 1j♀, 20 Apr 1974, D. J. Peters, HHH; 1♂I, 1♂II, 3♀, 2j♂, 3j♀, 1 ovig ♀, 19 Apr 1977, CEC, CWH, JEP, HHH. *Glascock County*: (8) burrows 2.1 mi E of Mitchell on St Rte 102, 1♀, 1j♂, 27 Apr 1966, E. T. Hall, Jr.,

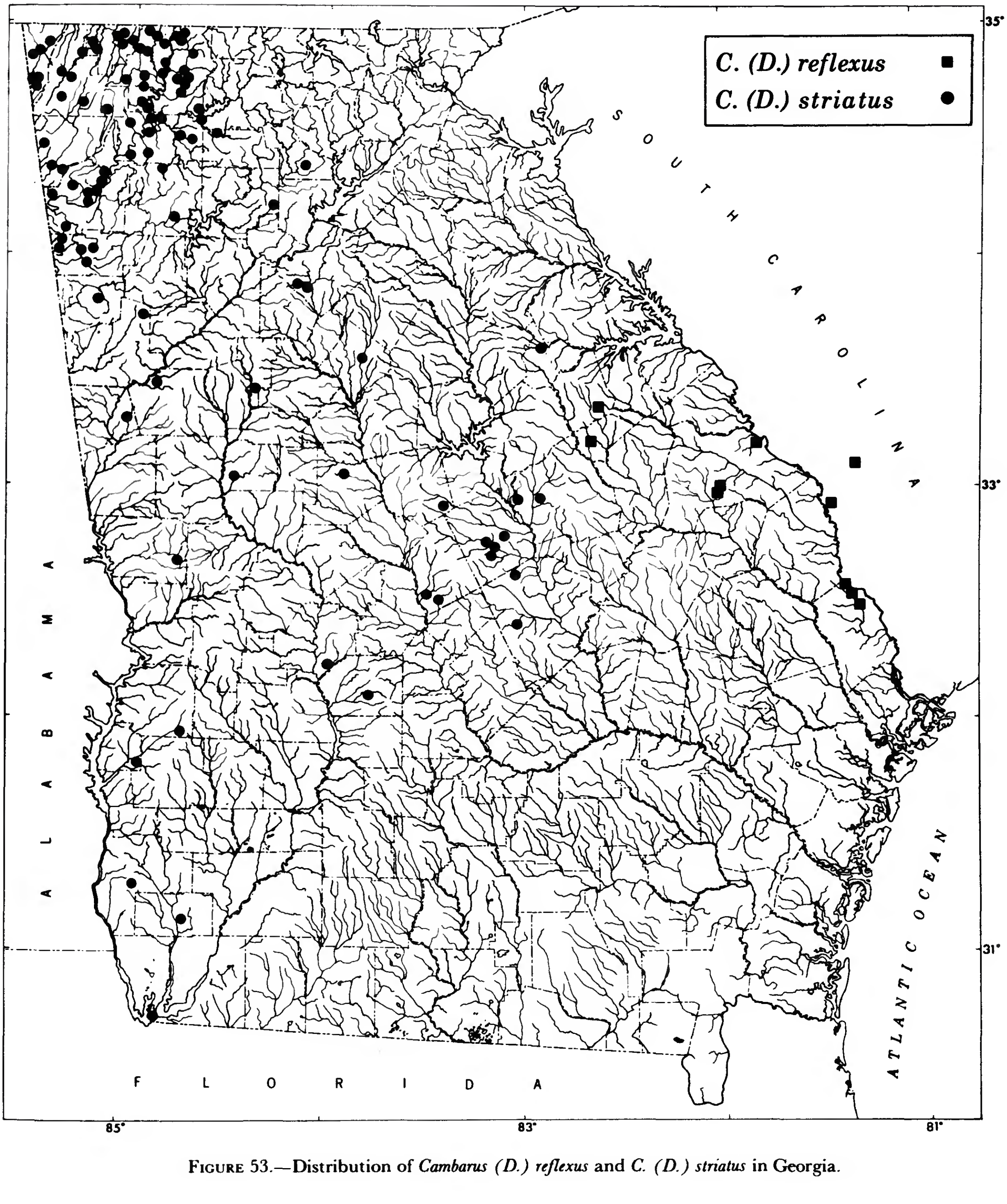


FIGURE 53.—Distribution of *Cambarus (D.) reflexus* and *C. (D.) striatus* in Georgia.

HHH. *Warren County*: (9) burrows 5.9 mi N of Glascock Co line on St Rte 80, 2♀, 27 Apr 1966, ETH, HHH. SOUTH CAROLINA. *Allendale County*: (10) type-locality, 1♂I, 31 Aug 1941, HHH; (11) 11.2 mi N of Allendale on US Hwy 278, 1♀, 15 Aug 1947, HHH. *Barnwell County*: (12) burrows along trib to Meyers Branch, 0.7 mi W of Rte 9 on Rte 14A, 2♂II, 13 May 1976, H. H. Hobbs III.

VARIATIONS.—In the very limited series, particularly of adult specimens, the range of variation is comparatively small. The rostrum is almost invariably short, rarely overreaching the base of the ultimate podomere of the antennular peduncle, and its shape departs little from that illustrated in Figure 52*j*. The suborbital angle, obtuse at best, is frequently obsolete. The range of variation in the width and length of the areola is pointed out in "Diagnosis." The mesial margin of the chela bears a row of six or seven (rarely eight) tubercles subtended by a row of four to six, and a tuft of setae may or may not be present at the mesial base of the fixed finger; the carpus of the chela may have one or two major tubercles mesially and the number of smaller ones varies from two to five; the ventrolateral row of tubercles on the merus consists of from three to five, and the ventromesial from eight to 11; the ischium bears two to four tubercles. Among the first form males, the variations in the secondary sexual characteristics seem negligible. The annuli ventrales of the females are remarkably similar except that mirror images of that illustrated for the allotype are present among the specimens.

SIZE.—The largest specimen available is the ovigerous female from Effingham County in which the carapace length is 37.6 (postorbital carapace length, 33.1) mm. The smallest first form male has corresponding lengths of 33.9 and 30.5 mm. The single female on the abdomen of which young were clinging when collected has corresponding lengths of 34.6 and 30.5 mm, and those of the smaller ovigerous female, 36.9 and 33.1 mm.

LIFE HISTORY NOTES.—The first form males were collected on 19 April, 31 August, and 9 September; ovigerous females on 17 and 19 April, and the female carrying young, on 29 August. The larger female (see "Size") was carrying 59 eggs, and the smaller, 31; the egg diameter ranged from 2.2 to 2.5 mm.

ECOLOGICAL NOTES.—All of the adult specimens of this crayfish have been dug from burrows or were found beneath logs in seepage areas as have some of the juveniles. A few of the latter were found in small rills flowing from bluffs along the Savannah River. On the bluff near State Route 119, my companions and I dug 15 specimens from complex burrows in a seepage area that extended from the level of the river to some 30 feet above it. The tunnels were, for the most part, in mats of roots, branched considerably, and communicated with the surface through at least two openings surrounded by poorly formed chimneys. The deepest passage excavated was slightly less than a meter. That the animals are not confined to seepage areas is evident from the type-locality, where the holotype was dug from a similarly complex burrow in a Savannah River swamp. Also, in the three localities in Burke County, the specimens were taken from burrows in low-lying boggy areas where the water table was a few centimeters below the surface.

In their report of the freshwater decapod crustaceans of the Savannah River Plant, South Carolina, Hobbs III, Thorp, and Anderson (1976:20–21) noted that in the single locality in which this crayfish was collected, it was found in

> a low-lying boggy area where the water table was only a few inches below the surface. The burrows are capped by poorly formed chimneys, consisting simply of a pile of black soil and the tunnels are complex and interwoven among numerous roots. The mouths of the burrows may be concealed beneath logs. The tunnels are relatively deep, one was dissected to a depth of approximately one meter.

RELATIONSHIPS.—There can be little question that the closest relatives of this crayfish are *Cambarus (D.) striatus* and *C. (D.) strigosus*. It differs from the former most conspicuously in the distinctly more strongly recurved central projection of the first pleopod of the male and by its reddish to orange brown or blue coloration. It also differs from *C. strigosus* most conspicuously in features of the first pleopod of the male: the central projection is longer, more tapering, and possesses a less clearly defined subapical notch, and the caudomesial margin of the mesial process is devoid of plumose setae.

Also closely allied is *C. (D.) truncatus*, which occurs in the Oconee Basin and differs from *C. reflexus* in several respects, including the absence of marginal spines on the mesial ramus of the uropod. It is highly probable that *C. reflexus* is vicariating for these three relatives in the Ogeechee and coastal plain section of the Savannah basins.

GEORGIA CRAYFISH ASSOCIATES.—The following crayfishes have been collected with *Cambarus (D.) reflexus* (the number of times they have been found together is noted in parentheses): *Cambarus (D.) latimanus* (4), *C. (L.) diogenes diogenes* (1), *P. (O.) acutus acutus* (1), *P. (O.) pubescens* (3), *P. (Pe.) petersi* (1), and *P. (Pe.) raneyi* (1).

ETYMOLOGY.—From the Latin *reflexus* (bent or turned back), so named because of the strongly recurved central projection of the first pleopod of the first form male.

Cambarus (Depressicambarus) striatus Hay

FIGURES 23*g*, 38*c*, *d*, 39*i*, 53–55, 204

Camburus sp. [Ashland City, Tennessee].—Faxon, 1885b:358 [lapsus for *Cambarus*].

Cambarus latimanus striatus Hay, 1902a:437–439.

Cambarus (Bartonius) latimanus var. *striatus*.—Ortmann, 1905a: 119 [by implication].

Cambarus (Cambarus) latimanus striatus.—Fowler, 1912:341 [by implication].

Cambarus (Cambarus) bartoni striatus.—Ortmann, 1931:142, 143.

Cambarus (Cambarus) bartonii striatus.—Fleming, 1938:303.

?*Cambarus Iatimanus*.—Fleming, 1939:311 [erroneous spelling].

?*Cambarus latimus*.—Fleming, 1939:319 [erroneous spelling].

Cambarus floridanus Hobbs, 1941b:113–118, figs. 1, 4, 5, 8, 9, 16, 19, 22, 25, 31, 32 [holotype and allotype, USNM 79341 (♂I, ♀), and "morphotype," USNM 79344 (♂II); paratypes, MCZ, USNM. Type-locality, 12 miles W of Tallahassee on St Rte 19, Leon County, Florida]; 1942a:356, pl. 3: figs. 1, 5; 1942b:6, 9, 14, 20, 32, 156–159, 161, 162, figs. 191–195; 1945a, fig. 14; 1959:897; 1968b:K-16*.—Hobbs and Hart, 1959:148, 151, 159, 161, 164, 172*, 186–187*, fig. 24.—Bouchard, 1978:27–29, 42.

Cambarus bartonii striatus.—Hobbs, 1942a:354 [by implication].—Hobbs and Shoup, 1942:637.

Cambarus bartoni striatus.—Rhoades, 1944:114, 142.

Cambarus striatus.—Hobbs, 1956b:61; 1968b:K-16*.—Hall, 1957:4, 22, 40, 41–47, 51–53, pl. 4, map 1.—Hobbs and Hobbs, 1962:41*.—Hobbs and Hall, 1969:293.—Anonymous, 1969a:C23, C24, C27–29, C31; 1970b:161, 163–166, 168.—Bouchard, 1978:27–29, 40, 43–46.—Wharton, 1978:220*.

Cambarus sp.—Anonymous, 1967j, tab. 3.—Holsinger and Peck, 1971:30*.

Cambarus (Depressicambarus) striatus.—Hobbs, 1969a:(102, 104, 105, 118, 136, 138, fig. 8)*; 1972b:115*, 147*; 1974b: 14* [the figures in these three publications are of *C. (D.) graysoni*].—Bouchard, 1978:30, 40–43*, figs. 2d,e, 10–14*.

Cambarus (Depressicambarus) floridanus.—Hobbs, 1969a:104, 105, 136, 138, 144, 171, figs. 8*, 18d; 1972b:116, 146*, fig. 98b; 1974b:12, fig. 34.

Cambarus latimanus.—Holsinger and Peck, 1971:30*.

Cambarus (Depressicambarus) sp.—Bouchard, 1972:91.—Hart and Hart, 1974:44*, 58, (63, 73, 88, 90, 134)*.

Cambarus species B.—Hobbs and Hall, 1974:204.

The above includes all of the synonyms for the species but does not contain many references to its occurrence in other states. References to Georgia are indicated by asterisks.

SUMMARY OF LITERATURE PERTAINING TO GEORGIA.—The first indication of the presence of this crayfish in Georgia was in the unpublished thesis of Hall (1957). On his distribution map, he noted four localities in the northwestern part of the state in Chattooga and Floyd counties and near the Dade-Walker county line. The first published Georgia record was that of Hobbs and Hart (1959), who recorded *Cambarus floridanus* (a junior synonym) from a ravine adjacent to the east end of Woodruff Dam in Decatur County. In 1962 Hobbs and Hobbs reported it to have been collected with *Cambarus (J.) conasaugaensis* in the type-locality of the latter, 2 miles east of Chatsworth, Murray County. Not until 1969 were a number of localities cited for the species in the Conasauga Basin in Gordon, Murray, and Whitfield counties (Anonymous, 1969a, 1970b).

Holsinger and Peck (1971), on the basis of my misidentifications, recorded specimens of this species from Byers and Hurricane caves in Dade County as *Cambarus latimanus* and that from Bible Cave in Walker County as *Cambarus* sp. Hart and Hart (1974) cited it as *Cambarus (Depressicambarus)* sp. in several localities in the Coosa Basin and from the Chickamauga and Flint drainage systems, where it served as host to several entocytherid ostracods.

As pointed out in the above synonomy and in the discussion under the subgenus *Depressicambarus*, *Cambarus (D.) floridanus* is a junior synonym of *C. (D.) striatus*. Both Bouchard (1978), in reviewing the subgenus, and I, in preparing this summary of the crayfishes of Georgia, encountered difficulties in separating the two species; however, in view of the following remarks of Hobbs and Hart (1959:186) concerning the color of *C. floridanus*, both of us were hesitant to synonymize them.

> All specimens except those collected at Torreya State Park, Liberty County, Florida, are purplish red dorsally fading to pinkish lavender along the lower lateral margins of the carapace. The chelipeds are also purplish red with dark tubercles. Specimens from Torreya State Park are concolorous, approximating the color of a boiled lobster.

The latter were described by Bouchard (1978:37) as *C. (D.) pyronotus*.

In order to determine whether such a difference in color exists between the two, I returned to the type-locality of *C. (D.) floridanus* and collected additional specimens, and, much to my chagrin, those obtained were brownish with conspicuous orange markings, particularly on the chelipeds. The only living specimen of *C. floridanus* that Hart and I saw during the preparation of our Apalachicola report was a small second form male from Decatur County, Georgia, and the statement was based on my faulty recollection of the color observed in specimens from the other localities cited.

Certainly the coloration of topotypes (Ochlockonee Basin) does not agree with my recollection, and specimens from the Apalachicola (especially the Chipola) Basin should be obtained to be certain that they are likewise drab olive brown and orange rather than purplish red! In view of this, Bouchard and I concur that *C. (D.) floridanus* is a synonym of *C. (D.) striatus* Hay.

Because of a lack of understanding of the identity of *Cambarus striatus*, all subsequent authors have followed the suggestion of Ortmann (1931:142) in considering *C. (D.) graysoni* Faxon (1914:393) its junior synonym. Not until Bouchard (1978:28) discovered that two species were represented among specimens referred to *C. striatus* was Rhoades' (1944:142) synonomy questioned. Surprising was the discovery that both species occur in Nashville, Davidson County, Tennessee, the type-locality of *C. striatus*, in the vicinity of which *C. (D.) graysoni* seems to be the more abundant of the two. Inasmuch as the only first form male cotype of *C. striatus* in the Smithsonian Institution is damaged, all of Hobbs' illustrations of this species were based on a supposed topotype that is now known to be a member of *Cambarus (D.) graysoni*! As a result the only illustrations of *Cambarus striatus* previously available are those of Bouchard (1978). For a full account of the confusion involved in the identity of these two species, the latter reference should be consulted. Included in it are redescriptions and illustrations of syntypes, a statement of its range, notes on variation (including illustrations) as well as on size, life history, and ecology. In addition, the species is treated in discussions of relationships and phylogeny of members of the subgenus *Depressicambarus*.

Most of the citations included in the above synonomy add nothing to our knowledge of the species. Hobbs and Hall (1974), utilizing data presented in Anonymous (1970b), indicated that *Cambarus* sp. B (=*Cambarus striatus*) is distinctly more tolerant to lower oxygen concentrations in the Conasauga River than are *Cambarus* sp. A (=*Cambarus coosae*) and *Orconectes spinosus*, occurring in a section of the stream where the concentration is only 1.6 mg/l.

DIAGNOSIS.—Eyes rather small. Rostrum without marginal spines or tubercles even in the young and seldom with inconspicuous median carina. Carapace without cervical spines (occasionally represented by small tubercle). Areola 7.8 to 78.0 (average 23.2) times as long as wide, constituting 35.7 to 44.3 (average 39.2) percent of entire length of carapace, 41.9 to 48.6 (average 45.7) percent of postorbital carapace length, and with 0 to 3 punctations in narrowest part. Suborbital angle obtuse to virtually obsolete (rarely subacute). Postorbital ridge terminating cephalically without spines and rarely tuberculiform. Antennal scale 2.4 to 2.6 times as long as wide, broadest

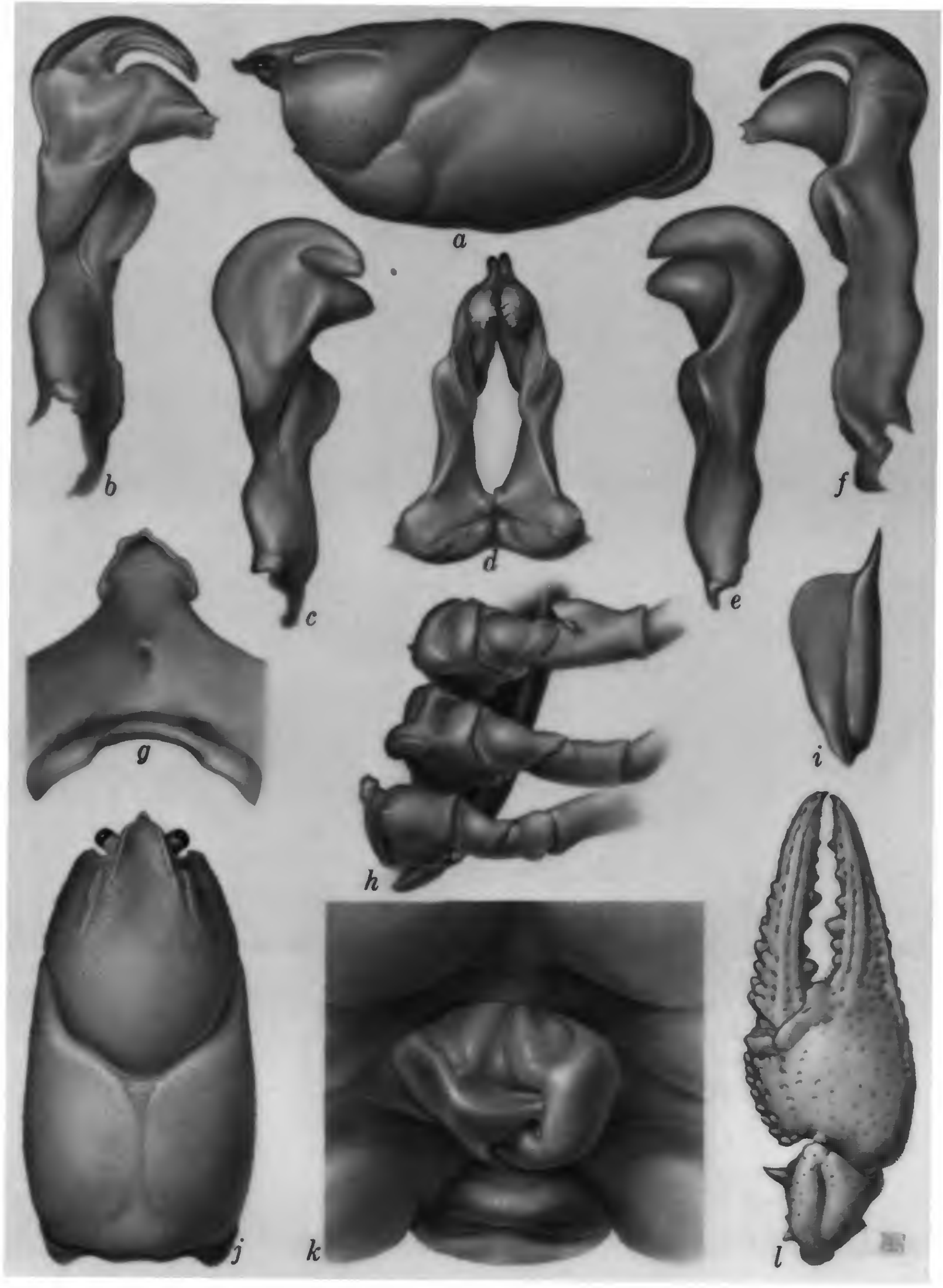


FIGURE 54.—*Cambarus (Depressicambarus) striatus* from Alcovy River floodplain at US Hwy 278, Newton Co, Georgia (all from male, form I, except *c*, *e*, from male, form II, and *k*, from female): *a*, lateral view of carapace; *b*, *c*, mesial view of first pleopod; *d*, caudal view of first pleopods; *e*, *f*, lateral view of first pleopod; *g*, epistome; *h*, basal podomeres of third, fourth, and fifth pereiopods; *i*, antennal scale; *j*, dorsal view of carapace; *k*, annulus ventralis; *l*, dorsal view of distal podomeres of cheliped.

distal to midlength. Palm of chela with 5 to 9 (usually 7) tubercles in mesialmost row. First pleopod of first form male with moderately long terminal elements; central projection tapering distally and rather strongly arched, shallow subapical notch seldom present, and tip reaching level proximal to position of caudal knob but not reaching so far caudally as mesial process; mesial process inflated, usually constricted in distal portion and frequently bearing 2 to 5 rounded or acute apical lobules, process disposed at angle of approximately 90 degrees to main shaft of appendage; caudal knob often well developed but occasionally reduced or absent. Mesial ramus of uropod with distomedian and distolateral spines. Carapace olive gray to tan; abdominal terga frequently with longitudinal stripes; rarely almost entirely dark blue. Female with first pleopod present.

COLOR NOTES (Figure 38*c*,*d*).—Hay (1902a: 438–439) described in some detail the color, noting two color phases (sage green and dark brown) as well as two patterns (with and without longitudinal stripes). Similar phases and patterns have been observed in specimens from Georgia; most of those collected by me exhibited the striped pattern, a description of which follows, based on a first form male from the Conasauga Basin in Gordon County.

Ground color of carapace and abdomen pale gray with tan and dark gray markings. Rostral margins orange tan, upper surface as well as dorsomedian gastric area suffused with tan; caudal gastric area with narrow transverse dark brown band adjacent to cervical groove, band broader on each side of median line but tapering rapidly and disappearing dorsolaterally. Hepatic region with almost white reticulations and tubercles and sparsely suffused with streaks of pale tan. Antennal area with almost white oblique spot. Areola grayish tan, its triangular cephalic area dark brown; dorsal region of branchiostegites with paired broad to narrow longitudinal dark brown stripes flanked ventrally by broader pale ones, latter irregular ventrally and adjacent dark coloration fading ventrally to almost white. Abdomen with median grayish tan stripe extending from cephalic extremity to base of telson (continuous with median grayish tan area on areola); this stripe flanked laterally by pair of slightly narrower dark grayish brown stripes continuing caudally from those on branchiostegites, stripes decreasing in width caudally and diverging on sixth abdominal tergum; caudal margin of each tergum edged with rust; bases of pleura with ventrally convex narrow dark stripes forming scalloped line from first to cephalic margin of sixth segment; each segment of stripe bleeding caudoventrally onto pleuron, cephaloventral portions of which very pale gray to white. Peduncles of antennule and antenna mostly pale gray with few darker markings, and antennal scale with longitudinal dark line laterally. Dorsal surface of cheliped from midlength of merus distally little different in color from dorsal surface of carapace, but much darker than proximolateral and ventral surfaces; carpus mostly dark brown with pale-tipped tubercles; chela with tan suffusion more intense on fingers than on palm; fingers light tan to cream preapically and with lateral costa of propodus and tubercles cream to white; apical spines orange to dark brown. Remaining pereiopods pale gray with slightly darker mottlings distal to midlength of merus.

Some individuals with tan and brown predominating rather than shades of gray but exhibiting same striped pattern. Others more nearly concolorous, ranging from pale gray to reddish brown, and only obvious pattern consisting of paired dark brown dorsolateral spots on abdominal terga and rather inconspicuous scalloped stripe along bases of pleura.

The color of other populations and that of "*C. floridanus*" are described by Bouchard (1978).

TYPES.—Syntypes, USNM 25019 (♂I, 3♂II, 4♀), MCZ 7348 (♂I, ♂II, 3♀).

TYPE-LOCALITY.—Nashville, Davidson County, Tennessee.

RANGE.—This crayfish ranges from the upper Savannah, Altamaha, and Coosa basins in Georgia and the Ochlockonee basin in Florida through much of Alabama and Mississippi, across Tennessee west of the Blue Ridge, and as far north as the Green watershed in Kentucky (see Bouchard, 1978:37). In Georgia, it is one of the dominant species in the northwestern part of the state, where it is abundant in tributaries of the Coosa River, especially in the Conasauga system and in the Coosawattee River basin below Carter's Reservoir. It is also present in the watersheds of Chickamauga and Lookout creeks. In the Etowah, Tallapoosa, Chattahoochee, Flint, Ocmulgee, and Oconee basins, it is less frequently encountered, but in the latter four it has become established on the upper part of the coastal plain as well as in the piedmont. Thus in Georgia, it ranges from the Appalachian Plateau and Ridge and Valley provinces onto the Dougherty Plain but appears to be absent from the Hiwassee, Little Tennessee, and Ogeechee river basins.

GEORGIA SPECIMENS EXAMINED.—Approximately 800 specimens have been examined by me from about 100 localities. A few of the localities are so close together that all could not be indicated on the accompanying map (Figure 53).

VARIATIONS.—Most conspicuous among the variations noted in the Georgia representatives of this species are the rather marked differences in the relative length and width of the areola. The extremely short ones (less than 37 percent of the total length of the carapace) occur in only 8 percent of the specimens measured, and those individuals with an areola length less than 44 percent of the postorbital carapace length comprise less than 17 percent of those measured. The extremely broad areola (less than 9.5 times longer than broad) occurs in less than two percent of the specimens measured. Those with such comparatively short and broad areolae to some extent appear to be limited to a restricted area of the range; most of those observed were collected in the Conasauga Basin in Murray and Whitfield counties, where few individuals have areolae with relative lengths as great as the average for the species in the state. The only other specimens with areolae of similar relative lengths are single individuals from the Catoosa and Chickamauga basins in Walker County and a single one from the Flint Basin in Pike County. Collected with the latter specimen was one with a longer (38.8 percent of the total length of the carapace) but comparatively broad (9.6 times as long as broad) areola.

The rostra of most of the specimens from the Conasauga Basin are broader and more obviously concave than in most individuals from elsewhere.

One of the most distinctive populations is that from the Alcovy River floodplain in Newton County, where the entire colony is apparently restricted to burrows, none having been found in the river. The areola is very narrow (Figure 55*q*), ranging from 29 to more than 70 (average about 52) times as long as broad and constituting 40.0 to 43.4 (average 42.8) percent of the total length of the carapace, 45.3 to 50.7 (average 47.8) percent of the postorbital carapace length. (The comparable ratios for all the specimens measured from elsewhere in Georgia are 7.8 to 48.5 (18.0); 35.7 to 44.3 (38.5); and 41.9 to 48.6 (45.4).) The rostra are distinctly shorter and the margins more convergent than in specimens from the Conasauga, and there are few specimens from elsewhere in which the rostrum is as short.

The range of differences existing in the pleopods of first form males available is illustrated in Figure 55. Some of the specimens from Gordon County bear plumose setae on the proximomesial surface of the mesial process (Figure 55*a*). In the specimens from the Coosa Basin (Figure 55*b–h*), the caudal knob may be strongly developed (Figure 55*c*) or obsolete (Figure 55*b,f*), and there is almost as much variation in the curvature of the central projection as is known to occur outside of the basin elsewhere in Georgia. A moderately well defined subapical notch is present on the central projection of the single first form male available from Harris County (Figure 55*j*), and a conspicuous one is present in specimens from Dawson and Wilkinson counties (Figure 55*f,l*).

The shorter rostrum, obliterated areola, and the tuft of setae at the opposable base of the fixed finger of the chela in specimens from Miller County (Spring Creek, 0.6 miles west of Colquitt) and Early County (Big Ditch, 0.7 mile east of Blakely on St Rte 62) make them stand quite apart from most of the seemingly more typical representatives of the species elsewhere in Georgia.

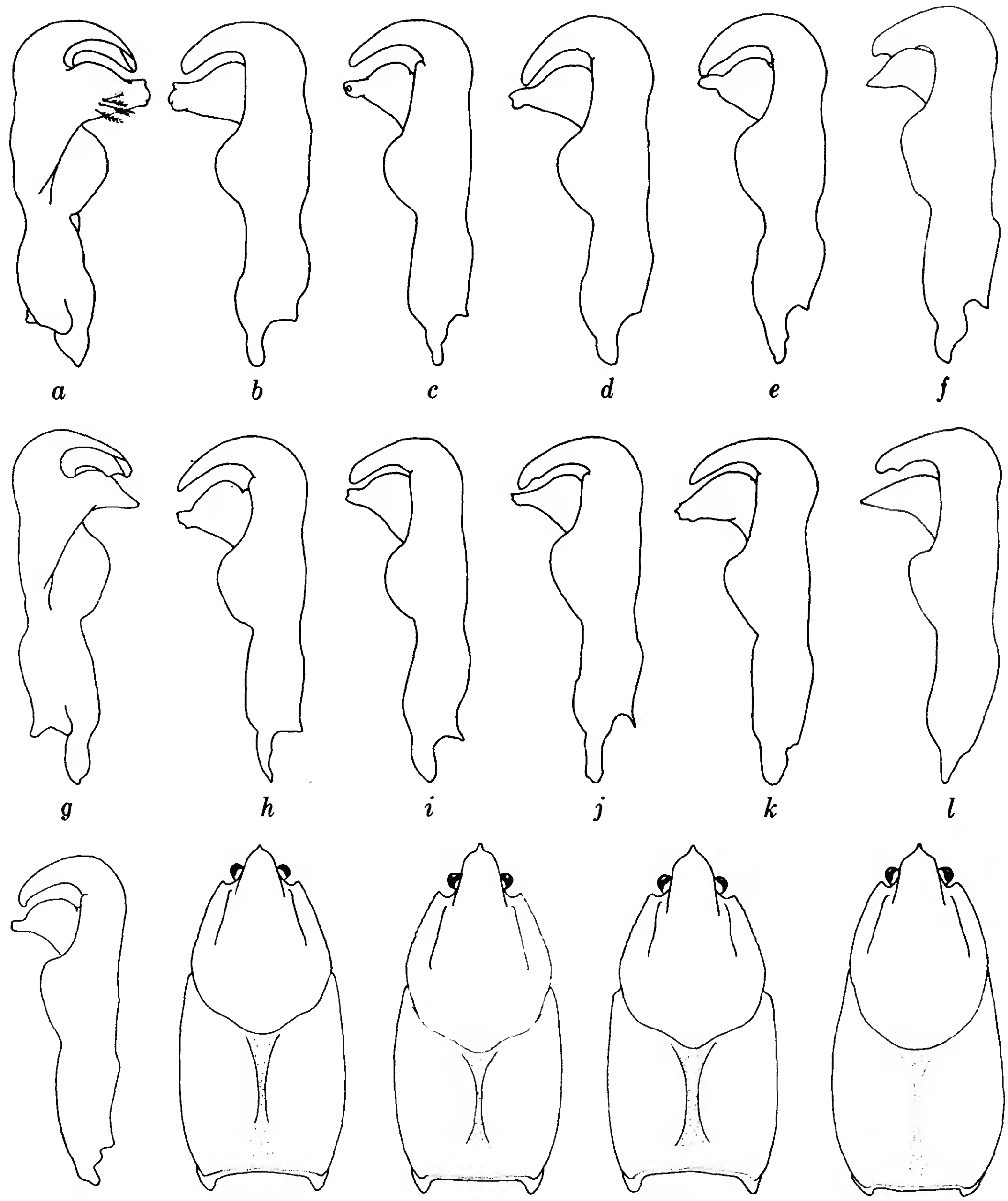


FIGURE 55.—*Cambarus (D.) striatus* (*a*, *g*, mesial view, and *b–f*, *h–m*, lateral view of first pleopods of male, form I; *n–q*, dorsal view of carapace of male, form I). Conasauga Basin: *a–d*, *p*, Gordon Co; *e*, Whitfield Co. Etowah Basin: *f*, *g*, Dawson Co. Coosa Basin: *h*, Floyd Co. Tennessee (Lookout Creek) Basin: *i*, *o*, Dade Co. Chattahoochee Basin: *j*, *n*, Harris Co. Ocmulgee Basin: *k*, *q*, Newton Co. Oconee Basin: *l*, Wilkinson Co. Chattooga Basin: *m*, Chattooga Co.

Variations in color have been pointed out in the paragraphs devoted to color notes.

SIZE.—The largest specimen collected in Georgia is a female from the Coosa Basin in Murray County that has a carapace length of 60.1 (postorbital carapace length 52.8) mm (see Bouchard, 1978:43). The corresponding lengths of the smallest and largest first form males are 31.5 (28.7) and 45.0 (38.1) mm.

LIFE HISTORY NOTES.—As shown on the chart of "Seasonal Data," first form males are known to occur in every month except June and August. In view of the seasonal occurrence of the first and second form males of relatives of this crayfish (and the single record for September being based on a specimen that molted in the laboratory on 28 September), it is probable that first form males are rare in naturally occurring populations from mid-July to early October. No ovigerous females have been observed, but Bouchard (1978:47) collected a female with young in Alabama on 9 October 1977. This suggests that such females probably conceal themselves in burrows until the young have hatched and become independent. On the basis of the size of juvenile specimens collected, one might suspect that egg laying occurs over a long period during the year.

Seasonal Data

Sex/stage	*J*	*F*	*M*	*A*	*M*	*J*	*J*	*A*	*S*	*O*	*N*	*D*
♂I	28	16	19	11	3		2	1		7	2	
♂II	3	1	4	43	11	6	1	5	3	2		
♀	4	1	2	47	12	13	1	14	1	8	1	
♂j	2			159	28	59		14	3	8	1	2
♀j	2		1	187	37	17		14	1	10		

ECOLOGICAL NOTES.—The habitats occupied by *Cambarus striatus* vary from mountain brooks to moderately large rivers and frequently to complex burrows far removed from standing water. Some unknown factors seem to influence its habits in different parts of its range, and at least some differences appear to occur when it shares a portion of a drainage basin with *Cambarus* (*D.*) *latimanus*. For example, in the Conasauga Basin from the Tennessee-Georgia line southward to the confluence of the Conasauga and Coosawattee rivers, *C.* (*D.*) *striatus* occurs abundantly within the river and its tributaries, where it is found among rocks in pools and among roots and in retreats along undercut banks of the stream, the precise kinds of places usually frequented elsewhere by *Cambarus* (*D.*) *latimanus*. For some reason, the latter is apparently rare in this section of the watershed and *C.* (*D.*) *striatus* is apparently vicariating for it. This is not to imply that individuals do not construct burrows in this part of the basin; to the contrary, within the western city limits of Chatsworth, I dug one specimen from a burrow adjacent to another occupied by *C.* (*D.*) *cymatilis*, a locality that is situated at least one mile from the nearest stream.

In contrast to its habitat distribution in this part of the Conasauga Basin is its apparent restriction to burrows in the Alcovy River floodplain in Newton County. Although more than 100 specimens were taken in small mammal traps (see "Life History Notes" for *C.* (*D.*) *latimanus*) near the U.S. Highway 78 crossing west of Monroe, neither adults nor juveniles of this species have been collected from the River proper, whereas *C.* (*D.*) *latimanus* occurs within it in numbers. In other localities where *C.* (*D.*) *latimanus* was found to be common in the streams, *C.* (*D.*) *striatus* seemed to be restricted to burrows removed from, and with no connection to, the water of the stream.

In a sluggish silt-laden creek about five miles west of Rome, Floyd County, numbers of specimens were taken from dense mats of *Myriophyllum* sp.

Unlike some of the burrowing species, *C.* (*D.*) *striatus* has never responded to my disturbing its tunnel by coming to the opening where it could be caught; all of the individuals I have obtained from burrows were either cornered in one of the horizontal galleries or, more usually, at the bottom of one of the flooded vertical tunnels. All of the burrows that I have dissected have been complex ones with one to three openings to the surface leading into a maze of subhorizontal tunnels and at least one vertical passageway penetrating well below the water table. While there is little evidence to support a conclusion that this species seeks wooded areas in which to construct its tunnels among matted roots, I have found few burrows constructed by this crayfish that were not well protected by winding among and occasionally spiraling around large roots; particularly is this true of the deep vertical passageway.

Soil types seems to be of little importance to the crayfish in its choice of site for constructing a burrow so long as there is enough claylike material to prevent the collapse of the walls in the deeper passages. I have followed subhorizontal tunnels that were constructed in a moist sandy soil that collapsed as rapidly as I was able to move my hand through it, but the deeper passageways were invariably supported by organic deposits or a sandy clay.

GEORGIA CRAYFISH ASSOCIATES.—Attesting to the wide range of ecological situations exploited by *Cambarus (D.) striatus* is the list of its crayfish associates, which frequent markedly diverse habitats (the number of times they have been found together is indicated in parentheses): *Cambarus (D.) cymatilis* (1), *C. (D.) latimanus* (20), *C. (D.) truncatus* (2), *C. (H.) girardianus* (9), *C. (H.) longirostris* (1), *C. (H.) manningi* (1), *C. (H.) speciosus* (1), *C. (J.) conasaugaensis* (3), *C.* '*(J.) unestami* (1), *C. (L.) acanthura* (9), *C. (L.) diogenes diogenes* (3), *C. (P.) coosae* (18), *C. (P.) extraneus* (4), *C. (P.) scotti* (3), *Faxonella clypeata* (5), *Orconectes erichsonianus* (11), *O. spinosus* (14), *Procambarus (O.) acutissimus* (1), *P. (O.) acutus acutus* (1), *P. (O.) enoplosternum* (3), *P. (O.) lophotus* (8), *P. (Pe.) spiculifer* (16), *P. (S.) howellae* (5), and *P. (S.) paeninsulanus* (1).

Cambarus (Depressicambarus) strigosus, new species

FIGURES 23*d*, 38*e*, 39*j*,*l*, 41, 56, 205

Cambarus sp.—Wharton, 1978:46.

DIAGNOSIS.—Eyes small. Rostrum without marginal spines or tubercles and lacking median carina. Carapace with cervical tubercles scarcely larger than others nearby. Areola linear to 44.5 times as long as broad, constituting 39.4 to 42.6 percent of entire length of carapace (45.3 to 48.8 percent of postorbital carapace length) and never with more than 1 punctation in narrowest part. Suborbital angle broadly rounded or obsolete. Postorbital ridge terminating cephalically without spines or tubercles. Antennal scale about 2.7 times as long as broad, widest distal to midlength. Palm of chela with 5 to 8 tubercles in mesialmost row. First pleopod of first form male with central projection, although arched, not reaching proximally to level of bulbous part of mesial process and provided with conspicuous subapical notch; mesial process strongly inflated proximally, with slender subacute apical terminal, and bearing row of plumose setae along caudomesial surface; caudal knob vestigial. Abdomen conspicuously reduced. Color mostly pale orange tan with dark brownish to black and orange markings. Female with first pleopod present.

HOLOTYPIC MALE, FORM I.—Body subovate, strongly compressed (Figure 56*a*,*j*). Abdomen conspicuously narrower than thorax (9.9 and 13.5 mm); maximum width of carapace greater than height at caudodorsal margin of cervical groove (13.5 and 12.6 mm, respectively). Areola linear along much of its length with no room for punctations; length 41.8 percent of total length of carapace (47.8 percent of postorbital carapace length). Rostrum with thickened convergent margins contracted rather suddenly at base of short subtriangular acumen, latter reaching distal margin of penultimate podomere of antennular peduncle; dorsal surface of rostrum deeply concave with comparatively few punctations except basally. Subrostral ridge moderately strong and evident in dorsal aspect to base of acumen. Postorbital ridge rather strong, ending abruptly anteriorly, lacking spine or tubercle, and swollen caudally. Suborbital angle poorly developed and rounded; branchiostegal spine lacking, only broad obtuse angle replacing it. Cervical spine represented by tubercle only slightly larger than others on branchiostegal region and smaller than several in hepatic and anteroventral branchiostegal regions. Carapace mostly punctate dorsally but bearing paired, slightly elevated, polished

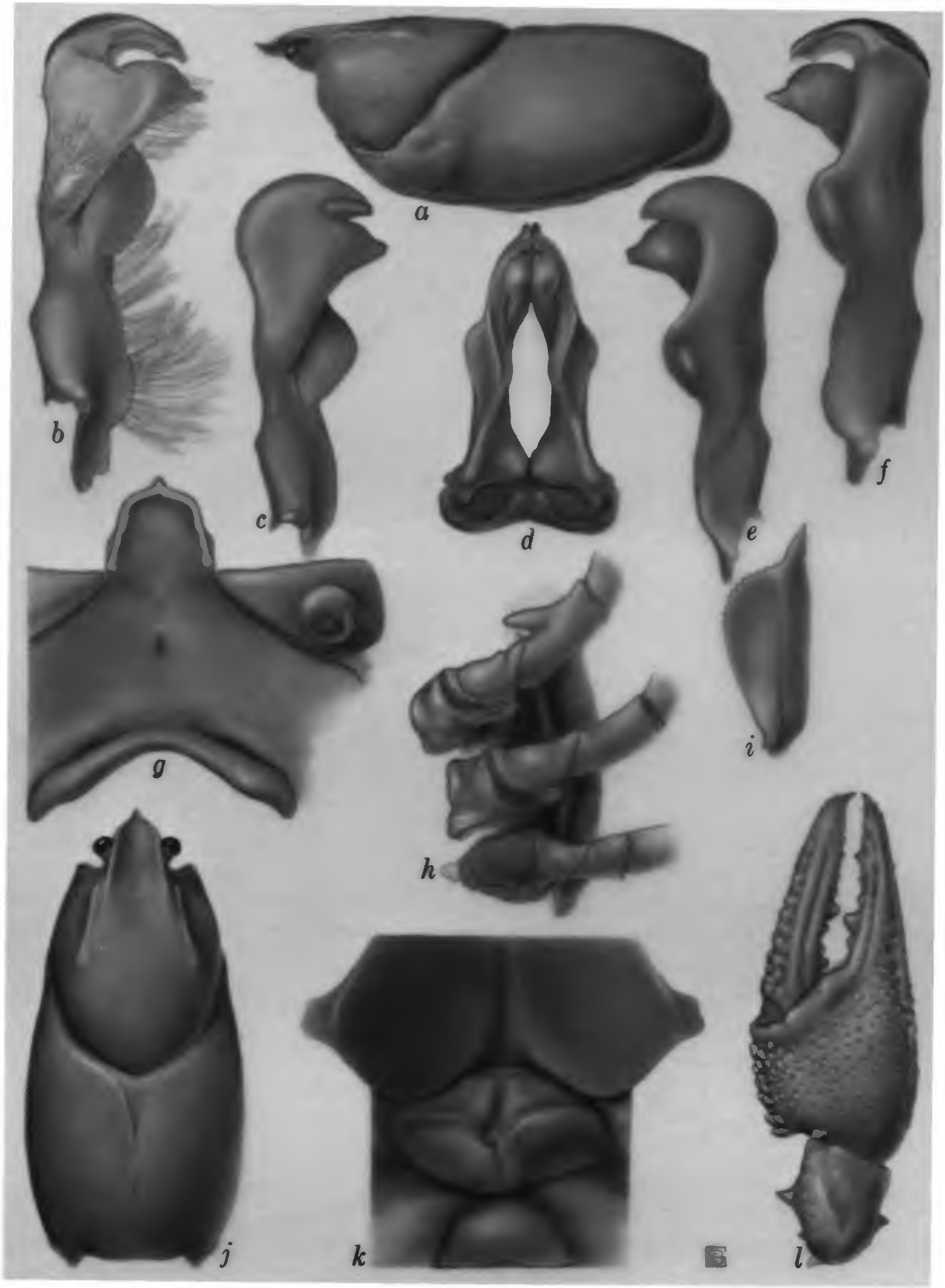


FIGURE 56.—*Cambarus (Depressicambarus) strigosus* (all from holotype except *c*, *e*, from morphotype, and *k*, from allotype): *a*, lateral view of carapace; *b*, *c*, mesial view of first pleopod; *d*, caudal view of first pleopods; *e*, *f*, lateral view of first pleopod; *g*, epistome; *h*, basal podomere of third, fourth, and fifth pereiopods; *i*, antennal scale; *j*, dorsal view of carapace; *k*, annulus ventralis; *l*, dorsal view of distal podomeres of cheliped.

areas between mandibular adductor regions; lateral surface of cephalic section, except for anterior part of orbital and posterior part of hepatic regions, tuberculate. Abdomen shorter than carapace (26.0 and 30.1 mm), pleura short, subtruncate ventrally and rounded caudoventrally (Figure 39*j*). Cephalic section of telson with single fixed spine in each caudolateral corner. Proximal podomere of uropod lacking spines; mesial ramus of uropod with moderately well developed submedian ridge terminating distally in spine, latter almost reaching distal margin of ramus, lateral margin of ramus with distolateral spine (Figure 39*l*).

Cephalomedian lobe of epistome (Figure 56*g*) subpentagonal with short rounded anteromedian projection; margins thickened and elevated ventrally; main body with small but distinct submedian fovea; epistomal zygoma arched. Ventral surface of proximal podomere of antennular peduncle with small spine at base of distal fourth. Antennal peduncle lacking spines; flagellum reaching fourth abdominal tergum; antennal scale (Figure 56*i*) about 2.7 times as long as wide, broadest distal to midlength; distomesial border forming broad gentle arc, dorsal surface of lateral part of thickened area with conspicuous, deep setiferous punctations, distolateral spine strong and reaching distal margin of penultimate podomere of antennular peduncle. Mesial half of ventral surface of ischium of third maxilliped with 2 rows of clusters of long stiff setae, submarginal lateral row of much smaller plumose ones, and 1 small cluster near base of polished lateral half; distolateral extremity of dextral member acute (sinistral member rounded, probably resulting from injury).

Right chela (Figure 56*l*) 2.3 times as long as broad, mesial margin of palm occupying slightly more than one-third of its length. Mesial surface of palm with 3 well-defined rows of tubercles, mesialmost of 6, adjacent dorsolateral one of 7 (left with 6), and ventrolateral one of 5 (left with 4); more than mesial half of both dorsal and ventral surfaces tuberculate, tubercles becoming smaller and more squamous laterally; lateral part of both surfaces with setiferous punctations. Ventral surface of palm with conspicuous distomedian tubercle and another large one on ridge opposite base of dactyl. Both fingers with well-defined submedian longitudinal ridge flanked by setiferous punctations on dorsal and ventral surfaces; opposable margin of fixed finger with row of 6 (left with 7) tubercles (third from base largest) along proximal three-fifths, large tubercle on lower level at base of distal third, and single (double distally) interrupted row of minute denticles extending from fourth tubercle from base to corneous tip, lateral margin of finger costate, with costa extending proximally along slightly more than distal half of palm and bearing single row of setiferous punctations; opposable margin of dactyl with row of 10 (left with 9) tubercles (fourth from base largest) and interrupted row of minute denticles extending distally from fourth tubercle from base to corneous tip of finger, mesial surface tuberculate along proximal two-thirds and punctate distally.

Carpus of cheliped with deep oblique submedian furrow dorsally, area mesial to it mostly tuberculate and that lateral to it punctate; mesial surface with large spikelike tubercle and smaller one proximal to it; ventral surface with 2 marginal tubercles (strong subacute median one and less conspicuous more rounded one on articular knob) and smaller one proximomesial to distomedian tubercle; lateral surface punctate. Merus with 2 (3 on left) prominent premarginal tubercles dorsally; ventrolateral row of 3 (only 2 well developed on left) tubercles, and ventromesial one of 12 (11 on left); podomere otherwise polished and with fine punctations laterally and similar ones along with very small tubercles mesially. Ventromesial margin of ischium with row of 4 tubercles.

Ischium of third pereiopod comparatively slender and bearing simple hook extending proximally beyond basioischial articulation (Figure 56*h*); hook not opposed by tubercle on basis. Coxa of fourth pereiopod with moderately prominent caudomesial boss and strongly elevated (ventrally) ridges mesially; coxa of fifth pereiopod lacking boss but with ventral membrane bearing setae.

First pleopod (Figure 56*b,d,f*) reaching coxa of third pereiopod and as described in "Diagnosis."

ALLOTYPIC FEMALE.—Differing from holotypic male in following respects: rostrum, with margins much more strongly convergent, reaching midlength of penultimate podomere of antennular peduncle; cervical tubercle slightly more conspicuous; epistome subtrapezoidal; chelae with mesialmost row of tubercles on palm consisting of 6, dorsolateral row (poorly defined on right) of 5, and adjacent ventrolateral row of 2 (left with only 1 representing row); less than mesial half of dorsal surface of palm tuberculate; tubercle on ventral ridge of palm at base of dactyl rudimentary; fixed finger of left chela atypical, bearing row of 8 tubercles (second from base largest) and additional lower row of 3 tubercles between levels of fifth and seventh tubercles in upper row; mesial surface of carpus lacking small proximal tubercle; merus with ventrolateral row of 4 tubercles on right (3 on left) and ventromesial row of 10 (11 on left). (See "Measurements.")

Annulus ventralis (Figure 56*k*) approximately 1.4 times as broad as long and strongly asymmetrical; cephalic two-fifths less calcified than caudal region and bearing shallow triangular median depression flanked by low caudally diverging ridges; caudal part of depression constricting where abutting transverse ridge, and becoming troughlike and turning sinistrally, initiating S-shaped sinus. Latter traversing massive caudal half of annulus, terminating slightly anterior to caudal margin. Surface of sinistral half of caudal region tilted but rather flat, marked by few low ridges mesially; dextral part, in contrast, greatly elevated ventrally and more strongly calcified than sinistral part; tongue from latter disappearing beneath wall of swollen dextral side. Postannular sclerite twice as broad as long, little more than half as long and two-fifths as wide as annulus, its ventral surface densely punctate. First pleopod reaching at least midlength of annulus when abdomen flexed.

MORPHOTYPIC MALE, FORM II.—Differing from holotype in following respects: cephalic section of telson with additional movable spine in caudodextral corner; both lobes of proximal podomore of uropod with spine; cephalomedian lobe of epistome almost square and bearing small, rounded, anteromedian projection; antenna reaching third abdominal tergum; distolateral extremity of ischium of third maxilliped produced in acute prominence; mesial margin of palm of right chela with mesialmost row of 5 tubercles flanked dorsally by row of 6 and ventrally by 2, left chela with 7, 5, and 0, respectively; ventral surface of palm with 2 tubercles on ridge flanking base of dactyl; opposable margin of fixed finger of chela with fourth tubercle from base largest; corresponding margin of dactyl with 11 tubercles; merus of right cheliped with ventrolateral row of 6 tubercles and ventromesial one of 9, that of left cheliped with 6 and 12, respectively. Hooks on ischia of third pereiopods much reduced in size, and boss on coxa of fourth pereiopod less prominent. (See "Measurements.")

First pleopod (Figure 56*c,e*) differing from that of holotype most conspicuously in lacking setae along caudal surface of mesial process and in more swollen, noncorneous central projection; former also with prominence on extremity much smaller and rounded.

COLOR NOTES (Figure 38*e*).—Carapace predominately olive dorsally, fading ventrally on branchiostegites to pinkish cream. Rostral margins, subrostral ridges, postorbital ridges, and small paired spots in posterior gastric region orange; remainder of rostral, orbital, and antennal areas adjacent to subrostral ridges dark olive, and mandibular and hepatic regions olive suffused with orange. Abdominal terga mostly olive but each with narrow orange band on caudal margin; pleura pinkish cream to cream. Telson and uropods pale olive but with margins and transverse sutures orange. Antennular and antennal peduncles dark olive with orange flanking articulations; flagella dark to pale olive. Third maxilliped with basal podomeres pinkish cream and more distal ones pale olive; proximal and distal ends of distal 3 podomeres light orange. Cheliped with coxa and basis cream, ischium with increased suffusion of orange distally, and with dorsal surface dark olive intensifying and broadening distal to midlength but with major dorsal tubercles orange;

carpus orange, mottled with dark olive dorsally, particularly mesially and distally; tubercles and dorsodistal articular area marked with orange; dorsomesial three-fourths of palm dark bluish green, fading laterally to orange, with orange tubercles and condyle flanking dactyl. Both fingers dark bluish green dorsally with mesial and lateral areas grading into orange on ventral surface; tips of fingers orange yellow. Remaining pereiopods pinkish cream basally, becoming pale olive on ischium and merus, but fading on propodus and dactyl. Sternal area cream to pinkish cream.

Measurements (mm)

	Holotype	*Allotype*	*Morphotype*
Carapace			
Height	12.6	14.4	13.0
Width	13.5	16.4	13.9
Entire length	30.1	34.2	30.1
Postorbital length	26.4	30.2	26.3
Areola			
Width	0	0	0
Length	12.6	14.2	12.2
Rostrum			
Width	4.4	5.5	4.6
Length	4.9	5.1	5.0
Chela			
Length of mesial margin of palm	7.6	7.3	6.6
Width of palm	10.5	10.7	8.9
Length of lateral margin	24.0	23.1	21.1
Length of dactyl	15.7	15.0	14.0
Abdomen			
Width	9.9	11.6	10.0
Length	26.0	30.1	27.8

TYPES.—The holotypic male, form I, allotypic female, and morphotypic male, form II (numbers 148284, 148574, and 148575, respectively), are deposited in the National Museum of Natural History, Smithsonian Institution, as are the paratypes consisting of two first form males, three second form males, 16 females, three juvenile males, five juvenile females, and three ovigerous females. (While the juvenile and second form males were being maintained alive in the laboratory, anticipating their attaining, at least, a greater size the juvenile male molted to form I.)

TYPE-LOCALITY.—Roadside ditch within 30 meters of Susan Smith Branch (tributary to Long Creek and the Broad River) west of State Route 17 on unnumbered county road, Wilkes County, Georgia. The ditch supported a dense growth of *Persicaria* sp. flanking several small pools on a sandy clay substrate. The burrows were comparatively simple and marked by low chimneys. One of the burrows that was excavated during October had two chimneys, and passageways from them united at a depth of some 20 centimeters and continued as a single vertical tunnel to a depth of about one meter; others that were opened in the spring descended well beyond the one-meter mark. The most conspicuous trees in the nearby woods were *Pinus* sp., *Liriodendron tulipifera*, and *Platanus occidentalis*.

RANGE.—This crayfish is known from only five localities in the Broad and Little river basins (tributaries of the Savannah River) in Elbert, Oglethorpe, and Wilkes counties, Georgia. These streams lie wholly within the Piedmont Province. Almost certainly the range of *C. (D.) strigosus* is greater that that indicated on Figure 41, for I can fathom no reason why it should not be more widespread in the basins of the Broad and Little rivers. Thorough searches have not been made for it in many parts of either basin. Appearing to vicariate for it in abutting or nearby watersheds are the following: in the upper Chattahoochee, *C. (J.) nodosus*; in the Ogeechee and Savannah (to the south), *C. (D.) reflexus*; in the Ocmulgee-Oconee, *C. (D.) striatus* and *C. (D.) truncatus*; and in the Etowah, *C. (D.) striatus*.

GEORGIA SPECIMENS EXAMINED.—I have examined 35 specimens from the following localities. *Elbert County*: (1) Nancy Hart State Park 1.6 mi E of St Rte 17 on Rte S2215, 3♀, 2j♂, 1j♀, 2 Apr 1978, R. J. Dubois, D. J. Peters, J. E. Pugh, HHH, collectors. *Oglethorpe County*: (2) seepage area adjacent to Big Indian Creek 4.5 mi N of Lexington on St Rte 77, 3♀, 1j♀, 2 Apr 1978, RJD, DJP, JEP, HHH; 3♂II, 3♀, 3 ovig ♀, 21 May 1979, E. T. Hall, Jr., HHH; 1♂I, 3♀, 23 May 1979, W. D. Kennedy, ETH, HHH; (3) roadside ditch near Goosepond Creek 2 mi E of St Rte 77 on Co Rd 195, 1♂II, 2 Apr 1978, RJD, DJP, JEP, HHH; 1♂I, 1♀, 22 May 1979, WDK, HHH. *Wilkes County*: (4) type-locality, 1♂I, 1j♀, 4 Oct 1977, T. A. English, Jr., HHH; 2♀, 1j♀, 2 Apr 1978, RJD, DJP, JEP, HHH; (5) along Beaver Dam Creek 4.1 mi

SW of Washington on St Rte 44, 2♀, 1j♂, 1j♀, 3 Apr 1978, RJD, DJP, JEP, HHH.

VARIATIONS.—In view of the limited number of specimens available from so few nearby localities, it is not surprising that the variations noted are so few, and, for the most part, hardly worthy of recording. The limits of variation in ratios of the length of the areola to its width, the carapace length, and the postorbital carapace length are cited in "Diagnosis." Whereas the numbers of tubercles in the mesialmost row on the palm of the chela range from five to eight, the usual is six, and on only one chela of a single specimen were there eight. The numbers of tubercles comprising the row on the opposable surface of the fixed finger of the chela range from five to seven, of which the third from the base is usually largest; those on the corresponding margin of the dactyl range from six to 10, and the fourth from the base is almost always largest. The mesial surface of the carpus of the cheliped bears from one to three tubercles, the latter occurring more infrequently than one or two; the number of spines on the ventral surface of the merus ranges from seven to 11 in the mesial row and two to six in the lateral one, the most frequently occurring are nine and four, respectively; and the row of tubercles on the mesial margin of the ischium consists of two to four, three most commonly. Two of the females, one from Elbert County and the other from the type-locality, were predominately dark blue instead of olive and orange.

SIZE.—The largest specimen available is a female having a carapace length and postorbital carapace length of 36.5 (31.9) mm. The smallest and largest first form males have comparable lengths of 29.9 (26.4) and 31.0 (27.2) mm, and of the smallest ovigerous female, 27.2 (24.0) mm.

LIFE HISTORY NOTES.—One of the first form males, the holotype, was collected on 4 October 1977 and the other two on 22 and 23 May 1979. Most of the females obtained in April 1978 possessed exoskeletons that were encrusted, indicating that they had not molted for several months. In contrast, the allotype, and at least one other female had molted recently. In none were the cement glands observed to be well developed, but had they been so in the encrusted specimens they probably would not have been noticed. In contrast, two of the females collected in May had well-developed cement glands, and four were ovigerous; the largest of the latter, with carapace lengths of 34.0 (30.2) mm, carried 39 yellow eggs, another with corresponding lengths of 31.9 (27.8) mm bore 31 eggs. The other two obviously had lost most of the eggs that had been attached to their pleopods for there were many empty "egg cases" present. The diameters of the viable eggs (not those that were degenerating) were 2.0 or 2.1 mm.

ECOLOGICAL NOTES.—The largest colony of this species observed by me is located in the Nancy Hart State Park. There, especially in the low-lying wooded area adjacent to the spring and spring-run, chimneys of this crayfish are one of the most conspicuous features of the leaf-littered forest floor. The sandy soil is rich in organic matter, almost black when wet, and the roots of trees, shrubs, and vines are so dense, especially in the upper 20 centimeters, that attempting to unearth a crayfish is exceedingly difficult. Not only is penetrating the root mats a laborious undertaking, but inasmuch as the burrows consist of many branches (some extending horizontally and others vertically, often passing between and winding about roots), securing the crayfish indeed becomes a task. In attempting to cut through the root mats in the sandy soil, nearly always some of the passageways of the burrow are at least partly destroyed, and more often than not the crayfish has sought refuge from the digger in one of the galleries of which the latter is unaware. In this locality, we attempted to excavate many more burrows than those five from which we obtained specimens!

In two of the four remaining localities, the burrows were far less complex than those in the Nancy Hart Park, having been constructed in a sandy clay soil in roadside ditches that had been cleared of shrubs and trees. Although there were far fewer burrows there, the digging could be accomplished much more easily. Unfortunately, the water table in one of the localities was more than a meter below the surface, and the crayfish was reached some distance below the surface of the water.

As is characteristic of the abodes of other primary burrowers, the system of galleries is far more complex (branching with several to many horizontal passageways) in areas where the water table remains near the surface than in habitats in which there is considerable fluctuation in its level.

RELATIONSHIPS.—This crayfish, a member of the *latimanus* Group of the subgenus *Depressicambarus*, has its closets affinities with *C. (D.) striatus*, *C. (D.) reflexus*, and *C. (D.) truncatus*. It differs most conspicuously from the former two in possessing a more slender body. Its reduced abdomen, more scabrous telson and uropods, and a single pair of fixed spines on the telson serve to distinguish it from all populations of *C. (D.) striatus* that I have observed; in addition, it differs from most populations of the latter species in that the central projection of the first pleopod of the first form male is short, not tapering, and bears a well-defined subapical notch. The presence of a row of plumose setae along the caudomesial side of the mesial process of the first pleopod, if typical of all first form males of the species, is a unique character in the genus; only in an occasional specimen of *C. (D.) striatus* have I observed two or three such setae similarly positioned.

It may be distinguished from *C. (D.) reflexus* most readily by the first pleopod of the first form male which, in addition to bearing plumose setae along the caudomesial margin of the mesial process, exhibits a much shorter, less tapering, less strongly reflexed central projection provided with a well-defined subapical notch. The telson with a single pair of fixed spines differs from all except the larger specimens of *C. (D.) reflexus* in late intermolt stages; in them the movable spines are occasionally absent, probably having been abraded or broken.

The orange and olive or blue coloration of *C. (D.) strigosus* serves readily to distinguish it from the almost concolorous vermilion orange *C. (D.) truncatus*. Distinctive also is the setiferous fringe on the mesial process of the first pleopod of the male and the presence of distolateral and (usually) distomesial spines on the mesial ramus of the uropod. Furthermore the distomesial margin of the antennal scale is distinctly rounded rather than being subangular.

GEORGIA CRAYFISH ASSOCIATES.—This crayfish was found in one locality with *C. (D.) latimanus* and *P. (D.) devexus*, and in another with only the latter.

ETYMOLOGY.—From the Latin *strigosus* (lean), selected because of the slender cephalothorax and abdomen of this crayfish.

Cambarus (Depressicambarus) truncatus, new species

FIGURES 23*b*, 38*f*, 39*k*,*m*, 41, 57, 206

Cambarus diogenes subsp.—Hart and Hart, 1974:33.

On the basis of my tentative identification of a specimen of this crayfish, from 8.1 miles east of Irwinton on State Route 52, Wilkinson County, Georgia, Hart and Hart (1974) recorded it as a host of *Ankylocythere tiphophila* (Crawford, 1959).

DIAGNOSIS.—Eyes small. Rostrum without marginal spines or tubercles and lacking median carina. Carapace without cervical spine or prominent tubercle. Areola obliterated or as much as 50 times as long as broad, constituting 38.2 to 42.5 (average 40.6) percent of entire length of carapace (44.0 to 47.7, average 46.0, percent of postorbital carapace length). Suborbital angle virtually obsolete. Postorbital ridge terminating cephalically without spine or tubercle. Antennal scale almost 3 times as long as wide, widest distal to midlength. Palm of chela with at least 2 rows of tubercles, mesialmost row consisting of 7 or 8. First pleopod terminating in short, moderately arched central projection, its tip directed somewhat caudoproximally at about 110 degrees to main shaft of appendage and bearing distinct subapical notch; mesial process robust and mammiform, extending beyond tip of central projection; caudal knob absent. Mesial ramus of uropod almost always lacking distomedian and distolateral spines. Color pinkish orange with tan to brown areas particularly evident on dorsal surfaces of distal part of merus, on carpus, and on mesial half of palm of chela; abdominal terga without stripes or bands. Female with first pleopod present.

Holotypic Male, Form I.—Body subovate, compressed (Figure 57*a,j*). Abdomen narrower than cephalothorax (9.1 and 12.8 mm); greatest width of carapace slightly greater than depth at caudodorsal margin of cervical groove (12.8 and 12.0 mm). Areola linear, lacking punctations in narrowest part, length 41.5 percent of total length of carapace (46.9 percent of postorbital carapace length). Rostrum slightly asymmetrical with convergent, thickened margins, contracted more abruptly sinistrally than dextrally into short acumen, base of which not clearly set off from remainder of rostrum; apex reaching slightly beyond midlength of penultimate podomere of antennular peduncle; dorsal surface of rostrum deeply concave, weakly punctate but with transverse striae in basal part. Subrostral ridges moderately strong and evident in dorsal aspect to base of acumen. Postorbital ridges weak, lacking tubercles or spines cephalically and not markedly swollen caudally. Suborbital angle obsolete, cephalic margin of carapace broadly rounded in area usually occupied by angle; branchiostegal spine rudimentary. Cervical spine represented by small tubercle scarcely larger than those in hepatic region. Carapace punctate dorsally and granulate laterally with tubercles in anteroventral branchiostegal region and in cephalic hepatic region. Abdomen shorter than carapace (22.8 and 27.5 mm), pleura (Figure 39*k*) short, truncate ventrally and rounded caudoventrally. Cephalic section of telson with single fixed spine in each caudolateral corner; usual paired incisions shallow and transverse suture not evident (Figure 39*m*). Uropod with proximal podomere lacking spines; mesial ramus with well-developed submedian ridge devoid of marginal or premarginal spine and lateral margin of ramus entire, lacking lateral spine.

Cephalomedian lobe of epistome (Figure 57*g*) subrhomboidal, narrow, and with cephalomedian projection; margins slightly thickened and elevated ventrally; main body with fovea represented by comparatively shallow depression, epistomal zygoma arched. Ventral surface of proximal podomere of antennular peduncle lacking usual spine or tubercle. Antennal peduncle without spines; flagellum reaching sixth abdominal tergum; antennal scale (Figure 57*i*) almost 3 times as long as broad, broadest distinctly distal to midlength with mesial margin subangular at base of distal two-fifths, distal spine almost reaching base of ultimate podomere of antennular peduncle. Mesial half of ventral surface of ischium of third maxilliped studded with irregular rows of long stiff setae and with submarginal lateral row of both smaller stiff and plumose ones, few additional setae in area between; distolateral angle subacute.

Right chela (Figure 57*l*) 2.1 times as long as broad, mesial margin of palm occupying about one-third of its length. Mesial surface of palm with 2 well-defined rows of 7 tubercles each, more lateral row on left chela consisting of only 6 tubercles, row of 3 tubercles adjacent to mesialmost row ventrally; entire ventral surface of palm and mesial half of dorsal surface tuberculate, lateral half of latter punctate; 2 prominent tubercles present ventrally on marginal thickening opposite base of dactyl; lateral surface of chela strongly costate. Both fingers of chela with well-defined submedian longitudinal ridges dorsally and ventrally; opposable margin of fixed finger with row of 7 tubercles (third from base largest) extending along proximal three-fourths of finger, additional large tubercle on lower level slightly proximal to distalmost tubercle of row; opposable margin of dactyl with row of 11 tubercles (left with 9), fourth from base largest, along proximal three-fourths of finger; single row of minute denticles between and distal to tubercles along distal half of both fingers; mesial surface of dactyl with cluster of large tubercles on basal half and row of punctations continuing distally.

Carpus of cheliped with distinct furrow dorsally flanked by setiferous punctations; mesial surface with moderately large tubercle near base of distal fourth, another slightly smaller one immediately proximal to it, and 2 much smaller ones within proximal half; ventral surface punctate and bearing usual 2 marginal tubercles dis-

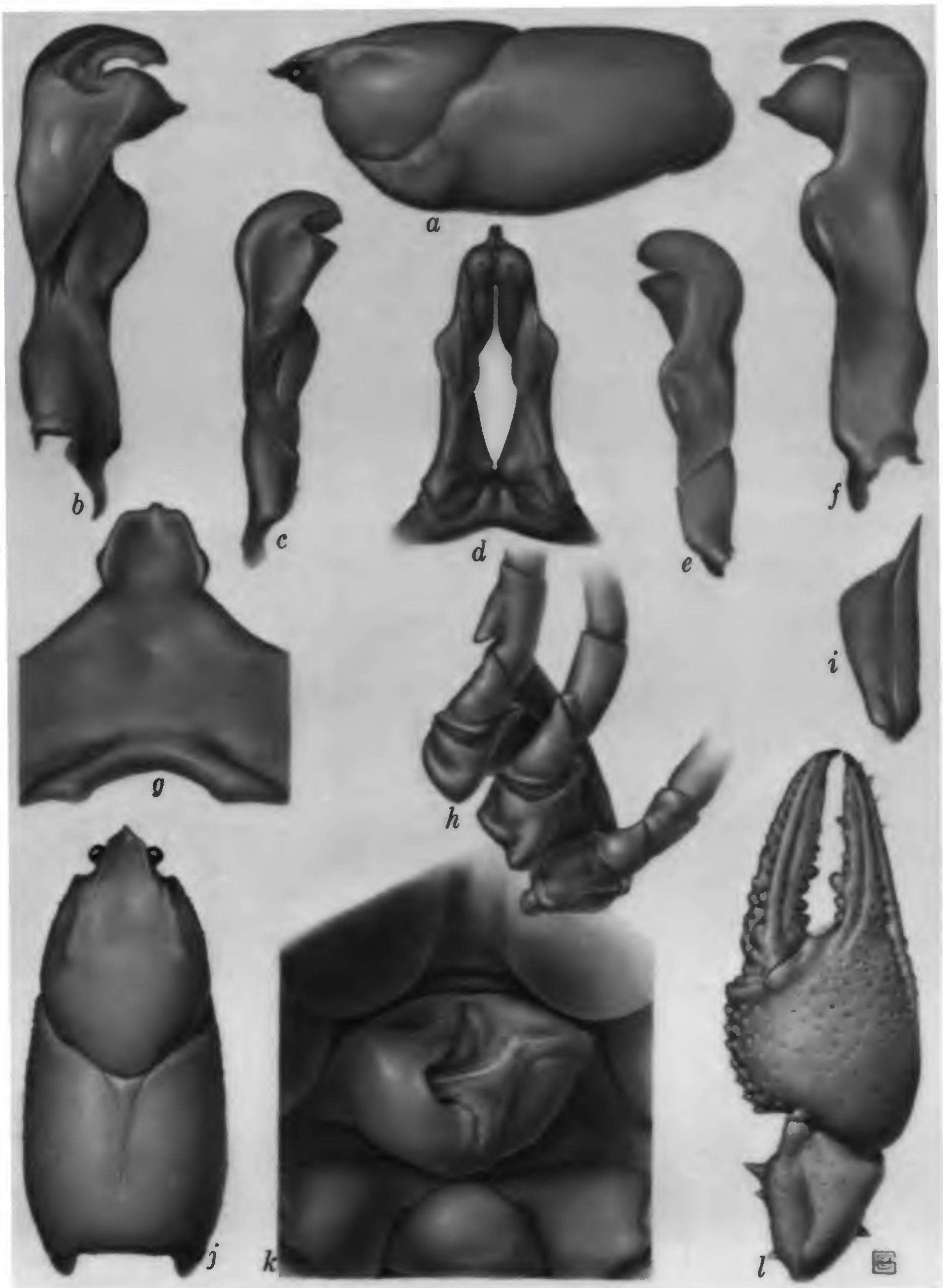


FIGURE 57.—*Cambarus (Depressicambarus) truncatus* (all from holotype except *c*, *e*, from morphotype, and *k*, from allotype): *a*, lateral view of carapace; *b*, *c*, mesial view of first pleopod; *d*, caudal view of first pleopods; *e*, *f*, lateral view of first pleopod; *g*, epistome; *h*, proximal podomeres of third, fourth, and fifth pereiopods; *i*, antennal scale; *j*, dorsal view of carapace; *k*, annulus ventralis; *l*, dorsal view of distal podomeres of cheliped.

tally and several additional small ones proximomesial to more mesial marginal tubercle. Merus with 4 (left with 2) premarginal tubercles dorsally, ventrolateral row of 8 (left with 6) tubercles, and ventromesial row of 11; podomere otherwise polished and/or punctate. Ventromesial margin of ischium with row of 4 small tubercles.

Ischium of third pereiopod with simple hook extending proximally over basioischial articulation (Figure 57*h*), opposed by very weak tubercle on basis. Coxa of fourth pereiopod with comparatively small subrectangular, vertically disposed caudomesial boss; that of fifth pereiopod lacking boss but with ventral membrane setiferous.

First pleopod (Figure 57*b,d,f*) reaching coxa of third pereiopod. (See "Diagnosis" for description.)

ALLOTYPIC FEMALE.—Differing from holotype, other than in secondary sexual characters, as follows: rostrum with margins contracted abruptly at base of triangular acumen; areola obliterated along part of its length; branchiostegal spine absent, not even represented by tubercle; mesial margin of palm of chela with 8 tubercles in mesialmost row and 6 (7 on left) in adjacent one, opposable margin of fixed finger with row of 5 tubercles, that of dactyl with 7 (6 on left); ventromesial row on merus of cheliped consisting of 10 tubercles (12 on left), and ventrolateral row of 7 (10 on left); ischium with ventromesial row of 3 (2 on left) tubercles. (See "Measurements.")

Annulus ventralis (Figure 57*k*) deeply embedded in sternum, subequal in length and width, strongly asymmetrical; cephalic region distinctly less calcified than caudal, with hinge action across junction of 2 areas; cephalic area with shallow submedian trough (dextral wall higher than sinistral), its caudal portion curving caudodextrally and with tongue extending beneath high thickened dextral wall, sinus originating there and following usual tilted S-shaped curve, ending on caudal wall in median line. Caudodextral wall inflated (convex) and caudosinistral wall concave. Postannular sclerite about 1.6 times as broad as long, length half that of annulus and width more than half that of latter. First pleopod reaching midlength of annulus when abdomen flexed.

MORPHOTYPIC MALE, FORM II.—Differing from holotype in following respects: shape of rostrum more nearly approaching that of allotype; no trace of branchiostegal spine; mesial margin of palm of left chela with 8 tubercles in mesialmost row and 6 in adjacent row on both chelae; opposable margin of fixed finger with small tuft of plumose setae at base, and with row of 5 tubercles on right and 4 on left; corresponding margin of dactyl with 6 tubercles on both right and left; dorsal surface of merus of cheliped with 3 (right) and 2 (left) preapical tubercles, ventral surface with mesial row of 10 tubercles and lateral one of 7; ischium of cheliped with only 2 tubercles ventromesially; hook on ischium of third pereiopod poorly developed, adnate, not overreaching basioischial articulation; boss on coxa of fourth pereiopod proportionately not much reduced. (See "Measurements.")

First pleopod (Figure 57*c,e*) reaching coxa of third pereiopod; central projection rounded distally, lacking subapical notch, and directed at about 75 degree angle to main shaft of appendage; mesial process less inflated and less constricted apically than in holotype.

COLOR NOTES (Figure 38*f*).—Basic color of body pale orange tan with darker tan markings. Rostrum with paired narrow longitudinal stripes immediately mesial to postorbital ridges, and subrostral ridges light orange tan. Remainder of cephalic region dark tan except for cream marginal antennal and mandibular regions, light transverse band across base of postorbital ridges, and paired light oval patches over posterior gastric region short distance cephalic to cervical groove. Branchiostegites pale tan, tinged with red dorsally and fading to cream ventrally; cephalic and caudal triangular parts of areola suffused with dark tan. Abdomen with cephalic part of tergum of first abdominal segment almost brown and succeeding terga with dorsal part suffused with dark tan extending onto cephalic part of telson; lateral portions of terga and much of pleura pale orange, latter with cream spot encompassing part of margin of each. Uropods and caudal part of telson cream. Antennular and antennal peduncles orange tan, flagella tan. Cheliped more orange than tan basically, with dark tan to brown reticulate markings on dorsal surfaces of distal part of merus, mesial half of carpus, and mesial half of palm of chela. Remaining pereiopods pinkish orange suffused with tan on merus and carpus, and ventral surface of body pinkish cream.

Measurements (mm)

	Holotype	*Allotype*	*Morphotype*
Carapace			
Height	12.0	11.7	7.9
Width	12.8	13.4	8.4
Entire length	27.5	27.8	19.9
Postorbital length	24.3	24.9	17.2
Areola			
Width	0.1	0	0.1
Length	11.4	11.5	8.0
Rostrum			
Width	3.9	4.2	3.1
Length	3.7	3.7	3.0
Chela			
Length of mesial margin of palm	6.5	6.4	3.8
Width of palm	9.2	8.7	5.4
Length of lateral margin	19.6	18.2	11.1
Length of dactyl	12.8	10.7	7.4
Abdomen			
Width	9.1	9.5	6.0
Length	22.8	23.6	14.7

TYPES.—The holotypic male, form I, allotypic female, and morphotypic male, form II (numbers 116966, 146649, and 146650, respectively), are deposited in the National Museum of Natural History, Smithsonian Institution, together with the paratypes comprising 2♂I, 1♂II, 8♀, 3j♂, and 1j♀.

TYPE-LOCALITY.—Roadside ditch 15.4 miles east of Irwinton, Wilkinson County, Georgia, on State Route 57, where specimens were dug from complex burrows in sandy clay soil.

RANGE.—Known from only 4 localities on the Fall Line Hills District in the Oconee Basin of Laurens and Wilkinson counties, Georgia.

GEORGIA SPECIMENS EXAMINED.—I have examined 18 specimens from the following localities. *Laurens County:* (1) roadside ditch 2.6 mi NW of St Rte 338 on US Hwy 441 (10.7 mi SW of Court House in Dublin), 2♀, 1j♀, 20 Jun 1975, D. J. Peters, J. E. Pugh, HHH, collectors; 1♂I, 1♂II, 1♀, 21 Apr 1977, C. E. Carter, JEP, HHH. *Wilkinson County:* (2) type-locality, 1♂I, 1♂II, 1♀, 26 Apr 1966, E. T. Hall, Jr., HHH; (3) roadside ditch 8.1 mi E of Irwington on St Rte 57, 1♂I, 26 Apr 1966, ETH, HHH; (4) roadside ditch 2.1 mi E of Toomsboro on St Rte 57, 5♀, 3j♂, 3 Apr 1978, R. J. Dubois, DJP, JEP, HHH.

VARIATIONS.—Most of the variations noted are minor ones involving numbers of tubercles on a podomere of the cheliped, and the only ones observed that are not pointed out in the descriptions of the primary types are rows of 10 tubercles on the opposable margins of both fingers in one of the males and the presence on the ischium of the cheliped of only a single tubercle ventromesially. The carpus of the right cheliped of one of the largest females has a row of four spines on the mesial surface. Most of the specimens possess spines on the basal segment of the antennular peduncle. A first form male is the only specimen in which there exists a small premarginal spine at the end of the median rib of the mesial ramus of the uropod, and in the same specimen, as well as in others, the telson is more deeply incised at the level of the base of the lateral spines than in the holotype. One of the first form males lacks virtually any trace of the tubercle on the basis of the third pereiopod opposing the ischial hook. No variation worthy of note is evident in the first pleopod of the first form males. The allotype and the second form male are the only specimens that possess a distolateral spine on one of the pairs of mesial rami of the uropods. The postannular sclerite is distinctly small in proportion to the annulus ventralis in the paratypic females.

SIZE.—The largest specimen available is a male, form I, in which the carapace length is 34.1 (postorbital carapace length 30.4) mm. The smallest first form male has corresponding lengths of 25.6 and 22.8 mm. No females with eggs or young have been observed.

LIFE HISTORY NOTES.—First form males have been collected only in April. No other data are available.

Ecological Notes.—Almost certainly, this crayfish is a primary burrower, for, although few specimens have been collected, all of them were dug from complex burrows. In two of the localities the tunnels were constructed in a sandy clay soil; in the third, however, the soil was a peculiar (to me) lumpy clay that flaked from the walls of the passageways into the water, forming a flocculent mixture similar in consistency to coarse cottage cheese from which the whey had not been filtered. In such a soil the passageways were exceedingly difficult to follow, becoming clogged with the packed lumps of clay. All of the burrows possessed at least two galleries leading to the surface and one that penetrated well below the water table; in addition there were always one to several side tunnels that extended for 0.3 to 1.0 meter obliquely or horizontally. None of the specimens collected could be lured into the open mouth of the burrow where it could be captured easily.

Relationships.—*Cambarus (D.) truncatus* probably has its closest affinities with *C. (D.) reflexus*, *C. (D.) strigosus*, and *C. (D.) striatus*, from which it differs primarily in the orange to red orange coloration and the lack of a marginal spine (two exceptions, see "Variations") on the mesial ramus of the uropod, which also rarely possesses a premarginal median spine. Also the central projection of the first pleopod is short and not nearly so strongly recurved as in *C. (D.) reflexus*. The absence of a distolateral spine on the mesial ramus of the uropod is apparently unique among the members of the genus *Cambarus*. Such a condition has been reported for the family Cambaridae only in a few members of the genus *Fallicambarus* (for summary, see Hobbs, 1973b:477–479, fig. 4). (See also "Relationships" under *C. (D.) reflexus* and *C. (D.) strigosus*.)

Georgia Crayfish Associates.—Only two species have been found in burrows adjacent to those of *C. (D.) truncatus*. In two of the localities *C. (D.) striatus* was present, and in one of them *Faxonella clypeata* was also found in a burrow.

Etymology.—The name *truncatus* refers to the comparatively short terminal elements of the first pleopod of the first form male.

Subgenus *Hiaticambarus*

Subgenus *Bartonius* Ortmann, 1905a:97 [in part].

Subgenus *Cambarus* Fowler, 1912:341 [in part; not Erichson, 1846:97].

Subgenus *Hiaticambarus* Hobbs, 1969a:105 [type-species: *Cambarus longulus* Girard, 1852:90].

Diagnosis.—Body pigmented, eyes well developed. Rostrum with thickened margins and with or without marginal spines or tubercles. Postorbital and cervical spines present or absent. Suborbital angle present or absent, sometimes acute. Branchiostegal spine reduced to very weak spine or tubercle. Areola broad, 2.3 to 6.0 (2.6 to 5.2 in Georgia) times as long as broad and comprising 30.3 to 40.4 percent of entire length of carapace (40.0 to 48.9 percent of postorbital carapace length), and bearing crowded deep punctations. Chela moderately heavy and usually with comparatively slender fingers bearing large deep punctations; mesial surface of palm usually with single row of low tubercles although sometimes tubercles rather prominent and occasionally with part of (or entire) second row; lateral margin of fixed finger rounded to costate, costa sometimes extending proximally along almost entire length of palm; fingers strongly gaping, especially in male, form I, and usually with poorly defined longitudinal ridges dorsally (occasionally well developed); conspicuous tuft of setae generally present at mesial base of fixed finger, lateral base inflated, rarely impressed, proximomesial surface of dactyl only occasionally with tubercles. First form male with first pleopods widely separated or contiguous basally; terminal elements consisting of (1) blade-like, distally notched (except in *C. (H.) speciosus*) central projection curved more than at right angle to main shaft of appendage, (2) swollen, distally tapering mesial process extending caudally or caudolaterally almost to, or slightly surpassing, apex of central projection, and (3) caudal process vestigial or absent. Annulus ventralis shallowly embedded in sternum and at least slightly asymmetrical. Female with or without first pleopod.

Range.—

The subgenus ranges from the upper Piedmont and lower mountain sections of the James and Yadkin drainage systems in Virginia and North Carolina through the New River system from West Virginia to North Carolina, southward through the Tennessee system to the Coosa in Georgia and Alabama and the upper Savannah in South Carolina (Hobbs, 1969a: 141).

In Georgia it is confined to the northwestern part of the State in the Coosa and Tennessee river basins.

SPECIES OCCURRING IN GEORGIA.—*Cambarus (H.) coosawattae*, *C. (H.) fasciatus*, *C. (H.) girardianus*, *C. (H.) longirostris*, *C. (H.) manningi*, and *C. (H.) speciosus*.

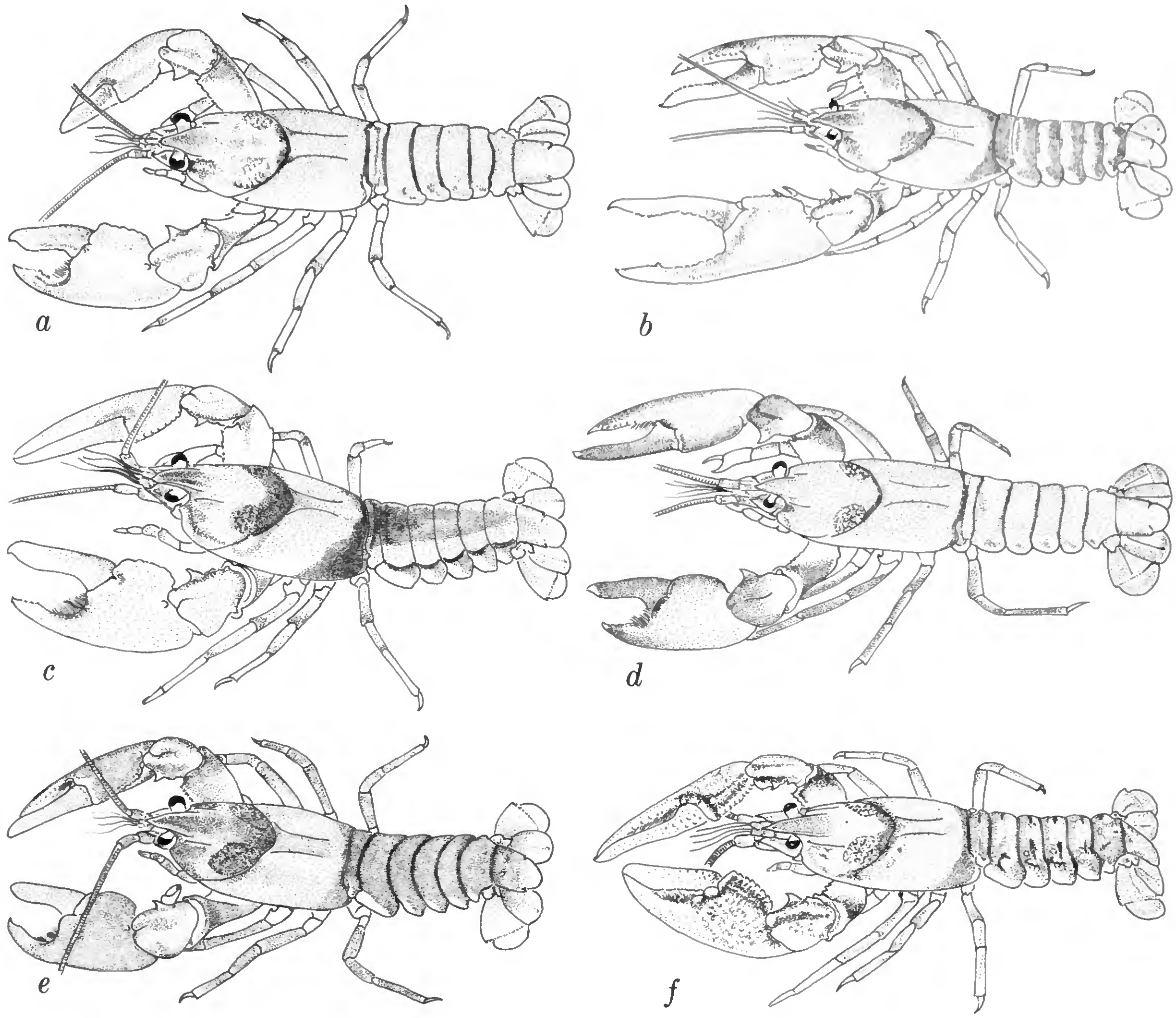


FIGURE 58.—Color patterns of Georgia representatives of subgenus *Hiaticambarus*: *a*, *Cambarus (H.) coosawattae* from 5.4 mi N of Ellijay on US Hwy 76, Gilmer Co; *b*, *C. (H.) fasciatus* from Amicalola Creek 6.4 mi W of Dawsonville on St Rte 53, Dawson Co; *c*, *C. (H.) girardianus* from tributary to Chickamauga Creek 4.6 mi W of St Rte 71, Catoosa Co; *d*, *C. (H.) longirostris* from East Fork of Wolf Creek at junction with West Fork, off US Hwy 19, Union Co; *e*, *C. (H.) manningi* from Little Cedar Creek at Cave Spring, Floyd Co; *f*, *C. (H.) speciosus* from Talking Rock Creek at St Rte 5, Pickens Co.

HABITAT.—The members of the subgenus *Hiaticambarus* are primarily inhabitants of riffles, although *C. (H.) girardianus* appears to be far less restricted to rocky areas of streams than are the other Georgia representatives of the subgenus. Whereas this crayfish is always found in streams, I have collected specimens in burrows in the stream bank as well as in leaf litter in eddies. There is some evidence that where it shares a stream with *C. (H.) longirostris*, the latter dominates the riffles and *C. (H.) girardianus* occurs more abundantly in the swift waters up- and downstream from them. Observations suggest also that *C. (H.) fasciatus* is less confined to riffles than are *C. (H.) coosawattae*, *C. (H.) longirostris*, *C. (H.) manningi*, and *C. (H.) speciosus*.

REMARKS.—Recently, Bouchard (1976b:592) placed Faxon's *Cambarus bartonii longirostris* Faxon (1885a:64) in synonomy with *Cambarus girardianus* Faxon (1884:117). Even though I do not hesitate to admit that among specimens of *Hiaticambarus* from Tennessee there exist individuals that seem to combine features of both, I am not convinced that the two species should be united. As pointed out in the treatment of *C. (H.) girardianus* that follows, it is an extremely variable species in Georgia (as it is in Tennessee), but the fact that I have collected it along with what I interpret to be *C. (H.) longirostris* in the same habitat, with no intermediate forms, necessitates my continued recognition of the two as distinct species. Perhaps I am in error in identifying the Georgia specimens ascribed to *C. (H.) longirostris* as conspecific with Faxon's species, in which case a new name must be proposed for them. The comparatively small, almost concolorous riffle-dwelling *Hiaticambarus* (forms that I have assigned to *C. (H.) longirostris*) in the Hiwassee Basin, in Lookout Creek, and in the Chattooga drainage system in northern Georgia are surely distinct from the more robust, colorful members of the genus (my *C. (H.) girardianus*) that at least occasionally share the same habitat, and indeed in one locality (Lookout Creek) were collected in the same seine haul. Not only are the color patterns markedly different but also there are other morphological distinctions in the Georgia material at hand. Suspect in the assumed synonomy of the two species are James' (1966:10) remarks related to the "concolorous" and "saddle pattern" of living specimens of *C. (H.) longirostris* examined by him. I suggest that those individuals with the "saddle pattern" are perhaps members of *C. (H.) girardianus* and the "concolorous" ones, *C. (H.) longirostris*.

I have compared the Georgia specimens here assigned to *C. (H.) longirostris* with topotypes of the species from the Doe River in Carter County, Tennessee, and find them to have most characters in agreement and to be quite distinct from those of *C. (H.) girardianus*, which compare favorably with my specimens from Lookout Creek. With the reservations stated above concerning the conspecificity of my *C. (H.) longirostris* and Faxon's species, I am recognizing it as distinct from *C. (H.) girardianus*. A description of Georgia representatives of *C. (H.) longirostris* is included herein.

According to my interpretation, the subgenus *Hiaticambarus* is composed of a group of eight species that are apparently both morphologically and ecologically (primarily riffle dwellers) allied. Only two of its recognized members, *C. (H.) longulus* Girard (1852:90) and *C. (H.) chasmodactylus* James (1966:14), are not found in Georgia. Two of the remaining ones, *C. (H.) girardianus* and *C. (H.) longirostris*, occur in the Tennessee River basin of Georgia and also in neighboring states. *Cambarus* (*H.*) *manningi* has been found in the Coosa Basin in Alabama and Tennessee, and, in all probability, *C. (H.) fasciatus* also occurs in Alabama. *Cambarus (H.) coosawattae* and *C. (H.) speciosus* are known only from the Coosawattee watershed (Coosa Basin) in Georgia and are probably endemic in the state.

The more generalized species, having more in common with members of the subgenus *Puncticambarus* than do the others, are *C. (H.) fasciatus*, *C. (H.) girardianus*, and *C. (H.) speciosus*; the latter has almost as many *Puncticambarus* characters as those typical of *Hiaticambarus*. Chief among those features prompting me to consider these species to be the more generalized members of the subgenus are the chelae, which tend to or have two rows of tubercles along the mesial surface of the palm, often moderately to well developed dorsal longitudinal ridges on the fingers, and a subcostate to costate lateral border. In addition, the rostra of virtually all members of *C. (H.) fasciatus* and some populations of *C. (H.) girardianus* possess marginal spines; these are always lacking in *C. (H.) speciosus*. Cervical spines are always strongly developed in the latter, in *C. (H.) fasciatus*, and occasionally in *C. (H.) girardianus*; and a comparatively strong suborbital angle is present in *C. (H.) speciosus* and *C. (H.) girardianus*, whereas it is obtuse or almost lacking in *C. (H.) fasciatus*.

Despite possessing what I consider to be the most generalized chela of any member of the subgenus, as well as strong cervical spines, *C. (H.) speciosus* has an acuminate rostrum devoid of marginal spines or tubercles and is unique in the subgenus in possessing a tapering central projection on the first pleopod, which also lacks a subapical notch. As is indicated above, some populations of *C. (H.) girardianus* lack marginal spines or tubercles on the rostrum; in addition, the cervical spines are frequently reduced to tubercles. *Cambarus (H.) fasciatus* departs from the more generalized condition most conspicuously in having a reduced suborbital angle and chelae that are not nearly so *Puncticambarus*-like as those of *C. (H.) speciosus*, and it is the only member of *Hiaticambarus* in which the female lacks a first pleopod.

At least in the retention of marginal tubercles on the usually strongly tapered rostrum, *C. (H.) coosawattae* serves to link the more generalized species with *C. (H.) longirostris*, *C. (H.) longulus*, *C. (H.) chasmodactylus*, and *C. (H.) manningi*. In lacking a trace of a cervical spine and a suborbital angle, however, it by no means represents an arrested stage in the evolution of the latter four. Nevertheless, at least in its color pattern, it more closely resembles the Georgia populations of *C. (H.) longirostris* than do any other members of the subgenus.

With little doubt, *C. (H.) chasmodactylus*, *C. (H.) longulus*, and *C. (H.) manningi* are the most specialized members of *Hiaticambarus*: tubercles comprising the single row borne on the mesial surface of the palm of the chela are greatly reduced, the more distal ones frequently so strongly adpressed as to be virtually absent; the cervical spines are at most tuberculiform; and the suborbital angle is very broadly obtuse or obsolete. *Cambarus (H.) manningi* appears to be the most divergent of the four; not only is the areola proportionately longer but also the color pattern is much more spectacular than that of the other two, with contrasting shades of almost black, red, blue, and white to cream markings. Ecologically, these three appear to be far more restricted to riffle areas of streams than are the supposedly more primitive *C. (H.) speciosus* and *C. (H.) girardianus*.

With respect to the ranges of the members of the subgenus, two pairs of species, *C. (H.) coosawattae* and *C. (H.) speciosus*, and *C. (H.) girardianus* and *C. (H.) longirostris*, are sympatric (occasionally syntopic), and it is highly probable that the ranges of *C. (H.) fasciatus* and *C. (H.) manningi* will be shown to overlap. Insofar as is known, the range of *C. (H.) chasmodactylus* (confined to the Kanawha Basin of North Carolina, Virginia, and West Virginia) does not overlap that of *C. (H.) longulus*, which occurs in the "Atlantic watershed from the James drainage in Virginia south to the Yadkin drainage in North Carolina . . ." (Hobbs, 1974b:16).

Reference has been made here to the presence of *C. (H.) manningi* in Alabama. Although I anticipated the occurrence of *Cambarus (H.) fasciatus* among the *Hiaticambarus* occurring in the upper Coosa Basin of that state, I did not find it; furthermore I am unable to assign what appears to be two distinct forms collected there to any of the currently recognized species.

Key to Georgia Members of Subgenus *Hiaticambarus*

1. Central projection of first pleopod of first form male without subapical notch; chela with at least 2 well-defined rows of tubercles on mesial

margin of palm and tubercles on proximomesial surface of dactyl .... ***speciosus***

Central projection of first pleopod of first form male with subapical notch; chela rarely with 2 rows of tubercles on mesial surface of palm and lacking tubercles on proximomesial surface of dactyl 2

2. Length of areola almost always at least 38 (average 39) percent of total length of carapace and no less than 45 (average 46.7) percent of postorbital carapace length; terga of abdomen dark with neither longitudinal stripe nor transverse bars .... ***manningi***

   Length of areola almost always less than 38 (no population averaging more than 36) percent of total length of carapace and less than 45 (no population averaging as much as 44) percent of postorbital carapace length; terga of abdomen with median longitudinal stripe, with transverse bars, or with caudal marginal lines 3

3. Rostral margins strongly convergent with small marginal tubercles (sometimes abraded in old or late intermolt individuals); suborbital angle obsolete; terga of abdomen with dark color largely limited to burgundy line on caudal margin of first 5 segments, first tergum often with additional transverse band .... ***coosawattae***

   Rostral margins not strongly convergent, or if so, lacking marginal tubercles; suborbital angle obtuse or acute, never obsolete; terga of abdomen with median longitudinal stripe or with transverse bands or caudal marginal lines 4

4. Cervical spine well developed; chela without tuft of setae at opposable base of fixed finger, or, if setae present, then lateral margin of chela costate with costa reaching proximally to midlength of palm; ischium of antennal peduncle with spiniform tubercle ventrally; terga of abdomen with broad transverse dark band on each segment, never with dark scalloped stripe extending along base of pleura. First pleopods of male not contiguous basally. Female lacking first pleopod .... ***fasciatus***

   Cervical spine seldom strongly developed, occasionally represented by low spiniform tubercle in *C. (H.) girardianus*; chela almost always with conspicuous tuft of setae at opposable base of fixed finger; if lateral margin of chela subcostate (never distinctly so), costa never extending so far proximally as midlength of palm; ischium of antennal peduncle without spiniform tubercle ventrally; terga of abdomen with posterior margins bearing very narrow dark border or with median longitudinal dark stripe, sometimes with dark scalloped stripe extending along base of pleura. First pleopods of male contiguous basally. Female with first pleopod 5

5. Marginal spines present or absent on rostrum; suborbital angle subacute, often conspicuously long; mesial margin of palm of chela with tubercles distinct along entire length; pleura of second through fifth abdominal segments with distinct posteroventral angle; carapace with 2 broad transverse dark bands at least dorsally; terga of abdomen with broad caudally tapering median longitudinal stripe, scalloped stripe extending along bases of pleura .... ***girardianus***

Marginal spines of rostrum always lacking; suborbital angle obtuse mesial margin of palm of chela with tubercles along distal half or third so strongly adpressed as to be obscured in silhouette and sometimes replaced by punctations; pleura of second through fifth abdominal segments rounded posteroventrally; carapace lacking transverse dark bands; terga of abdomen with very narrow transverse burgundy or dark brown band on posterior margin of each, first sometimes with broad similarly colored band on anterior section; lacking scalloped stripe along bases of pleura .... ***longirostris***

Cambarus (Hiaticambarus) coosawattae, new species

FIGURES 22*b*, 58*a*, 59, 60, 207

Cambarus (Cambarus) extraneus.—Ortmann, 1931:98*.
Cambarus longulus.—Anonymous, 1967a, tab. 3.
Cambarus (Hiaticambarus) species G.—Hobbs, 1969a:106, 141, fig. 10* [in part].

The first record of the occurrence of this species is that of Ortmann (1931), which was based upon two second form males from the Cartecay River, East Ellijay, Gilmer County, Georgia. As indicated above, he erroneously identified these specimens as *Cambarus (C.) extraneus*. Anonymous (1967a) recorded this crayfish as *C. longulus* from the Coosawattee River, 2 miles south of Ellijay at State Route 5, Gilmer County. The distribution map provided by Hobbs (1969a) for his "species G" encompasses the ranges of two species of the subgenus (both described herein: *C. (H.) coosawattae* and *C. (H.) fasciatus*), as do the references to it on pages 106 and 141. No specific localities were cited by him.

DIAGNOSIS.—Rostrum with strongly tapering margins bearing small spines or tubercles (sometimes abraded in individuals in late intermolt stage) at base of acumen. Postorbital ridge terminating cephalically in spine. Cervical spine and suborbital angle obsolete. Areola 2.8 to 4.0 times as long as broad and comprising 34.8 to 37.8 percent of entire length of carapace (41.8 to 44.3 percent of postorbital carapace length). Chela with tubercles along mesial margin of palm adpressed, more distal ones sometimes virtually lacking, always with conspicuous setal tufts at mesial base of fixed finger; lateral margin of propodus costate or subcostate. Hook on ischium of third pereiopod opposed by tubercle on basis. Pleura of third through fifth abdominal segments truncate ventrally and with caudoventral angle. First pleopod of first form male with moderately short terminal elements: central projection bearing distinct subapical notch, not tapering, and directed at about 120 degrees to shaft of appendage; mesial process inflated, tapering, with acute tip directed caudally at about right angle. Terga of abdomen with narrow, dark marginal band posteriorly, first with slightly paler transverse band across midlength, and pleura lacking scalloped stripe at base. Female with first pleopod present.

HOLOTYPIC MALE, FORM I.—Body subovate, depressed (Figure 59*a,j*). Abdomen narrower than cephalothorax (10.8 and 12.5 mm); maximum width of carapace markedly greater than depth at caudodorsal margin of cervical groove (12.5 and 9.4 mm). Areola 3.9 times as long as broad, constituting 36.6 percent of total length of carapace (44.2 percent of postorbital carapace length), densely punctate with about 9 punctations across narrowest part. Rostrum with thickened margins converging strongly to base of acumen, there subangular and bearing small corneous tubercles; acumen with strongly upturned tip, reaching end of basal third of ultimate podomere of antennular peduncle; dorsal surface of rostrum weakly concave and bearing crowded, deep punctations, those in basal portion coalescing into striae. Subrostral ridges rather strong but evident in dorsal aspect only posterior to acumen. Postorbital ridge short, grooved dorsolaterally, and terminating cephalically in acute spine. Suborbital angle obsolete; branchiostegal spine re-

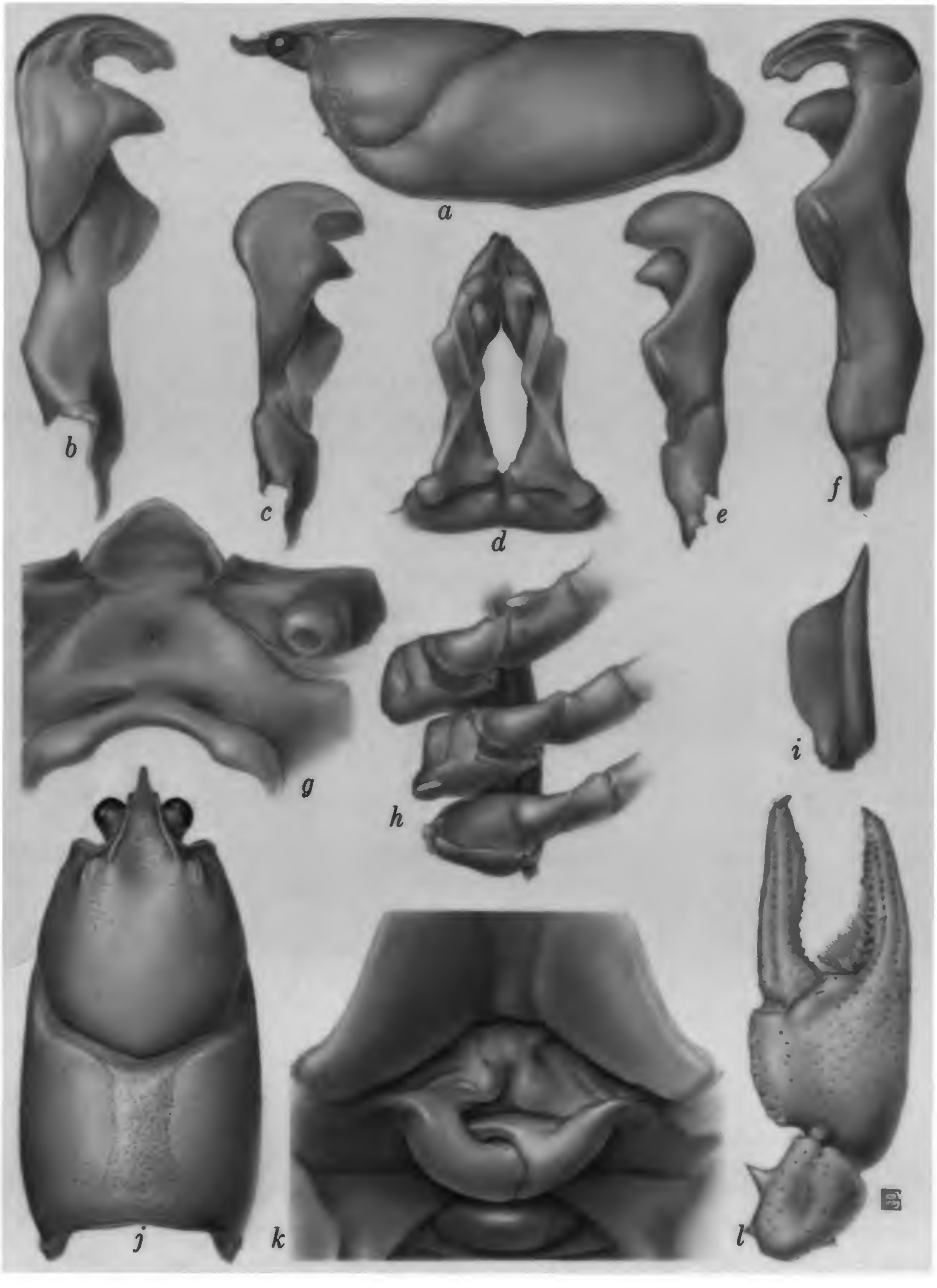


FIGURE 59.—*Cambarus (Hiaticambarus) coosawattae* (all from holotype except *c*, *e*, from morphotype, and *k*, from allotype): *a*, lateral view of carapace; *b*, *c*, mesial view of first pleopod; *d*, caudal view of first pleopods; *e*, *f*, lateral view of first pleopod; *g*, epistome; *h*, proximal podomeres of third, fourth, and fifth pereiopods; *i*, antennal scale; *j*, dorsal view of carapace; *k*, annulus ventralis; *l*, dorsal view of distal podomeres of cheliped.

duced to subacute tubercle. Cervical spine lacking, not even represented by tubercle. Carapace densely punctate dorsally except for polished median gastric area and that interrupted by 2 or 3 punctations, lateral surface mostly granulate but tubercles present in ventral hepatic, antennal, and mandibular regions and flanking cervical groove in anteroventral branchiostegal area. Abdomen shorter than carapace (23.3 and 24.6 mm); pleura moderately long, truncate ventrally, and angular posteroventrally. Cephalic section of telson with 2 spines in each caudolateral corner, usual lateral incision deep and transverse suture clearly defined. Uropod with both lobes of proximal podomere bearing corneous spine; mesial ramus with distolateral spine and poorly defined submedian ridge ending in distomedian spine.

Cephalomedian lobe of epistome (Figure 59*g*) subtriangular, central area somewhat elevated, lacking cephalomedian prominence; main body with distinct fovea and arched epistomal zygoma, latter flanked anterolaterally by deep elongate pits. Ventral surface of proximal podomere of antennular peduncle with short acute tubercle very near distal end. Antennal peduncle with strong lateral spine on basis and with subacute corneous tubercle on ventral surface of ischium; flagellum reaching sixth abdominal tergum; antennal scale (Figure 59*i*) about 2.8 times as long as broad, widest along area contiguous to midlength, distolateral spine strong and reaching distal margin of antennular peduncle. Ventral surface of ischium of third maxilliped with broad longitudinal band of both stiff and plumose setae and with submarginal lateral row of smaller stiff and plumose ones; irregular row of punctations bearing short plumose setae between band and submarginal row; distolateral extremity subacute but not produced.

Right chela (Figure 59*l*) 2.2 times as long as broad, mesial margin of palm occupying about one-third its length. Mesial surface of palm with single row of 8 adpressed tubercles flanked dorsally by row of punctations; dorsal and ventral surfaces with large, deep punctations, and palm subcostate distolaterally. Fingers moderately widely gaping and with prominent setal tuft protruding into gap from proximal half of opposable margin of fixed finger; deep punctations and depression flanking subcostate lateral margin of finger, setting off well-defined median longitudinal ridge on dorsal surface of finger; opposable margin with row of 9 rounded tubercles along proximal two-thirds of finger and single large tubercle on lower level between seventh and eighth of row; band of minute denticles extending distally from proximal base of large tubercle to corneous tip of finger; opposable margin of dactyl with row of 11 tubercles along proximal four-fifths of finger and band of minute denticles, interrupted by tubercles, extending from sixth tubercle from base to corneous tip of finger; median longitudinal ridge on dorsal surface not so prominent as that on fixed finger; mesial surface of dactyl punctate.

Carpus of cheliped with well-developed longitudinal furrow dorsally, flanked by setiferous punctations; mesial surface with large spikelike tubercle, lacking more proximal tubercle present in some other members; ventral surface punctate and 2 tubercles present on distal margin, 1 on lateral condyle and other on mesioventral angle. Merus with 1 premarginal tubercle dorsally; ventrolateral row of tubercles represented by only 2, and ventromesial row consisting of 7 (left member with 6), all acute, and distal members of both rows spikelike; distolateral surface with minute corneous tubercle. Mesial margin of ischium with 2 small tubercles.

Ischium of third pereiopod with simple hook overreaching basioischial articulation and opposed by strong tubercle on basis (Figure 59*h*). Coxa of fourth pereiopod with transverse boss vertically disposed, that of fifth pereiopod devoid of boss but with ventral membrane sparsely setiferous.

First pleopods (Figure 59*b*,*d*,*f*) reaching coxa of third pereiopod, symmetrical, with gap between their bases. (See "Diagnosis" for description.)

ALLOTYPIC FEMALE.—Excluding secondary sexual characters, differing from holotype in following respects: flagellum of antennae reaching fifth abdominal tergum, antennal scale broadest distal to midlength; mesial margin of palm of chela with adpressed row of 9 tubercles on right chela and 7 on left; opposable margin of fixed finger with row of 7 tubercles along basal two-thirds and large tubercle on lower level between sixth and seventh tubercles from base; corresponding margin of dactyl with row of 9 tubercles; mesial surface of carpus of cheliped with small tubercle proximal to large spikelike one; 6 tubercles present in ventromesial row on merus; mesial margin of ischium with 3 small tubercles. (See "Measurements.")

Annulus ventralis (Figure 59*k*) approximately 1.5 times as broad as long, slightly movable, subsymmetrical, cephalic and central areas less sclerotized than caudal part; cephalic area with subparallel longitudinal ridges flanking median trough leading to depressed central area; sinus originating at caudal end of trough, from there extending dextrally, making hairpin turn, to median line before turning rather sharply and forming arc slightly sinistral to median line, returning to latter on caudal wall. Postannular sclerite with straight caudal margin and broadly arched cephalic margin, almost one-third as long and little less than three-fourths as wide as annulus. First pleopods reaching midlength of annulus when abdomen flexed.

MORPHOTYPIC MALE, FORM II.—Differing from holotype in following respects: margins of rostrum continuous with base of acumen, lacking angle but with minute tubercle marking position of angle in other specimens; branchiostegal spine vestigial; ischium of antennal peduncle on right side lacking small acute tubercle (injured?), flagellum reaching fourth abdominal tergum; opposable margin of fixed finger of right chela with row of 8 tubercles (left cheliped regenerated), that of dactyl with 10; mesial surface of carpus with small tubercle proximal to spikelike one; ventromesial surface of ischium with 4 tubercles; hook on ischium of third pereiopod much reduced, not overreaching basioischial articulation. First pleopod (Figure 59*c,e*) with juvenile suture on shaft; central projection inflated with subacute apex directed caudally at right angle; mesial process little different from that of holotype.

COLOR NOTES (Figure 58*a*).—Entire body basically pale olive to brown with darker olive to dark brown reticulations on mandibular adductor region and dark brown cervical groove; posterior margin of carapace and corresponding margin of all abdominal terga with narrow band of burgundy; rostral margins and postorbital ridges orange to vermilion; antennal and mandibular regions pinkish cream; telson and uropods pale olive to brown with orange to vermilion spines and spots on proximal podomere of latter; basal podomeres of all pereiopods cream to midlength of ischium, from there distally pale to dark olive and with orange to vermilion articular margins, knobs, spines, and tubercles.

Measurements (mm)

	Holotype	*Allotype*	*Morphotype*
Carapace			
Height	9.4	8.6	8.1
Width	12.5	11.9	10.2
Entire length	24.6	23.5	21.4
Postorbital length	20.4	19.3	17.6
Areola			
Width	2.3	2.3	2.4
Length	9.0	8.2	7.6
Rostrum			
Width	3.7	3.4	3.5
Length	5.4	5.5	5.1
Chela			
Length of mesial margin of palm	7.4	5.8	5.5
Width of palm	10.0	7.3	7.1
Length of lateral margin	22.1	17.2	16.2
Length of dactyl	13.5	9.8	9.3
Abdomen			
Width	10.8	11.8	9.1
Length	23.3	23.8	21.1

TYPES.—The holotypic male, form I, allotypic female, and morphotypic male, form II (numbers 148112, 148113 and 148114, respectively), are deposited in the National Museum of Natural History, Smithsonian Institution, as is the paratypic series, which is restricted to those specimens listed from localities 1-4, 8, and 9 under "Specimens Examined."

TYPE-LOCALITY.—Cartecay River, 6 miles east southeast of Ellijay, just off Route S1010, near Flint Hill Church, Gilmer County, Georgia.

There the stream, some 17 meters wide and less than 1 meter deep, flows with a swift current over a sandy, rock-littered bottom. The water is clear and shaded along the margins of the stream by *Liriodendron tulipifera*, *Plantanus occidentalis*, *Quercus* sp., and *Prunus* sp. Only one other crayfish, *C. (J.) conasaugaensis*, was found in company with *Cambarus (H.) coosawattae*.

RANGE.—This crayfish is known only from the Coosawattee watershed (Coosa River basin) in

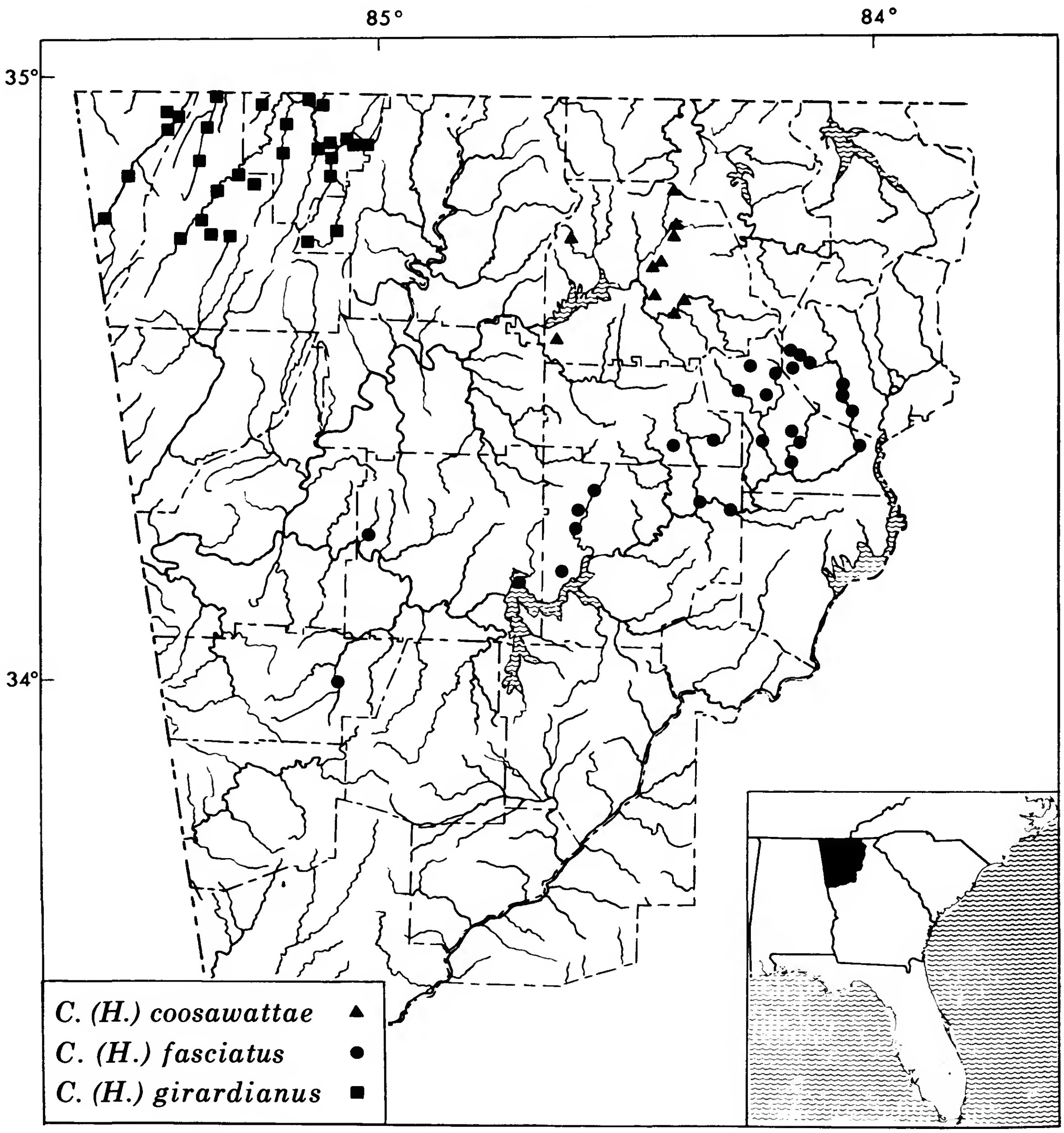


FIGURE 60.—Distribution of *Cambarus (H.) coosawattae*, *C. (H.) fasciatus*, and *C. (H.) girardianus* in Georgia.

Gilmer County, Georgia. Although a number of crayfish collections are available from the same watershed in Gordon and Pickens counties, no members of *C. (H.) coosawattae* were among them.

GEORGIA SPECIMENS EXAMINED.—I have examined 187 specimens from the following localities. *Gilmer County*: (1) type-locality, 4♂I, 3♂II, 6♀, 23 Oct 1976, T. A. English, Jr., HHH, collectors; (2) Little Turniptown Creek 7.3 mi SW of Fannin Co line on US Hwy 76, 1♂I, 1♂II, 1♀, 1j♀, 16 Apr 1962, J. F. Fitzpatrick, Jr., HHH; (3) trib to Ellijay River 5.4 mi N of Ellijay on US Hwy 76, 5♂I, 4♀, 5j♂, 1j♀, 10 Oct 1969, K. R. Martin, HHH; 2♂I, 1♀, 21 Sep 1972, HHH; (4) Rock Creek 8 mi NE of Ellijay, 1♂II, 1♀, 1j♀, 3 Sep 1953, R. H. Gibbs, Jr., et al.; 1♂I, 9 Oct 1955, R. W. Yerger et al.; 13♂I, 13♂II, 17♀, 1j♂, 4 ovig ♀, 28 Apr 1967, Torgny Unestam, HHH; (5) Cherry Log Creek just W of Fannin Co line on US Hwy 76, 2♂II, 1♀, 8 Sep 1945, G. B. Hobbs, HHH; 2♂I, 1j♂, 1j♀, 28 Apr 1967, TU, HHH; (6) trib to Cherry Log Creek 7.9 mi NE of Ellijay on US Hwy 76, 1♂I, 2♂II, 1♀, 1j♀, 8 Sep 1945, GBH, HHH; (7) Conasauga Creek 9.7 mi NW of Ellijay on US Hwy 76, 2♂I, 18♂II, 17♀, 2j♂, 3j♀, 6 ovig ♀, 16 Apr 1962, JFF, HHH; (8) Cartecay River 3.0 mi SE of Ellijay on St Rte 52, 1♂I, 1j♀, 1 ovig ♀, 22 Apr 1968, C. R. Gilbert et al.; 1♂II, 3♀, 15 Aug 1970, F. J. Schwartz et al.; (9) Cartecay River 1 mi N of Cartecay on St Rte 52, 2♀, 1j♂, 1j♀, 23 Jul 1960, A. L. Metcalf; (10) Hells Creek on secondary road between St Rtes 5 and 156, 2j♀, 2 ovig ♀, 28 Apr 1967, TU, HHH; (11) Coosawattee River 2 mi S of Ellijay on St Rte 5 (Anonymous, 1967a, tab. 3), 2j♂, 1j♀, 29 Jul 1966, L. Carrick.

Accurate locality data are lacking for 1♂I, 4♂II, 2♀, 11j♂, 5j♀, and 2 ovig ♀ collected in June.

VARIATIONS.—In all of the specimens examined, except those from Little Turniptown Creek, the rostral margins are strongly convergent; in the few specimens available from this stream, however, the rostral margins are not strongly inclined anteriorly toward the median line and resemble the rostra of *C. (H.) fasciatus*; otherwise the crayfish from there are typical of *C. (H.) coosawattae*. In the specimens from Hells Creek, there are as many as 13 punctations across the narrowest width of the areola. In many of the crayfish, especially those in the Ellijay River watershed, the ventral surface of the ischium of the antennal peduncle does not bear a well-defined spine, and indeed in a number of them the podomere is conspicuously reduced in size. Prominent tufts of setae may or may not be present at the opposable base of the fixed finger of the chela. In any part of the range, the mesial surface of the carpus of the cheliped may or may not have a small tubercle proximal to the major spikelike one, and the ventral surface of the merus rarely has three tubercles in the lateral row, but the mesial row has from five to 13.

Except for these features, there are no conspicuous variations that exceed the ranges pointed out in the descriptions of the primary types and that are apparent in "Measurements."

SIZE.—The largest specimen available is a second form male having a carapace length of 34.5 (postorbital carapace length 28.9) mm. Corresponding lengths of the smallest and largest first form males and of the smallest ovigerous female are 19.4 (16.2) and 34.1 (28.7) mm, and 22.1 (18.2) mm, respectively.

LIFE HISTORY NOTES.—Collections are available from April and June to October. First form males were obtained in April, June, September, and October, and ovigerous females were found in April and June. Thus it is probable that, in general, the adult males of *C. (H.) coosawattae*, like other members of the subgenus *Hiaticambarus*, molt to second form in late June and return to first form in September, and the egg-laying period occurs in the spring. On the basis of the specimens at hand, no more than three generations are present in the streams in April. Among the ovigerous females that have retained a near-complete complement of eggs following preservation are the following:

Carapace and postorbital carapace lengths (mm)	*Number of eggs*	*Diameter of eggs (mm)*
22.1 (18.2)	30	2.5–2.6
22.3 (18.1)	27	2.5
24.9 (20.3)	46	2.4–2.5
25.3 (20.8)	42	2.4–2.5
25.5 (21.2)	55	2.5–2.6
27.2 (22.6)	57	2.4–2.5
28.2 (23.0)	85	2.5–2.6
30.1 (24.8)	101	2.5

ECOLOGICAL NOTES.—This crayfish, like most members of the subgenus, is primarily an inhabitant of riffle areas of streams. In all of the localities in which I have observed it, the individuals had sought cover under rocks in moderately to swiftly flowing water that was clear to slightly

Seasonal Data

Sex/stage	*J*	*F*	*M*	*A*	*M*	*J*	*J*	*A*	*S*	*O*	*N*	*D*
♂I				19		1			3	10		
♂II				32		4		1	5	3		
♀				35		2	2	3	4	10		
♂j				4		9	3			5		
♀j				8		4	2		2	1		
♀ ovig				13		2						

cloudy. I have not found it in eddies where fallen leaves have accumulated, but I do not doubt that at least the young and an occasional adult will be found in such habitats near riffles.

Relationships.—The closest affinities of this crayfish seem to be with *Cambarus (H.) longirostris* and *C. (H.) fasciatus*. It may be distinguished readily from *C. longirostris* by the presence of marginal tubercles on the rostrum, the spiniform or subspiniform spine on the ischium of the antennal peduncle in many individuals, in lacking a suborbital angle, and by the brilliant orange to vermilion markings on the carapace and pereiopods. It may be separated from *C. (H.) fasciatus* by the strongly tapered rostral margins, the absence of a suborbital angle and cervical spine, the presence of first pleopods in the female, and by the absence of a dark saddle on the caudal part of the carapace and the presence of narrow burgundy transverse bands on the caudal margins of the abdominal terga, as opposed to broad dark bands.

Georgia Crayfish Associates.—*Cambarus (H.) coosawattae* has been collected with the following crayfishes (the number of times is indicated in parentheses): *Cambarus (C.) bartonii* (1), *C. (D.) latimanus* (5), *C. (H.) speciosus* (1), *C. (J.) conasaugaensis* (11), *C. (L.) acanthura* (1), *Orconectes erichsonianus* (1), and *Procambarus (Pe.) spiculifer* (2).

Etymology.—The name is derived from the Coosawattee River, in the basin of which this crayfish seems to be endemic.

Cambarus (Hiaticambarus) fasciatus, new species

Figures 22*e*, 58*b*, 60, 61, 208

Cambarus (Hiaticambarus) species G.—Hobbs, 1969a:106, 141, fig. 10 [in part].
Cambarus sp. nov. B.—Anonymous, 1970b:180, 182, 184.
Cambarus (Puncticambarus) sp.—Hart and Hart, 1974:79.
Cambarus nov. sp. B.—Wharton, 1978:220.

Summary of Literature.—Hobbs (1969a) referred to this crayfish as one of two members of the subgenus occurring in the "upper Coosa system," and in his distribution map (fig. 10) he relegated both this species and *C. (H.) coosawattae* to his "species G" but cited no specific localities. Anonymous (1970b) reported it from three localities on the Etowah River, one each in Cherokee, Dawson, and Lumpkin counties (see "Specimens Examined"). It was cited as a host to *Donnaldsoncythere hiwasseensis (= D. donnaldsonensis)* by Hart and Hart (1974) in Shoal Creek, Dawson County, Georgia.

Diagnosis.—Rostrum with margins not strongly tapered, angular at base of acumen, and bearing spines or tubercles (many individuals in late intermolt stages with abraded margins lacking spines or tubercles). Postorbital ridges terminating cephalically in small spine or spiniform tubercle. Cervical spine well developed. Suborbital angle acute to strongly obtuse. Areola 2.8 to 5.2 times as long as broad and constituting 32.2 to 38.2 percent of entire length of carapace (41.6 to 45.4 percent of postorbital carapace length); of 80 specimens measured only 4 with ratio of 45 percent or more. Chela with row of tubercles on mesial margin of palm strongly or weakly developed, second row of less well developed tubercles sometimes present, with or without setal tuft at mesial base of fixed finger; lateral margin of propodus costate or subcostate. Hook on ischium of third pereiopod opposed by tubercle on basis. Pleura of third through fifth abdominal segments truncate ventrally, subangular caudoventrally. First pleopod of first form male with moderately short terminal elements: central projection bearing distinct subapical notch, not tapering, and directed at about 120 degrees to shaft of appendage; mesial process inflated, tapering, with acute tip directed caudally at about right angle. Terga of abdomen with broad dark bands spanning no less than posterior third of each; first tergum entirely dark; no dark scalloped line evident along bases of pleura. Female without first pleopods—unique in subgenus.

Holotypic Male, Form I.—Body subovate, depressed (Figure 61*a,j*). Abdomen narrower than cephalothorax (13.3 and 16.0 mm); maximum width of carapace distinctly greater than depth at caudodorsal margin of cervical groove (16.0 and 11.7 mm). Areola almost 4 times as long as broad, constituting 36.0 percent of total length of carapace (43.4 percent of postorbital carapace length), densely punctate with about 7 punctations across narrowest part. Rostrum with thickened margins gently converging to base of acumen, there distinctly angular and bearing minute corneous tubercles; acumen, with strongly upturned tip, reaching midlength of ultimate podomere of antennular peduncle; dorsal surface of rostrum concave with conspicuous deep punctations in basal half. Subrostral ridge rather strong and evident in dorsal aspect along entire length of rostrum, continuing onto acumen. Postorbital ridge short, deeply grooved dorsolaterally, and terminating cephalically in short, acute, upturned spine. Suborbital angle obtuse; branchiostegal spine moderately strong and acute. Cervical spine well developed. Carapace densely punctate dorsally except for polished median gastric area, granulate laterally and with prominent tubercles in hepatic and posterior orbital regions as well as flanking cervical groove in anteroventral branchiostegal region. Abdomen shorter than carapace (28.4 and 32.0 mm); pleura moderately long, truncate ventrally, and subangular caudoventrally. Cephalic section of telson with 2 spines in each caudolateral corner, usual lateral incision deep and transverse suture clearly defined. Uropod with both lobes of proximal podomere bearing short corneous spine or tubercles; mesial ramus with low submedian ridge bearing premarginal spine, and spine present on distolateral extremity.

Cephalomedian lobe of epistome (Figure 61*g*) broadly rounded, subplane, with submedian acute prominence cephalically; main body with distinct fovea and arched epistomal zygoma, latter flanked anterolaterally by elongate pits. Ventral surface of proximal podomere of antennular peduncle with short acute spine at base of distal fourth. Antennal peduncle with strong lateral spine on basis and with well-defined corneous-tipped tubercle on ischium; flagellum reaching fourth abdominal tergum; antennal scale (Figure 61*i*) about 2.4 times as long as broad, widest slightly proximal to midlength, distal spine strong and reaching base of distal fourth of ultimate segment of antennular peduncle. Ventral surface of ischium of third maxilliped with broad longitudinal band of long stiff setae and with submarginal lateral row of smaller both stiff and plumose ones, few additional setae in area between rows; distolateral extremity subangular but not produced.

Right chela (Figure 61*l*) 2.2 times as long as broad, mesial margin of palm occupying about one-third of its length. Mesial surface of palm with single row of 7 well-defined tubercles flanked dorsolaterally by row of 6 decidedly smaller ones; dorsal and ventral surfaces with many large, deep punctations, lateral margin of palm strongly costate, costa extending along almost entire length of fixed finger; lateral base of latter rather deeply impressed. Fingers widely gaping, lacking setal tuft at opposable base of fixed finger; dorsal longitudinal ridges not sharply defined on either finger (punctations in Figure 61*l* responsible for ridges appearing sharply delimited), both fingers with large deep punctations; opposable margin of fixed finger with row of 10 rounded, corneous tubercles extending from base almost to corneous tip of finger, distal fourth of finger with row of minute tubercles present on level slightly below tubercular row, and prominent tubercle on yet lower level situated opposite base of row of denticles; opposable margin of dactyl with row of 9 tubercles (10 on left chela) similar in form and disposition to those on fixed finger, large tubercle on lower level and minute denticles situated as on fixed finger; mesial surface of dactyl punctate.

Carpus of cheliped with prominent longitudinal furrow dorsally, flanked by setiferous punctations; mesial surface with large procurved spine, and smaller knoblike tubercle situated more proximally; ventral surface with smaller punctations, and 2 tubercles present on distal margin, one on lateral condyle and other on mesioventral angle. Merus with 2 premarginal tubercles dorsally; ven-

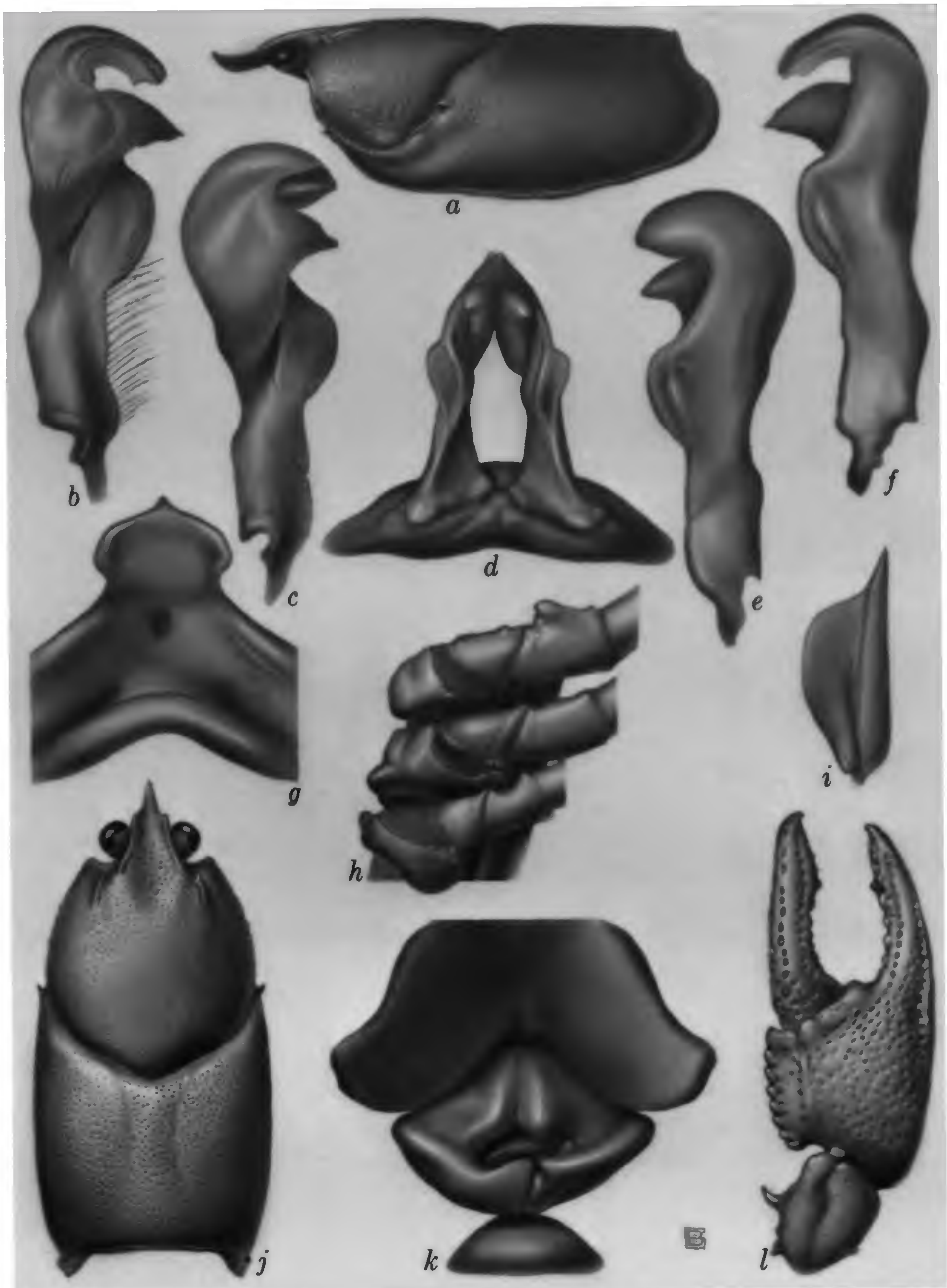


FIGURE 61.—*Cambarus (Hiaticambarus) fasciatus* (all from holotype except *b*, *f*, from paratopotypic male, form I, *c*, *e*, from morphotype, and *k*, from allotype): *a*, lateral view of carapace; *b*, *c*, mesial view of first pleopod; *d*, caudal view of first pleopods; *e*, *f*, lateral view of first pleopod; *g*, epistome; *h*, proximal podomeres of third, fourth, and fifth pereiopods; *i*, antennal scale; *j*, dorsal view of carapace; *k*, annulus ventralis; *l*, dorsal view of distal podomeres of cheliped.

trolateral row of tubercles represented by only 2, and ventromesial row consisting of 10 (9 on left cheliped), distal members of both rows strongest and spikelike; distolateral surface with minute subacute corneous tubercle. Mesial margin of ischium with 1 very small tubercle.

Ischium of third pereiopod with simple hook (that on right deformed) overreaching basioischial articulation and opposed by tubercle on basis (Figure 61*h*). Coxa of fourth pereiopod with transverse boss vertically disposed, that of fifth pereiopod devoid of boss but with ventral membrane sparsely setiferous.

First pleopods (Figure 61*b,d,f*) reaching coxae of third pereiopods, symmetrical, with gap between their bases. (See "Diagnosis" for description.)

ALLOTYPIC FEMALE.—Excluding secondary sexual characters, differing from holotype in following respects: distal spine on antennal scale almost (left) or reaching (right) distal end of ultimate podomere of antennular peduncle; mesial margin of palm of chela with row of only 6 tubercles on left member, more lateral row on both chelae rudimentary, represented by punctations; opposable margin of fixed finger with setal tuft along proximal three-fourths, in addition, row of 8 tubercles along proximal two-thirds on right chela (6 on left), row of minute denticles along distal third (half on left), and large tubercle on lower level at base of distal third; merus with ventrolateral row of 8 tubercles on right member (9 on left); mesial margin of ischium with 2 small tubercles. (See "Measurements.")

Annulus ventralis (Figure 61*k*) approximately 1.5 times as broad as long, slightly movable, subsymmetrical, cephalic and central areas decidedly less sclerotized than caudal part; cephalic area with subparallel longitudinal ridges flanking trough leading to depressed central area; sinus originating at caudal end of trough, from there extending gently caudodextrally, making hairpin turn, continuing cephalosinistrally across median line before turning sharply caudodextrally, and ending on caudal wall at median line. Postannular sclerite, little more than one-third as long as annulus and about three-fifths as wide, with straight caudal margin and arched cephalically. First pleopods lacking. Ovigerous, bearing 73 eggs, diameter of which 2.6 to 2.8 mm.

MORPHOTYPIC MALE, FORM II.—Differing from holotype in following respects: rostrum reaching distal end of antennular peduncle, marginal spines larger; mesial margin of palm of right chela with row of 8 tubercles; adjacent, more lateral row much weaker, some tubercles represented by punctations; fingers of chelae not so conspicuously gaping, opposable surface of fixed finger with setal tufts present on proximal half and with row of 9 tubercles and another of minute denticles, latter extending along distal half of finger, and tubercle on lower level situated at base of distal two-fifths; ventromesial row of tubercles on merus of right cheliped consisting of 7 tubercles (left with 9); mesial margin of ischium of right cheliped with 2 tubercles; ischium of third pereiopod with shorter hooks, latter not overreaching basioischial articulation. First pleopod (Figure 61*c,e*) with juvenile suture of shaft evident; neither terminal element corneous; central projection inflated and directed caudally at right angle; mesial process, except for being shorter, strongly resembling that of holotype. (See "Measurements.")

COLOR NOTES (Figure 58*b*).—Carapace with background tan to olive brown, bearing following dark brown markings: reticulate pattern over mandibular adductor region joined by narrow, dark area covering and flanking cervical groove, another extending across orbital and ventral hepatic regions, and saddle extending across posterior part of carapace. Antennal and mandibular regions pinkish cream; areola slightly darker than branchiostegites, latter fading ventrally. Abdomen with caudal part of tergum of first segment very dark brown, remaining terga with broad, transverse dark brown bands caudally, extending ventrally onto pleura, caudal margins edged in burgundy, also second through fifth terga with much narrower dark band anteriorly, separated from broader posterior band by pale pinkish area expanding ventrally and covering anteroventral part of pleura. Telson and uropods bluish olive with margins, ridges, and sutures orange tan. Dorsal surface of chelipeds distal to midlength of merus mostly pale tan to light brown, fingers fading to cream distally; tubercles and articular ridges and knobs orange; sternal area and proximal podomeres of all pereiopods pinkish cream, more distal podomeres (merus through dactyl) olive, distal margins of each reddish orange.

Measurements (mm)

	Holotype	*Allotype*	*Morphotype*
Carapace			
Height	11.7	12.1	10.1
Width	16.0	15.4	13.2
Entire length	32.0	30.6	28.0
Postorbital length	26.5	24.9	22.2
Areola			
Width	2.9	2.8	2.4
Length	11.5	10.4	9.6
Rostrum			
Width	4.5	4.2	4.0
Length	6.9	7.4	6.8
Chela			
Length of mesial margin of palm	10.1	7.8	7.4
Width of palm	13.6	9.6	9.3
Length of lateral margin	29.8	21.9	22.6
Length of dactyl	17.5	13.0	13.3
Abdomen			
Width	13.3	14.8	12.2
Length	28.4	30.3	26.8

TYPES.—The holotypic male, form I, allotypic female, and morphotypic male, form II (numbers 147917, 147918, and 147919, respectively), are deposited in the National Museum of Natural History, Smithsonian Institution, as is the paratypic series, which is restricted to those specimens listed under "Georgia Specimens Examined" from Lumpkin County (specimens cited under the type-locality include the holotype, allotype, and morphotype).

TYPE-LOCALITY.—Etowah River 0.2 mile west of State Route 52 on an unpaved road near Davis Chapel, Lumpkin County, Georgia. There the river was some 12 meters wide and no more than one meter in depth, and the clear water flowed with a moderate to swift current over a sand bottom littered with rocks and woody debris (Anonymous, 1970b:88).

RANGE.—This crayfish is known only from the Coosa River basin in Georgia, where it occurs throughout the Etowah drainage system above Allatoona Lake, from three localities in downstream tributaries in Bartow and Polk counties, and an additional locality, in Bartow County, which is now submerged in the waters of Allatoona Lake.

GEORGIA SPECIMENS EXAMINED.—I have examined 393 specimens from the following localities. *Bartow County*: (1) Bouldery Ford on Stamp Creek, 0.3 mi above jct with McKaskey Creek, 4♂I, 1♂II, 2j♂, 4j♀, 3 ovig ♀, 1 May 1948, D. C. Scott, collector; (2) trib to Coosa River 5.3 mi W of Kingston, 1♂I, 2j♂, 6 Apr 1952, E. A. Lachner et al. *Cherokee County*: (3) Etowah River at Rte S2551, 0.7 mi SE of St Rte 5, 2 mi W of Ball Ground (Anonymous, 1970b:184), 1♂I, 2♂II, 1♀, 3j♀, 1 ovig ♀, 13 May 1969, E. T. Hall, Jr.; (4) Shoal Creek, 1♀, 6 Jul 1948, DCS; (5) Sweetwater Creek, 1♂I, 3 Apr 1953, DCS; (6) Lost Town Creek, 3♂II, 2♀, 7 Jul 1948, DCS; (7) Upper Moores Mill on Shoal Creek, 1♀, 7 Jul 1948, DCS; (8) Etowah River 1 mi NW of Hightower Church near confluence of Board Tree Creek (Anonymous, 1970b:182), 1 specimen, 13 May 1969, ETH. *Dawson County*: (9) Amicalola Creek 6.4 mi W of US Hwy 19 on St Rte 53, 1♂II, 2♀, 3j♂, 18 Jun 1975, D. J. Peters, J. E. Pugh, HHH; (10) Etowah River 0.7 mi NW of Landrum on St Rte 136, 1♂I, 1♂II, 21 Apr 1968, C. R. Gilbert; (11) trib to Amicalola Creek 19 mi S of Ellijay on St Rte 52, 2♂I, 4♂II, 2♀, 18j♂, 32j♀, 4 May 1967, Torgny Unestam, HHH; (12) trib to Etowah River 2 mi N of Dawsonville on St Rte 136, 11♂I, 11♂II, 27♀, 2j♂, 3j♀, 26 Mar 1951, E. C. Raney; (13) stream at base of Amicalola Falls, 3♂II, 1♀, 1j♂, 1j♀, 14 Jun 1966, J. M. Odell; (14) Amicalola Creek 3 mi SW of Johntown, 3♂I, 4♂II, 4♀, 18 Apr 1968, coll ?; (15) Shoal Creek, 5 mi SW of Dawsonville, 12♂II, 2♀, 3 Jun 1950, DCS; 1♂II, 8 Jul 1948, DCS; (16) trib to Etowah River 3.4 mi W of Dawsonville on St Rte 53, 2♂I, 2♂II, 2♀, 31 Mar 1950, ECR; (17) Clear Creek about 2 mi SE of Amicalola Falls, 6♂II, 4♀, 8 Jul 1948, DCS; (18) Shoal Creek 2.5 mi W of Dawsonville on St Rte 85, 1♀, 17 Jul 1961, R. W. Yerger. *Lumpkin County*: (19) Etowah River at St Rte 52 (Anonymous, 1970b:180), 7♂I, 5♂II, 9♀, 5j♂, 4j♀, 4 May 1967, TU, HHH; (20) Etowah River at Castleberry Bridge on US Hwy 19, 1j♂, 10 Apr 1947, ECR; 10♂II, 9♀, 18 Jun 1975, DJP, JEP, HHH; (21) Etowah River at Jay Bridge Rd, at first bridge upstream from St Rte 52, 3♂I, 1♂II, 6♀, 1j♂, 1j♀, 25 Mar 1978, B. A. Caldwell; (22) Etowah River at Castleberry bridge, 1 mi W of Auraria, 1♀, 1j♂, 25 Mar 1978, BAC; (23) Jones Creek NE of Nimblewill Church off St Rte 52, 1♂I, 1♂II, 1♀, 1j♂, 1j♀, 25 Mar 1978, BAC; (24) Poverty Creek in extreme W Lumpkin Co, 5♂I, 2♂II, 1♀, 25 Apr 1954, DCS; (25) Etowah

River near Dahlonega, 3♂II, 1948, DCS; (26) type-locality, 5♂I, 1♀, 1j♂, 5j♀, 2 ovig ♀, 27 May 1969, ETH; (27) trib to Etowah River 3 mi N of St Rte 52 off Jones Creek Rd, 1♂I, 8♂II, 13♀, 12 Apr 1968, HHH; (28) stream 7 mi W of Dahlonega, 1♀, 1j♂, 2j♀, 23 Jul 1960, A. Metcalf. *Pickens County*: (29) East Branch of Long Creek 5.3 mi W of Dawson Co line on St Rte 53, 1♂II, 11 Jun 1952, R. H. Gibbs; 3♂II, 18 Jun 1975, DJP, JEP, HHH; (30) trib to Little River 1 mi W of Tate on St Rte 156, 2♂I, 7j♂, 4j♀, 29 Apr 1967, TU, HHH. *Polk County*: (31) Euharlee Creek at Rockmart, 12♂I, 3♂II, 2♀, 4j♂, 5j♀, 5 ovig ♀, 18 Apr 1966, ETH, HHH; 3♂II, 1j♂, 6 ovig ♀, 3♀ with young, 11 May 1967, TU, HHH; 2♂I, 2♂II, 23 Apr 1977, JEP, HHH.

VARIATIONS.—One of the most conspicuous variations occurs in the rostral margins. In late intermolt individuals (particularly in larger, presumably older ones) the marginal tubercles may be absent; even the angle marking their usual position is occasionally rounded. The suborbital angle, while rather consistently obtuse, is sometimes so broad as to appear virtually obsolete. As few as six and as many as nine punctations span the narrowest part of the areola. The mesialmost row of tubercles on the mesial surface of the palm in unregenerated chelae contains seven or eight; the adjacent more dorsolateral row is much more variable, possessing as many as eight although usually less than seven and sometimes being entirely replaced by prominent punctations. The number of tubercles on the opposable margin of the fingers and on the ventral surface of the merus of the cheliped is also variable, particularly those constituting the ventromesial row on the merus, which range from six to 12. The setal tuft at the opposable base of the fixed finger of the chela is seldom conspicuous and often entirely absent. A single second form male from the Etowah River at U.S. Highway 19 differed from all of the other members of the species collected with it in lacking well-defined transverse bands on the abdomen, and the saddle on the carapace was very pale. Other variations are indicated in the "Diagnosis" and in "Measurements."

SIZE.—The largest specimen available is a first form male having a carapace length of 51.1 mm (postorbital carapace length, 42.3 mm). Corresponding lengths of the smallest first form male are 21.4 (16.6) mm and of the smallest ovigerous female, 26.7 (21.6) mm.

LIFE HISTORY NOTES.—Collections have been made during the period of March through August, and only one juvenile specimen was obtained in the latter month. First form males were found from March to June, and it is highly probable that most if not all of the adult males molt to second form (or die) by the first of July, reverting to first form in late September and October. Ovigerous females were found in May and June, and three females carrying young were collected in May. A tabulation of the number of eggs carried by the females follows. Unfortunately, three of the females (nos. 1, 6, 7) were preserved in a single container and 29 eggs became detached from their pleopods and were found in the bottom of the jar. Likewise, 36 eggs were lost from one or more of the females (nos. 2, 5, 9, 10, 12, 14) in another container, and 33 from one or more females (nos. 3, 4, 8, 13, 15) in a third bottle.

	Carapace and postorbital carapace lengths (mm)	*Number of eggs (young)*	*Diameter of eggs (mm)*
1.	26.7 (21.6)	55	2.2–2.3
2.	29.4 (23.2)	72	2.3–2.5
3.	31.4 (25.7)	124	2.1–2.3
4.	31.7 (25.2)	131	2.2–2.3
5.	32.3 (25.9)	61	2.4–2.5
6.	33.3 (27.3)	29(8)	2.3–2.5
7.	33.8 (27.3)	117	2.3–2.4
8.	37.2 (30.0)	114	2.3–2.5
9.	38.5 (30.2)	13	2.4–2.5
10.	38.7 (31.1)	166	2.5–2.6
11.	38.7 (31.9)	138	2.5–2.7
12.	41.0 (33.6)	196(3)	2.5–2.6
13.	41.9 (33.3)	177	2.5–2.6
14.	43.2 (35.0)	194	2.5–2.6
15.	44.3 (36.7)	263	2.3–2.4

Seasonal Data

Sex/stage	*J*	*F*	*M*	*A*	*M*	*J*	*J*	*A*	*S*	*O*	*N*	*D*	*?*
♂I			17	28	19								
♂II			15	20	16	30	10						3
♀			37	20	14	14	10						
♂j			5	14	27	4	1						
♀j			5	9	51	1	2						
♀ ovig				5	12								
♀ with young					3								

ECOLOGICAL NOTES.—In every locality for which data on the habitat are available, the clear to slightly cloudy water was flowing over a rock-littered bottom with a moderate to swift current, and most of the adult crayfish were found beneath rocks or in debris that had been trapped in or adjacent to riffle areas. Occasional adults and young were present in leaf litter that had accumulated in eddies.

RELATIONSHIPS.—*Cambarus (H.) fasciatus* probably has its closest affinities with *C. (H.) girardianus* and *C. (H.) coosawattae*, vicariating for them in the Etowah Basin. Angulate rostral margins occur in many populations of *C. (H.) girardianus* and in all populations of the latter, and the conformation of the chela and secondary sexual characters of the male is remarkably similar in the three. A combination of well-developed cervical spines, spiniform tubercle on the ischium of the antennal peduncle, broad transverse dark bands (almost always) on the abdominal terga, the central projection of the first pleopod of the first form male bearing a subapical notch, and the absence of first pleopods in the female will serve to distinguish this crayfish from any of its congeners.

GEORGIA CRAYFISH ASSOCIATES.—Occurring with *Cambarus (H.) fasciatus* were the following crayfishes (the number of times they were collected together is indicated in parentheses): *C. (C.) bartonii* (2), *C. (D.) latimanus* (11), *C. (J.) conasaugaensis* (5), *C. (L.) acanthura* (1), *Orconectes spinosus* (2), and *Procambarus (Pe.) spiculifer* (7).

ETYMOLOGY.—From the Latin *fascio* (enveloped in bands), denoting the dark transverse bands on the abdominal terga of members of this species.

Cambarus (Hiaticambarus) girardianus Faxon

FIGURES 22*f*, 58*c*, 60, 62, 63, 209

Cambarus Girardianus Faxon, 1884:117–119, 145; 1885a:59, 78–79, 84, 160, 174, 178, pl. IV: fig. 1, pl. IX: fig. 2a, a′; 1885b:359.—Underwood, 1886:369.

Cambarus extraneus girardianus.—Faxon, 1898:650; 1914:422.—Harris, 1903a:59, 97, 98, 146, 151, 154.—Ortmann, 1931: 97.—Fleming, 1938:300.

Cambarus girardianus.—Hay, 1899b:959, 966.—Steele, 1902:7.—Harris, 1903a:98.—Ortmann, 1931:97–104.—Rhoades, 1944:136.—Hobbs, 1956c:115; 1968b:K-17.—Anonymous, 1970c:35, 36, 38.—Bouchard, 1974:41; 1976a:571–575 [in part]; 1976b:585–596 [in part].—Hart and Hart, 1974:63, 75, 136, 138, 141.—Wharton, 1978: 220*.

Cambarus extraneus.—Ortmann, 1905b:310–311 [in part]; 1931:97–105, 141 [in part].—Rhoades, 1944:136 [in part]. —Fleming, 1938:299–301 [in part]; 1939:311 [in part]. —Hobbs, 1956c:115, 120* [in part]; 1959:896* [in part]. —Hobbs and Hart, 1966:50.

Cambarus (Bartonius) girardianus.—Ortmann, 1931:97.

Cambarus longulus longirostris.—Ortmann, 1931:123* [in part]. —James, 1966:9–13, 21, fig. 2b [in part, probably all of those populations with a "saddle pattern" as illustrated in fig. 2b].

Cambarus extraneus Girardanius.—Fleming, 1938:299 [erroneous spelling].

Cambarus (Hiaticambarus) girardianus.—Hobbs, 1969a:106, 141*, figs. 10*, 18 l; 1972b:120*, 146*, 154*, figs. 89c, 104a; 1974b:16*, fig. 47.—Hobbs and Bouchard, 1973:47 [by implication].—Bouchard, 1976a:572, 574, 575 [in part]; 1976b:588, 592* [in part].—Hobbs and Walton, 1977:602, 609, 612.

Cambarus longirostris.—Anonymous, 1970c: (42, 43, 45, 49–52)*.

The above synonomy is believed to be complete except for records of this species misidentified as *Cambarus longulus longirostris* from Tennessee and North Carolina. Those references marked with an asterisk denote at least the mention of Georgia.

SUMMARY OF LITERATURE PERTAINING TO GEORGIA.—The first notice of the occurrence of this species in Georgia is that of Ortmann (1931:123), who recorded it from South Chickamauga Creek, Ringgold, Catoosa County, as *Cambarus longulus longirostris*. In a report of a biological investigation of Tennessee Basin streams in northwestern Georgia, Anonymous (1970c) cited seven localities for this species (based on my misidentifications) in the Chickamauga Creek basin as *Cambarus longirostris*. No other specific localities have been cited, although all of the above references bearing an asterisk note that the species occurs in the state.

DIAGNOSIS.—Rostrum with or without marginal spines or tubercles. Postorbital ridge terminating cephalically in short spine or very small tubercle. Suborbital angle well developed and usually acute. Cervical spine ranging from well-developed spine to low subspiniform tubercle. Areola 2.7 to 4.0 times as long as broad and constituting 32.5 to 37.1 (rarely as much as 36.0

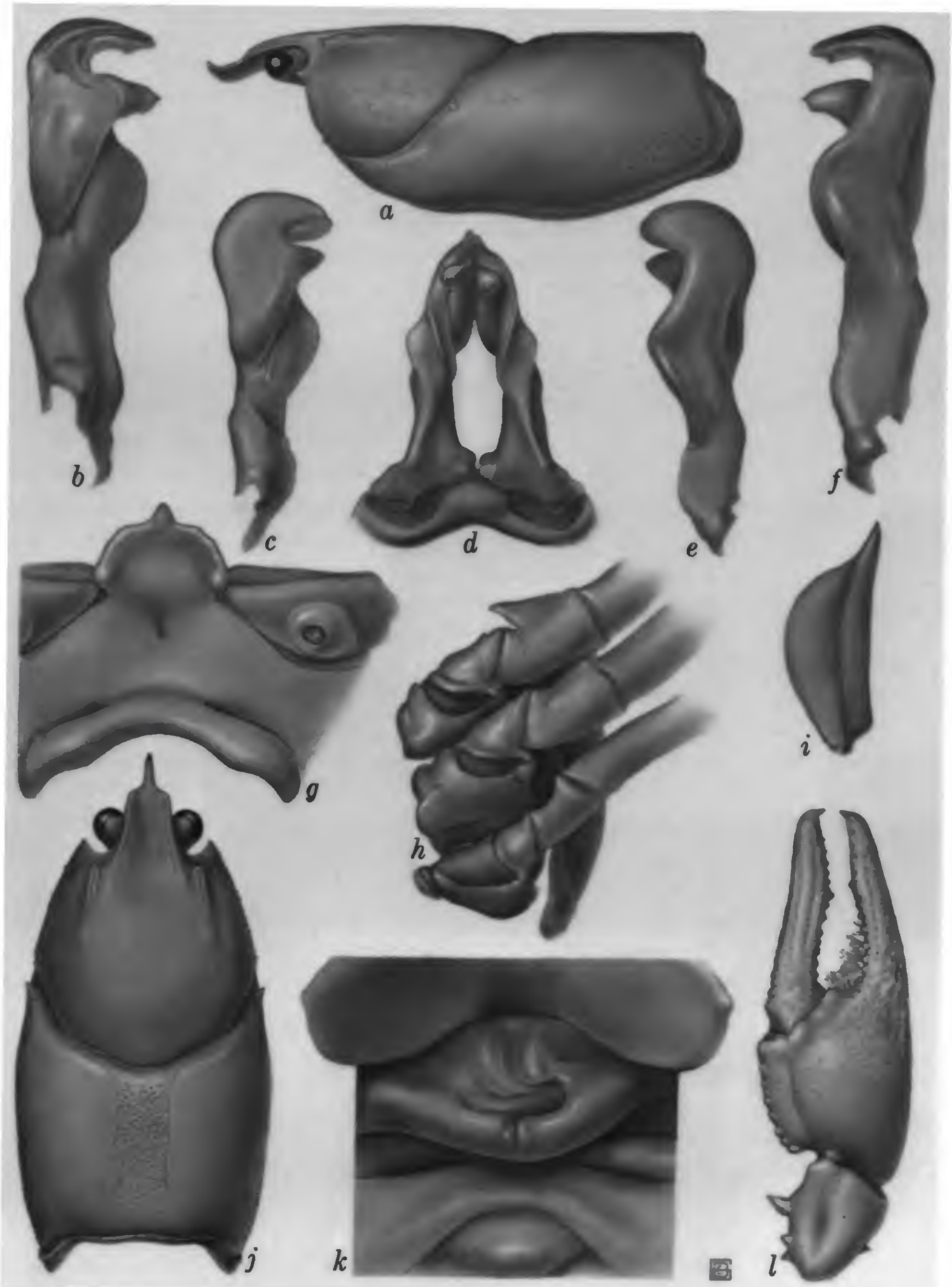


FIGURE 62.—*Cambarus (Hiaticambarus) girardianus* from Lookout Creek, E of Rising Fawn, Dade Co (all from male, form I, except *c*, *e*, from male, form II, and *k*, from female): *a*, lateral view of carapace; *b*, *c*, mesial view of first pleopod; *d*, caudal view of first pleopods; *e*, *f*, lateral view of first pleopod; *g*, epistome; *h*, proximal podomeres of third, fourth, and fifth pereiopods; *i*, antennal scale; *j*, dorsal view of carapace; *k*, annulus ventralis; *l*, dorsal view of distal podomeres of cheliped.

or less than 33.5) percent of entire length of carapace and 41.1 to 44.7 (one specimen 45.8) percent of postorbital carapace length. Chela always with well-defined row of tubercles along mesial margin of palm (sometimes with traces of adjacent second row dorsolaterally), and almost always with conspicuous setal tuft at mesial base of fixed finger; lateral margin of propodus rounded to weakly costate. Hook on ischium of third pereiopod often opposed by tubercle on basis. Pleura of third through fifth pereiopods subtruncate ventrally and angulate caudoventrally. First pleopod of first form male with central projection rather short, bearing distinct subapical notch, and recurved at approximately 110 to 120 degrees to main shaft of appendage; mesial process inflated, seldom with acute tip, and directed caudally at about 90 degrees. Terga of abdomen with broad, median, caudally tapering dark stripe extending from first tergum to or onto telson, and pleura always with broadly U-shaped (ventrally concave) dark band at base, thus forming scalloped line extending along bases of pleura.

Color Notes (Figure 58*c*).—Rostral margins yellowish to bright orange, area between them and most of gastric area brown suffused with orange; mandibular adductor regions with chocolate reticulations anteriorly, their posterior parts, much of posterior gastric region, and cervical groove dark brown. Postorbital ridges cream with orange suffusion. Hepatic region mostly pinkish cream to cream with white tubercles and few small irregular gray markings. Orbital region and narrow area along ventral hepatic regions straw brown. Antennal and mandibular regions cream, latter suffused with brown. Areola tan. Branchiostegites largely pale orange tan fading ventrally to pinkish cream and bearing white granulations, but brown adjacent to cervical groove and similarly colored patch surrounding cervical tubercle; chocolate saddle covering caudal part of carapace, bar very narrow but flaring conspicuously ventrolaterally. Abdominal terga with broad dark brown median stripe extending from first segment to or onto anterior region of telson; stripe narrowing and becoming paler posteriorly; pleura white anteroventrally, and all with U-shaped chocolate band at base, together forming longitudinal scalloped line extending from first through sixth segments. Telson and uropods rather uniformly tan, and each ramus of latter with small brown spot at base, sutures and margins orange to orange tan. Antennular and antennal peduncle olive with pinkish cream markings, latter more cream than olive; flagella pale olive with brown bands; antennal scale with pinkish brown lateral margin, lamellar area pinkish cream with longitudinal brown band flanking thickened lateral pinkish area, distolateral spine cream with corneous reddish brown tip. Dorsum of palm of chela olive tan with light brown reticulations and orange cream tubercles. Fingers also pale olive proximally, fading distally; distal third of finger orange cream with reddish brown corneous tips; tubercles and lateral surface of propodus cream to orange cream; dorsodistal part of merus and entire dorsal, mesial, and lateral surfaces of carpus with same color and markings as palm. Remaining pereiopods mostly cream but dorsal area of merus through proximal part of propodus pinkish cream. Venter, third maxillipeds, and ventral surface of chelipeds also pinkish cream.

Types.—Syntypes, MCZ 3560 (♂II, ♀), USNM 4882 (♂II, 2♀).

Type-Locality.—Cypress Creek, Lauderdale County, Alabama.

Range.—The Tennessee River basin from northeastern Mississippi to Georgia and northward at least to the vicinity of Knoxville. In Georgia, it is known only from the basins of Lookout, Chattanooga, and Chickamauga creeks in Dade, Walker, Catoosa, and Whitfield counties.

Georgia Specimens Examined.—A total of 479 specimens have been examined by me from 29 localities (Figure 60) in the area cited immediately above.

Variations (Figure 63).—While considerable variation exists among the specimens at hand, particularly in the ornamentation (spines and tubercles) of the chelipeds and in the degree of development of the cervical spine—which may be well developed or reduced to a small tubercle—none of these variations have been invari-

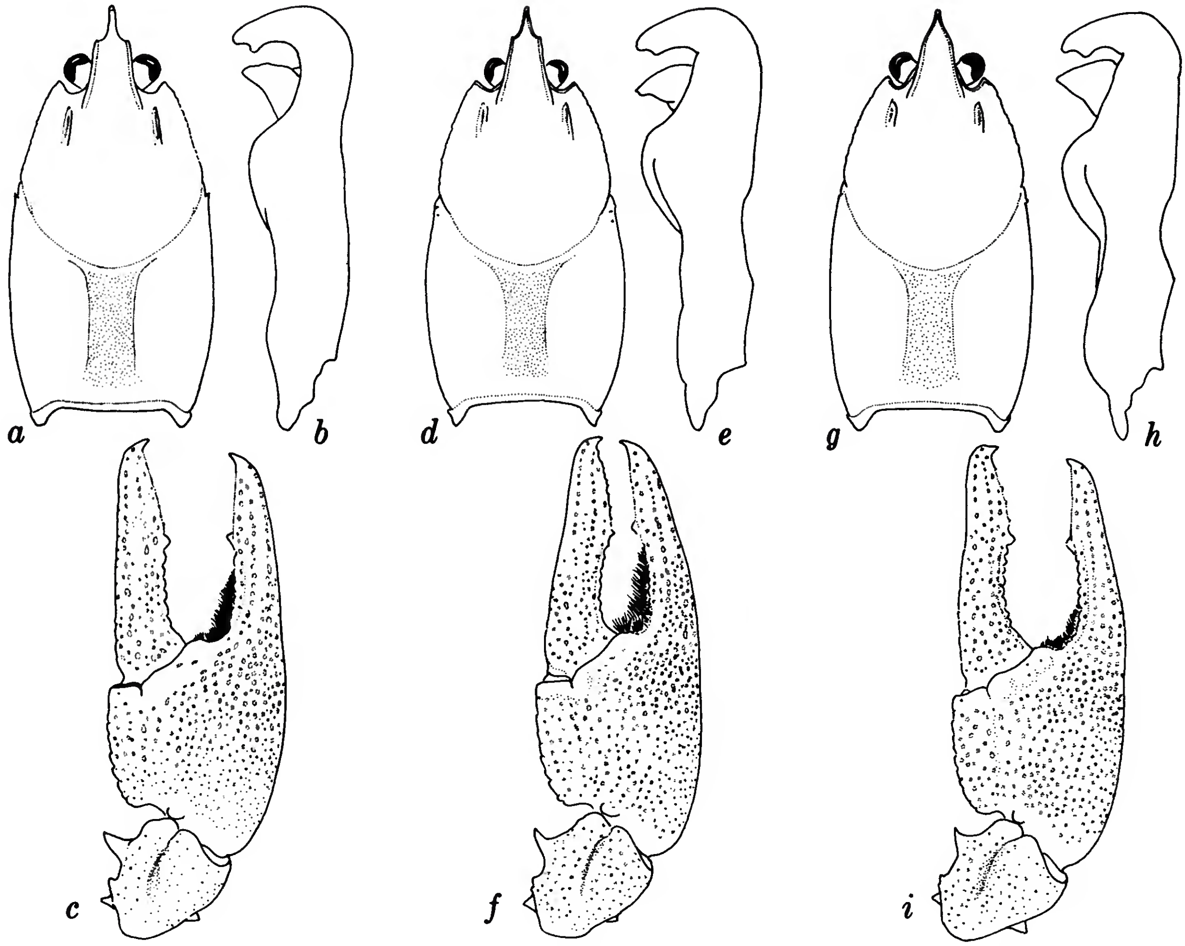


FIGURE 63.—*Cambarus (H.) girardianus* (*a, d, g*, dorsal view of carapace; *b, e, h*, lateral view of first pleopod of first form male; *c, f, i*, dorsal view of distal podomeres of cheliped of first form male): *a–c*, from Squirrel Town Creek in community of New England, Dade Co; *d–f*, from Chattanooga Creek 0.1 mi E of High Point, Walker Co; *g–i*, from Peavine Creek (to Chickamauga Creek) 2 mi upstream from St Rte 2, Catoosa Co.

ably correlated with a part of any of the three drainage basins. In Lookout Creek, however, the cervical spine ranges from a small tubercle to a well-developed spine; in Chattanooga Creek it may be absent or represented by a small subspiniform tubercle; and in Chickamauga Creek, it is absent or, at most, reduced to a small rounded tubercle. In contrast, the rostrum of specimens from Lookout and Chattanooga creeks bear marginal spines or tubercles, or, at least, the acumen is set off from the rest of the rostrum by distinct angles. In specimens from Chickamauga Creek, however, the rostrum tapers from its base to the tip of the acumen; rarely is there an angle at the base of the latter. The color pattern shows little variation except that occasionally the dorsomedian dark stripe on the abdomen is very pale, but the scalloped line along the base of the pleura always furnishes a ready means for separating this species from the other members of the subgenus occurring in Georgia.

SIZE.—The largest specimen available is a first form male having a carapace length of 43.2 (postorbital carapace length 36.3) mm. The corresponding lengths of the smallest first form male are 24.0 (19.5) mm, and those of the smallest ovigerous female, 25.6 (20.6) mm.

LIFE HISTORY NOTES.—Collections have been made only during April, May, June, August, and October, and first form males were found in April, May, and October. Seven ovigerous females were collected in April. On the basis of the sizes of the specimens in the larger series obtained, three generations seem to be represented in the populations during April and October.

The number of eggs carried by the seven females from Georgia are as follows:

Carapace and postorbital carapace lengths (mm)	*Number of eggs*	*Diameter of eggs (mm)*
25.6 (20.0)	83	2.3
31.9 (26.0)	154	2.2–2.3
33.8 (28.2)	97	1.8–2.2
34.3 (28.0)	169	2.5–2.7
34.8 (27.8)	163	2.3–2.4
36.8 (29.6)	203	2.3–2.5
38.8 (31.5)	224	2.4–2.5

Seasonal Data

Sex/stage	*J*	*F*	*M*	*A*	*M*	*J*	*J*	*A*	*S*	*O*	*N*	*D*
♂I				9	2					10	1	
♂II				39	1		1	21		13		
♀				79	43	2	1	14		53	2	
♂j				30	3			11		5	7	
♀j				23	36			17		4	5	
♀ ovig				7								

Three series of specimens were examined from Little Tiger Creek, near the Catoosa-Whitfield County line, just south of State Route 2. On 2 May 1967, of the 69 specimens obtained, all were females. On 24 April 1968, 35 specimens were collected, and except for one second form male, again all were females. On 22 October 1976, 32 specimens were examined and released, and all were females. Inasmuch as collections were made both during the spring and fall, it seems unlikely that the males are migrating, and finding only one male (it in the nonbreeding state) during the time when egg laying occurs suggests the possibility of parthenogenesis or hermaphroditism in this population. Unfortunately, improper fixation of the gonads prevents determining whether or not testicular elements are present in them. In all other localities where the species was found and in which as many as a half dozen specimens were collected, males were present in the populations.

ECOLOGICAL NOTES.—Although this crayfish is limited to lotic habitats, within the streams it is not restricted to riffle areas, frequently being abundant in water where the current is not so swift but where adequate cover (rocks, matted roots, and/or leaf litter) is available. In a tributary to Lookout Creek, I found numbers of them occupying shallow, gently sloping tunnels constructed in a clay bank, the openings of which were beneath the water. Some of the crayfish were at the mouths of the cavities with their chelae and antennae partially exposed. In a swift riffle area on Lookout Creek at State Route 189, immediately east of Rising Fawn, *C. (H.) girardianus* was far less abundant than *C. (H.) longirostris*.

GEORGIA CRAYFISH ASSOCIATES.—Collected with this crayfish were the following species (the number of times they were found together is indicated in parentheses): *Cambarus (C.) bartonii* (2), *C. (D.) latimanus* (2), *C. (D.) striatus* (9), *C. (H.) longirostris* (3), *C. (L.) acanthura* (1), *C. (P.) extraneus* (12), *Orconectes erichsonianus* (27), *O. forceps* (3), and *Procambarus (O.) lophotus* (3).

Cambarus (Hiaticambarus) longirostris Faxon

FIGURES 22*d*, 58*d*, 64–66, 210

Cambarus Bartonii, var. *longirostris* Faxon, 1885a:64.
Cambarus bartonii longirostris.—Faxon, 1890:623.
Cambarus bartonii spinirostris.—Faxon, 1890:623 [lapsus for *C. b. longirostris*].
Cambarus longulus longirostris.—Hay, 1899b:959.—James, 1966:3, 12 [not references to Georgia], 13, 17, 21, 22 [in part], figs. 2a, 2b, pl. lc,f,g,n,o,r,s.—Holt, 1968b:32*.—Bouchard, 1976a:574.
Cambarus (Bartonius) bartoni longirostris.—Ortmann, 1905a:135 [by implication].

Cambarus (Cambarus) bartonii longirostris.—Fowler, 1912:341 [by implication].
Cambarus (Cambarus) longulus longirostris.—Ortmann, 1931: 121, ?123*.—Bouchard, 1976a:572 [in part].
Cambarus longerosilis.—Brimley, 1938:503 [erroneous spelling].
Cambarus bartonii var. *longirostris.*—James, 1966:2.
Cambarus longirostris.—James, 1966:2.—Hobbs, 1968b:K-17*[in part].—Anonymous, 1970c:35*; 1973b:66*, 67*.—Bouchard, 1976a:574 [in part]; 1976b:588, 592 [in part]. —Wharton, 1978:220*.
Cambarus (Hiaticambarus) longirostris.—Hobbs, 1969a:141*, 142* [in part], figs. 10*, 18m; 1972b:120*, 146*, 154* [in part], figs. 104b, 105a; 1974b:16* [in part], fig. 48.—Bouchard, 1976a:574, 575 [in part].—Bouchard and Hobbs, 1976:13.
Cambarus girardianus.—Bouchard, 1976a:572-575 [in part].
Cambarus (Hiaticambarus) girardianus.—Bouchard, 1976a:572 [in part]; 1976b:588, 592* [in part].

The above synonomy is believed to include all of the synonyms and misidentifications of specimens from Georgia but does not include all records or erroneous determinations from elsewhere in the range of the species. Those citations marked by an asterisk include references to Georgia or to specimens from the state.

Summary of Literature Pertaining to Georgia.—The earliest reference to the occurrence of this crayfish in the state was that of Ortmann (1931:123). His specimens, however, are believed to have been members of *C. (H.) girardianus*, for subsequent collections of representatives of the subgenus *Hiaticambarus* in South Chickamauga Creek in the vicinity of Ringgold contain only members of that species. James' (1966:12) record is based on a misidentification of *C. (H.) manningi*. The first notice of the presence of *C. (H.) longirostris* in Georgia that I have been able to confirm is that of Holt (1968b), who cited it as a host of an unidentified branchiobdellid worm belonging to the genus *Pterodrilus* collected in Union County. Two additional localities were included in faunistic surveys (Anonymous, 1970c and 1973b), one each in Dade and Union counties. Specimens on which these three localities are based are included among the "Georgia Specimens Examined," all of which are deposited in the National Museum of Natural History, Smithsonian Institution. The reference to the association of this crayfish with *C. (J.) nodosus* by Bouchard and Hobbs (1976) is based on specimens obtained at the second locality listed under " Georgia Specimens Examined."

The most comprehensive work cited is that of James (1966). All other references include synonyms, misidentifications, or statements concerning the range of the species. (See "Remarks" under subgenus *Hiaticambarus*.)

Diagnosis.—Rostrum strongly tapering and lacking marginal spines or tubercles. Postorbital ridge terminating cephalically with or without small tubercle. Cervical spine absent, usually not even represented by low tubercle. Areola 3.1 to 4.7 times as long as broad and constituting 34.6 to 38.2 percent of entire length of carapace (41.5 to 44.7 percent of postorbital carapace length). Chela with row of tubercles on mesial margin of palm so strongly adpressed (or lacking) that not evident in silhouette, never with part of second row dorsolaterally, and almost always with conspicuous setal tuft along opposable base of fixed finger; lateral margin of propodus never distinctly costate. Hook on ischium of third pereiopod sometimes opposed by tubercle on basis. Pleura of third through fifth abdominal segments more rounded than angular. First pleopods of first form male contiguous basally; terminal elements comparatively short; central projection bearing distinct subapical notch, not tapering, and rather strongly recurved with notch directed almost proximally; mesial process inflated, with acute to subacute tip disposed at about right angle to shaft of appendage. Terga of abdomen with narrow, dark marginal band posteriorly, first segment often with broad similarly colored band in anterior section; longitudinal dark stripe lacking, and pleura without scalloped stripe at base. Female with first pleopod present.

Male, Form I (from Lookout Creek, Dade County, Georgia).—Body subovate, depressed (Figure 64*a,j*). Abdomen narrower than cephalothorax (10.2 and 12.0 mm); maximum width of carapace greater than depth at caudodorsal margin of cervical groove (12.0 and 8.7 mm). Areola 3.1 times as long as broad, densely punctate with 7 punctations across narrowest part, length 36.5

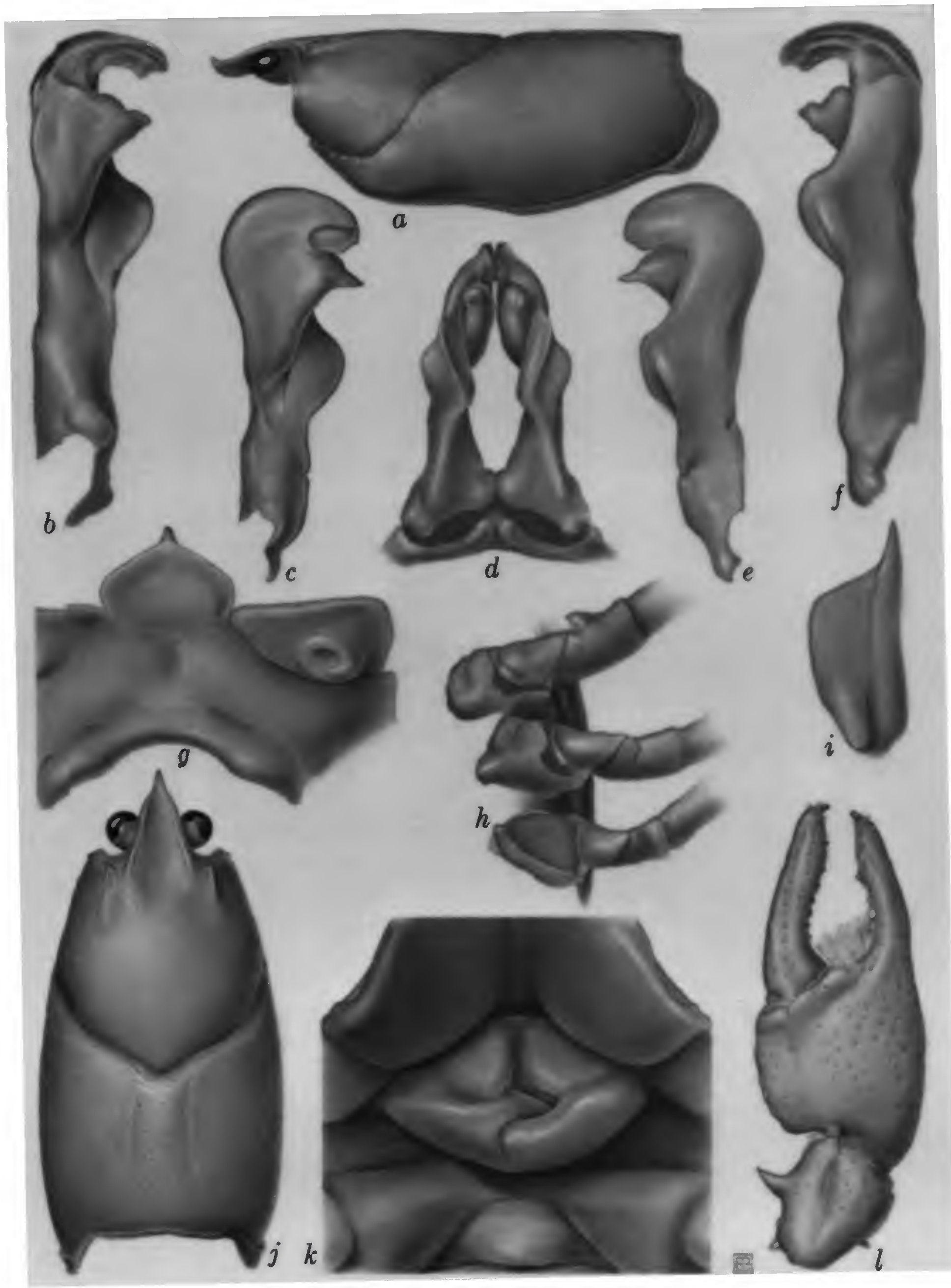


FIGURE 64.—*Cambarus (Hiaticambarus) longirostris* from East Fork of Wolf Creek at junction with West Fork off US Hwy 19, Union Co (all from male, form I, except *c*, *e*, from male, form II, and *k*, from female): *a*, lateral view of carapace; *b*, *c*, mesial view of first pleopod; *d*, caudal view of first pleopods; *e*, *f*, lateral view of first pleopod; *g*, epistome; *h*, proximal podomeres of third, fourth, and fifth pereiopods; *i*, antennal scale; *j*, dorsal view of carapace; *k*, annulus ventralis; *l*, dorsal view of distal podomeres of cheliped.

percent of total length of carapace (43.8 percent of postorbital carapace length). Rostrum with strongly convergent thickened margins ending rather suddenly at base of acumen; latter distinctly upturned, reaching base of ultimate podomere of antennular peduncle; dorsal surface of rostrum concave with prominent punctations; subrostral ridges well developed and, although in dorsal aspect disappearing beneath rostral ridges just anterior to orbit, reappearing posterior to base of acumen and continuing to tip. Postorbital ridge short, deeply grooved dorsolaterally, terminating cephalically in small tubercle. Suborbital angle subacute, branchiostegal spine represented by angulation ventral to cephalic margin of cervical groove. Cervical spine or tubercle absent. Carapace densely punctate dorsally except for median gastric region and wedge-shaped area in anterior half of areola where punctations sparse, lateral part of cephalic section also mostly punctate, majority of punctations conspicuously large; posterior orbital area swollen and with few tubercles; lateral part of branchiostegal region granulate to weakly tuberculate. Abdomen and carapace subequal in length (23.0 and 22.5 mm); pleura rather long and rounded posteroventrally and with gently sloping cephaloventral margins. Cephalic section of telson with 2 spines in each caudolateral corner, usual lateral incision deep and transverse suture distinct. Uropod with proximal podomere bearing acute mesial lobe, lateral lobe rounded; mesial ramus with median ridge obsolete but with premarginal distomedian spine and small distolateral spine.

Cephalomedian lobe of epistome (Figure 64*g*) subtriangular with slightly elevated (ventrally) margins, surface convex posteriorly; main body with prominent fovea and arched epistomal zygoma, usual elongate pits flanking anterolateral side of zygoma reduced to rather shallow grooves. Ventral surface of proximal podomere of antennule with small spine at base of distal fourth or fifth. Antennal peduncle without spines or prominent tubercles; flagellum reaching third abdominal tergum; antennal scale (Figure 64*i*) about 2.4 times as long as wide, sides subparallel but broadest distal to midlength, distal spine strong and reaching almost to midlength of ultimate podomere of antennular peduncle. Ventral surface of ischium of third maxilliped with broad longitudinal band of long stiff setae, submarginal lateral row of smaller plumose setae, and additional short plumose setae dispersed between; distolateral angle subacute but not produced.

Right chela (Figure 64*l*) 2.2 times as long as broad, mesial margin of palm occupying about one-third of its length. Mesial surface of palm with 3 moderately well defined tubercles followed distally by row of 5 punctations; dorsal, ventral, and lateral surfaces punctate, latter surface with slight suggestion of costa. Fingers widely gaping and proximal half of opposable surface of fixed finger with prominent tufts of long plumose setae; neither finger with clearly defined longitudinal ridges dorsally or ventrally, both conspicuously punctate; opposable margin of fixed finger with row of 9 low, rounded corneous tubercles, another on lower level opposite seventh tubercle from base, and band of minute denticles situated between sixth tubercle and corneous tip of finger; opposable margin of dactyl with irregular row of 12 (left with 11) tubercles similar to those on fixed finger, third and fifth from base larger than others, and band of minute denticles present between ninth tubercle and corneous tip of finger.

Carpus of cheliped with distinct oblique furrow dorsally, single spikelike tubercle mesially, and 2 tubercles on ventrodistal margin (one submedian and other forming articular knob), podomere otherwise punctate. Merus of right cheliped with 2 (left with 1) premarginal tubercles dorsodistally; ventrolateral row of tubercles represented by 1 (2 on left) and ventromesial consisting of 6 (7 on left), only distal members of latter row spikelike. Mesial margin of ischium without tubercles.

Ischium of third pereiopod with simple hook (Figure 64*h*) overreaching basioischial articulation and opposed by small tubercle on basis. Coxa of fourth pereiopod with caudomesial boss bearing transverse ridge caudoventrally, that of fifth lacking boss but bearing scattered setae on ventral membrane.

First pleopods (Figure 64*b*,*d*,*f*) reaching coxae of third pereiopods, symmetrical, and with contiguous bases (see "Diagnosis" for description).

FEMALE (from Lookout Creek, Dade County, Georgia).—Excluding secondary sexual characters, differing from male, form I, in following respects: tubercle lacking from cephalic end of postorbital ridges; suborbital angle obtuse; several tubercles in area occupied by cervical spine in other crayfishes slightly larger than others nearby on branchiostegite; median ridge on mesial ramus of uropod evident but weak; cephalomedian lobe of epistome irregularly but broadly rounded cephalically; antennal scale broadest at about midlength; mesial surface of palm of chela with 4 tubercles followed distally by 3 punctations; fixed finger with weak median longitudinal ridge; opposable margin of fixed finger of right chela with row of only 8 tubercles; mesial surface of carpus of cheliped with additional small tubercle proximally; merus of cheliped with 1 premarginal tubercle dorsodistally, only 1 tubercle representing ventrolateral row.

Annulus ventralis (Figure 64*k*) about 1.8 times as broad as long, almost quadrangular, and rather shallowly embedded in sternum; cephalic section, more weakly sclerotized than caudal, with median longitudinal furrow flanked by paired ridges; caudal region broadly excavate anteriorly, inflated, forming convex caudal wall dextrally and angular, somewhat concave one, sinistrally; sinus originating at caudodextral end of median furrow, and following tilted S-shaped course, ending on edge of protruding midcaudal wall. Postannular sclerite about 2.8 times as broad as long, little more than half as wide and almost one-third as long as annulus, bearing punctate oval elevation (ventrally). First pleopods reaching slightly anterior to midlength of annulus when abdomen flexed.

MALE, FORM II (from West Fork of Wolf Creek, Union County, Georgia).—Differing from first form male in following respects: areola with 5 punctations across narrowest part; rostral margins not ending abruptly at base of acumen and merging imperceptibly with subrostral ridges, latter evident in dorsal aspect to base of acumen where joining rostral ridges, postorbital ridges with well-developed corneous tubercles cephalically; suborbital angle obtuse; posterior part of orbital area less swollen and tubercles on it much reduced; cephalic section of telson with only 1 spine in caudodextral corner; cephalomedian lobe of epistome with broadly arched cephalic margin as in female; antennal peduncle with acute spine on lateral surface of basis; antennal scale broadest at about midlength, distolateral spine reaching end of antennular peduncle; mesial surface of palm of chela with row of 6 very low tubercles becoming progressively more squamous and inconspicuous distally; fixed finger with poorly developed median longitudinal ridge dorsally, opposable margin of that finger on right chela with row of 10 tubercles; corresponding margin of dactyl also with 10; merus of both chelipeds with 2 premarginal tubercles dorsodistally, ventrolateral row represented by 2 tubercles and ventromesial by 7 on right and 8 on left cheliped; ventromesial margin of ischium with 2 very small tubercles; hook on ischium of third pereiopod not reaching basioischial articulation and not opposed by tubercle on basis; boss on coxa of fourth pereiopod with much suppressed caudal ridge.

First pleopods (Figure 64*c*,*e*) reaching coxae of third pereiopods, symmetrical, and separated basally by very narrow gap. Noncorneous terminal elements contiguous at base; mesial process directed at about right angle to shaft of appendage and tapering to subacute tip; and central projection deflected caudoproximally at about 110 degrees, rounded apically but with suggestion of subapical notch. Juvenile oblique suture present on shaft.

COLOR NOTES (Figure 58*d*).—Dorsum of carapace olive to orange tan or brown; mandibular adductor regions with dark brown reticulations, these flanked caudally and joined dorsally across posterior gastric region by very narrow dark band along cervical groove; rostral ridges pale olive to brownish cream; broad, marginal pinkish cream band extending from antennal region caudoventrally across mandibular and anteroventral branchiostegal regions; hepatic area with oval dark patch continuing over orbital region but pale more caudally and ventrally. Thoracic region olive to orange tan, fading ventrally almost to cream and with pale orange or tan semiovate spot abutting dorsomedian caudal ridge; latter, including flange, dark greenish gray or dark burgundy. Tergum of first abdominal segment sometimes with dark brown to burgundy rectangular band, its cephalic section, median transverse ridges, and caudal margin red to burgundy; pleura pale. Remaining terga pale olive or orange tan with narrow red to burgundy caudal band extending onto posterior margin of pleura, latter pale cephaloventrally. Telson olive to orange tan bordered in brown to red. Uropods similarly colored but with lateral parts of both rami darker and distal parts suffused with reddish orange to brown. Chelipeds with basal podomeres cream, dorsodistal part of merus dark olive to brown; dorsal part of carpus pale olive or tan basally and darker distally; dorsal part of palm pale proximolaterally and with pale knob opposite mesial base of dactyl, olive tan over most of surface, and mesial margin dark olive to brown; both fingers dark olive with pale tips, and setal tuft at base of fixed finger gray. Remaining pereiopods with cream or pinkish cream basal podomeres and olive to tan distal to ischium; distal part of merus and carpus darker than propodus and dactyl.

TYPE.—Holotype, MCZ 3629 (♂II).

TYPE-LOCALITY.—Eastern Tennessee and West Virginia (Faxon, 1885a). Restricted to Doe River, Elizabethton, Carter County, Tennessee, by Ortmann (1931:121).

RANGE.—The range of this crayfish has not been accurately defined, and in view of the difference of opinion concerning its relationship to *C. (H.) girardianus* (see "Remarks" under "Subgenus *Hiaticambarus*"), a detailed study of the two, particularly in Tennessee, needs to be made. It is a common species in the Tennessee Basin, especially in the Holston and Watauga watersheds. From Knoxville southward what seems to me to be the typical form is less abundant. In Georgia, it has been found only in the headwaters of the Nottely River (Hiwassee Basin) in Union County, in Lookout Creek in Dade County, and in Cane Creek (introduced?), a tributary of the Chattooga River in the southern part of Walker County, thus being confined to the Appalachian Plateau, Ridge and Valley, and Blue Ridge provinces of the state.

Measurements
(mm; based on specimens described herein)

	Male, form I	*Female*	*Male, form II*
Carapace			
Height	8.7	11.8	9.8
Width	12.0	15.9	13.9
Entire length	23.0	30.2	26.6
Postorbital length	19.2	25.3	22.1
Areola			
Width	2.7	3.4	2.5
Length	8.4	11.1	9.6
Rostrum			
Width	3.8	4.8	4.3
Length	4.8	5.9	5.2
Chela			
Length of mesial margin of palm	7.1	8.2	7.8
Width of palm	10.0	11.5	10.1
Length of lateral margin	21.7	25.0	22.9
Length of dactyl	13.1	15.1	13.3
Abdomen			
Width	10.2	14.9	11.0
Length	22.5	30.3	25.5

GEORGIA SPECIMENS EXAMINED.—I have examined 119 specimens from the following localities. *Dade County:* (1) Lookout Creek at St Rte 189, E of Rising Fawn (Anonymous, 1970c:35), 1♂I, 23 Apr 1968, E. T. Hall, Jr., HHH, collectors; 3♀, 1j♂, 3j♀, 29 Sep 1969, M. W. Walker, ETH; 2♂I, 9♀, 1j♂, 21 Oct 1976, T. A. English, Jr., HHH. *Union County:* (2) East Fork of Wolf Creek 0.5 mi NE of Vogel State Park on US Hwy 19 (Holt, 1968b:32; Bouchard and Hobbs, 1976:13), 3♂I, 2♀, 5 May 1958, K. W. Simonds; (3) East Fork of Wolf Creek at confluence with West Fork, near Self Mountain (Anonymous, 1973b:67), 5♂II, 1♀, 9 Aug 1972, ETH, W. D. Kennedy; 2♂I, 7♀, 1j♀, 24 Oct 1976, TAE, HHH; (4) West Fork of Wolf Creek at confluence with East Fork near Self Mountain (Anonymous, 1973b:66), 2♂II, 3♀, 9 Aug 1972, ETH, WDK; (5) Nottely River 1.0 mi N of jct of St Rte 180E on US Hwy 19, 5♂I, 1♂II, 1♀, 9j♂, 8j♀, 3 ovig ♀, 27 Apr 1967, T. Unestam, HHH. *Walker County:* (6) Cane Creek at St Rte 151, 3♂II, 6 Jun 1977, R. W. Bouchard, J. R. Weaver; 1♀, 5j♂, 6j♀, 8 Oct 1977, WDK, HHH; 2♂I, 7♀, 12j♂, 10j♀, 9 Oct 1977, WDK, HHH.

VARIATIONS.—The most conspicuous difference

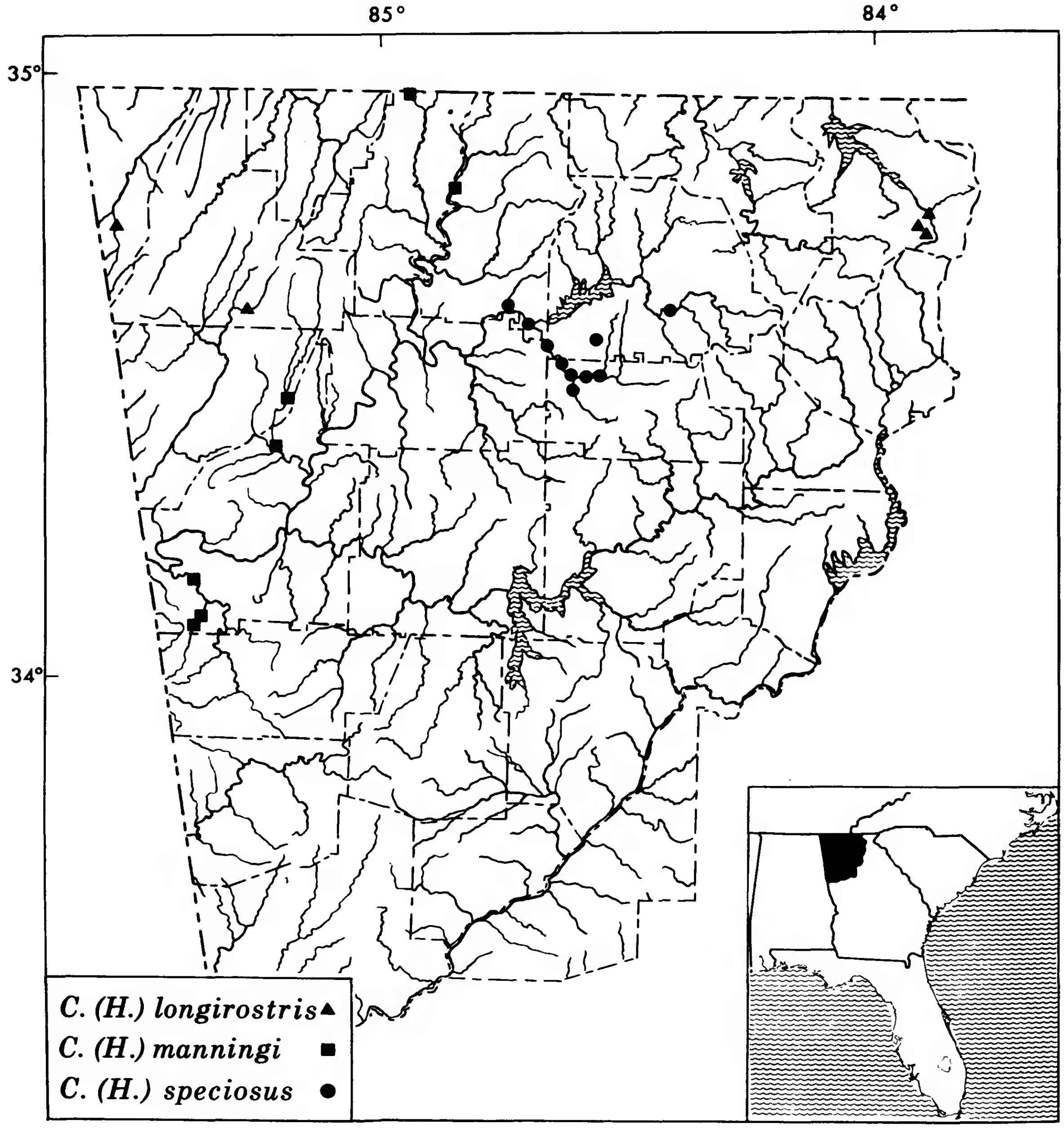


FIGURE 65.—Distribution of *Cambarus (H.) longirostris*, *C. (H.) manningi*, and *C. (H.) speciosus* in Georgia.

noted between the Georgia specimens assigned to this species and topotypes of *C. (H.) longirostris* from the Doe River in Carter County, Tennessee, is in the position of the first pleopods of the male: in the Georgia specimens the bases of these appendages are contiguous, whereas in the topotypes there is a comparatively broad gap between them. The anticipated importance of such a dif-

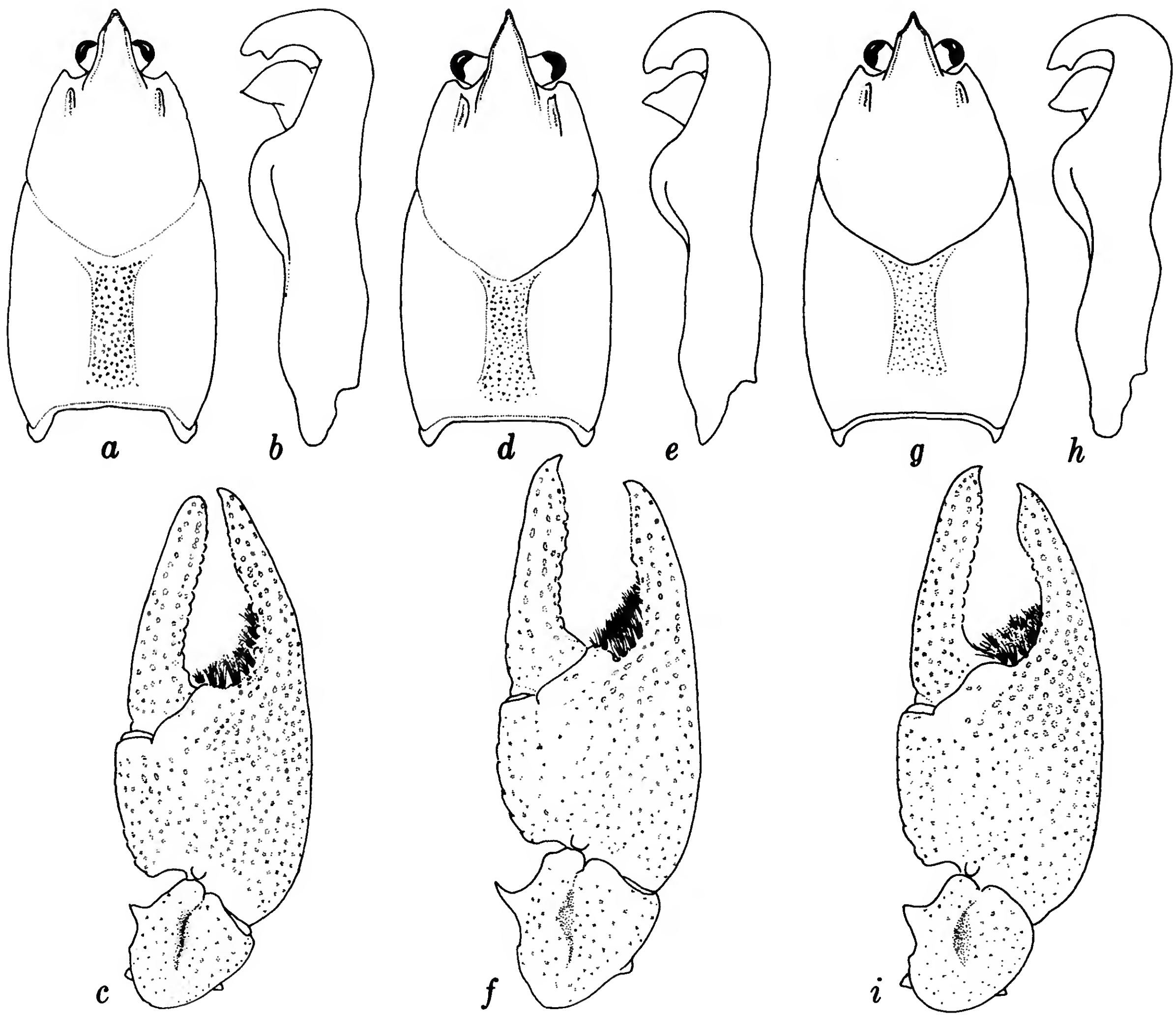


FIGURE 66.—*Cambarus (H.) longirostris*, variations (*a, d, g*, dorsal view of carapace; *b, e, h*, lateral view of first pleopod of first form male; *c, f, i*, dorsal view of distal podomeres of cheliped of same): *a–c*, from Lookout Creek at Rising Fawn, Dade Co; *d–f*, from Nottely River 1.0 mi N of St Rte 186 on US Hwy 19, Union Co; *g–i*, from Cane Creek at St Rte 151, Walker Co.

ference, however, is negated by the occurrence of contiguous pleopods in specimens from another tributary of the Watauga River in Carter County. Other differences noted in the pleopods from the two areas are almost certainly insignificant. The rostra of the Georgia specimens from the Hiwassee Basin are markedly similar to those of topotypes, but those in populations frequenting Lookout Creek and the Chattooga basins are distinctly different (see below). The suborbital angle in none of the Georgia representatives is so prominent as in those from the Doe River. The chelae of specimens from Lookout Creek, and especially those of individuals from the Chattooga River basin, are distinctly more robust than those of the topotypes. Only two tubercles are present on the ventral surface of the carpus of the cheliped in the Georgia specimens, but a third one situated proximomesial to the distomedian tubercle is present, although sometimes very poorly developed, in the topotypes; even the distomedian tubercle in some of the latter is almost obsolete. Most of the topotypes possess only one well-developed tubercle representing the ventrolateral row on the merus of the cheliped, in this respect resembling most members of the Lookout Creek population and differing from most specimens from the Hiwassee Basin that possess two. Among available material from the Chattooga watershed neither one nor two tubercles seem to predominate.

Many of the variations noted among the Georgia specimens seem to be associated with the age or stage in the molt cycle of the specimens. For example, the young usually have well-developed postorbital spines, whereas in the larger, presumably older, individuals they are frequently reduced to rounded tubercles that are sometimes hardly evident in specimens in the late intermolt stage.

Characteristics exist among the Georgia specimens (Figure 66) that in most instances seem to distinguish those representatives occurring in the three watersheds: in the Hiwassee Basin, the rostral margins are evenly tapered to the tip of the acumen; there are two spines or tubercles representing the ventrolateral row on the merus of the cheliped; and the caudal wall of the annulus ventralis is almost symmetrical. In specimens from Lookout Creek, the rostral margins become suddenly thinner, actually ending, at the base of the acumen; almost always there is only one tubercle (sometimes acute) representing the ventrolateral row on the merus of the cheliped; and the caudal wall of the annulus is distinctly asymmetrical, with the side from which the tongue arises somewhat concave instead of being evenly rounded. In specimens from the Chattooga Basin locality, the rostrum is not strongly tapered and the rostral margins end abruptly at the base of the acumen, the latter feature resembling that of the population in Lookout Creek; not only do the adults attain a greater size but the chelae appear to be more robust than those of topotypes and specimens from the other two basins in Georgia. The annulus ventralis is nearly symmetrical as it is in the populations occurring in the Hiwassee Basin.

The ranges and averages (in parentheses) of three ratios obtained from specimens from the type-locality and the three drainage basins in Georgia are presented in the accompanying tabulation. Otherwise, no consistent differences in individuals from the three basins have been observed. The ratios of areola length (AL) to carapace length (CL) and to postorbital carapace length (POCL) are expressed in percentages. The relationship of areola length to areola width (AW) is expressed directly as a ratio.

River basin	*AL/CL × 100*	*AL/POCL × 100*	*AL/AW*
Watauga (type-locality)	35.9–38.9 (37.1)	43.4–45.2 (44.5)	3.9–4.6 (4.4)
Hiwassee	34.6–36.3 (35.3)	42.3–44.3 (42.9)	3.6–4.3 (3.9)
Lookout Creek	35.0–37.7 (35.9)	41.5–43.7 (42.7)	2.8–3.8 (3.4)
Chattooga	36.3–38.1 (37.1)	43.1–44.7 (43.8)	3.4–4.5 (4.0)

Size.—The largest specimen available is a second form male having a carapace length of 33.1 (postorbital carapace length 28.2) mm. The smallest and largest first form males have corresponding lengths of 21.1 (17.1) and 30.5 (26.0) mm, respectively, and those of the smallest ovigerous female are 20.0 (16.4) mm.

Life History Notes.—First form males have been collected in April, October, and November. The seven males collected on 9 August were in the second form suggesting that, as Smart (1962: 86) found in its relative *C. (H.) longulus* in Virginia, the majority of the adult male population molts to first form in the fall.

Similar also to *C. (H.) longulus* was the occurrence of ovigerous females in late April. The number of eggs carried by the three females from Georgia, which were preserved together, are as follows (seven eggs became detached in the bottle):

Carapace and postorbital carapace lengths (mm)	*Number of eggs*	*Diameter of eggs (mm)*
20.0 (16.4)	42	2.3
21.8 (18.9)	47	2.1–2.2
22.6 (18.8)	53	2.2–2.3

ECOLOGICAL NOTES.—*Cambarus (H.) longirostris* is confined to riffle areas of streams, where it occurs beneath rocks even in the most swiftly flowing areas. I have not found it in leaf litter or among other debris accumulated in the stream, and rarely has it been taken in quieter water above and below riffles. In the East Fork of Wolf Creek, some three to five meters in width and no more than 0.5 meter deep, the clear water flows swiftly over a rock-strewn bed of sand on clay. Sharing this segment of the stream, although in fewer numbers, is *C. (P.) hiwasseensis*. In Cane Creek at State Route 151, *C. (H.) longirostris* occurs only in the swiftest part of the stream. Even though there are extensive riffle areas at this locality, only in two of the swiftest segments where there were comparatively large rocks were adult specimens taken. Also frequenting the stream in this area are *C. (D.) latimanus*, *C. (P.) scotti*, and *Orconectes erichsonianus*.

GEORGIA CRAYFISH ASSOCIATES.—*Cambarus (H.) longirostris* has been collected in the same localities as the following crayfishes (the number of times is indicated in parentheses): *Cambarus (C.) bartonii* (2), *C. (D.) latimanus* (1), *C. (D.) striatus* (1), *C. (H.) girardianus* (3), *C. (J.) nodosus* (1), *C. (P.) hiwasseensis* (4), *C. (P.) scotti* (1), and *Orconectes erichsonianus* (2).

Cambarus (Hiaticambarus) manningi, new species

FIGURES 22*c*, 58*e*, 65, 67, 68, 211

Cambarus longulus longirostris.—James, 1966:12 [in part: map based on list of localities deposited in the Smithsonian Institution (file no. 254736)].

Cambarus (Hiaticambarus) longirostris.—Hobbs, 1974b:16 [in part: Coosa drainage system in Georgia].

Untitled color photograph.—Bouchard in Anonymous, 1978:195.

SUMMARY OF LITERATURE PERTAINING TO GEORGIA.—The single female specimen from Georgia examined by James (1966) from Armuchee Creek, north of Armuchee, is in the Smithsonian collection. I have examined it and am assigning it to *C. (H.) manningi*. This and additional specimens from other localities listed below led Hobbs (1974b) to include northwestern Georgia within the range of *C. (H.) longirostris*. A beautiful color photograph, by R. W. Bouchard, of a specimen from the type-locality is included in Anonymous (1978).

DIAGNOSIS.—Rostrum strongly tapering and lacking marginal spines or tubercles. Postorbital ridge terminating cephalically in acute corneous tubercle. Suborbital angle obtuse to rounded. Cervical spine represented at most by low tubercle. Areola 3.7 to 4.3 times as long as broad and constituting 37.1 to 40.4 percent of entire length of carapace (45.0 to 48.9 percent of postorbital carapace length). Chela with row of tubercles on mesial margin of palm strongly depressed, sometimes reduced to few tubercles proximally, and lacking any part of second dorsolateral row; always with setal tuft at mesial base of fixed finger; lateral margin of propodus never costate. Hook on ischium of third pereiopod opposed or not by low tubercle on basis. Pleura of third through fifth abdominal segments with oblique cephaloventral margin, and subangular posteroventrally. First pleopod of first form male with short terminal elements: central projection bearing distinct subapical notch, not tapering, and directed at slightly more than right angle to shaft of appendage; and mesial process inflated, with acute tip directed caudally at about right angle and slightly laterally. Terga of abdomen uniformly dark and pleura with dark coloration extending from corresponding tergum posteroventrally leaving cream to white anteroventral section; no dark scalloped line evident along bases of pleura. Female with first pleopod present.

HOLOTYPIC MALE, FORM I.—Body subovate, depressed (Figure 67*a,j*). Abdomen narrower than cephalothorax (10.2 and 12.2 mm); maximum width of carapace distinctly greater than depth at caudodorsal margin of cervical groove (12.2 and 9.9 mm). Areola 3.8 times as long as broad, densely punctate, with 7 punctations

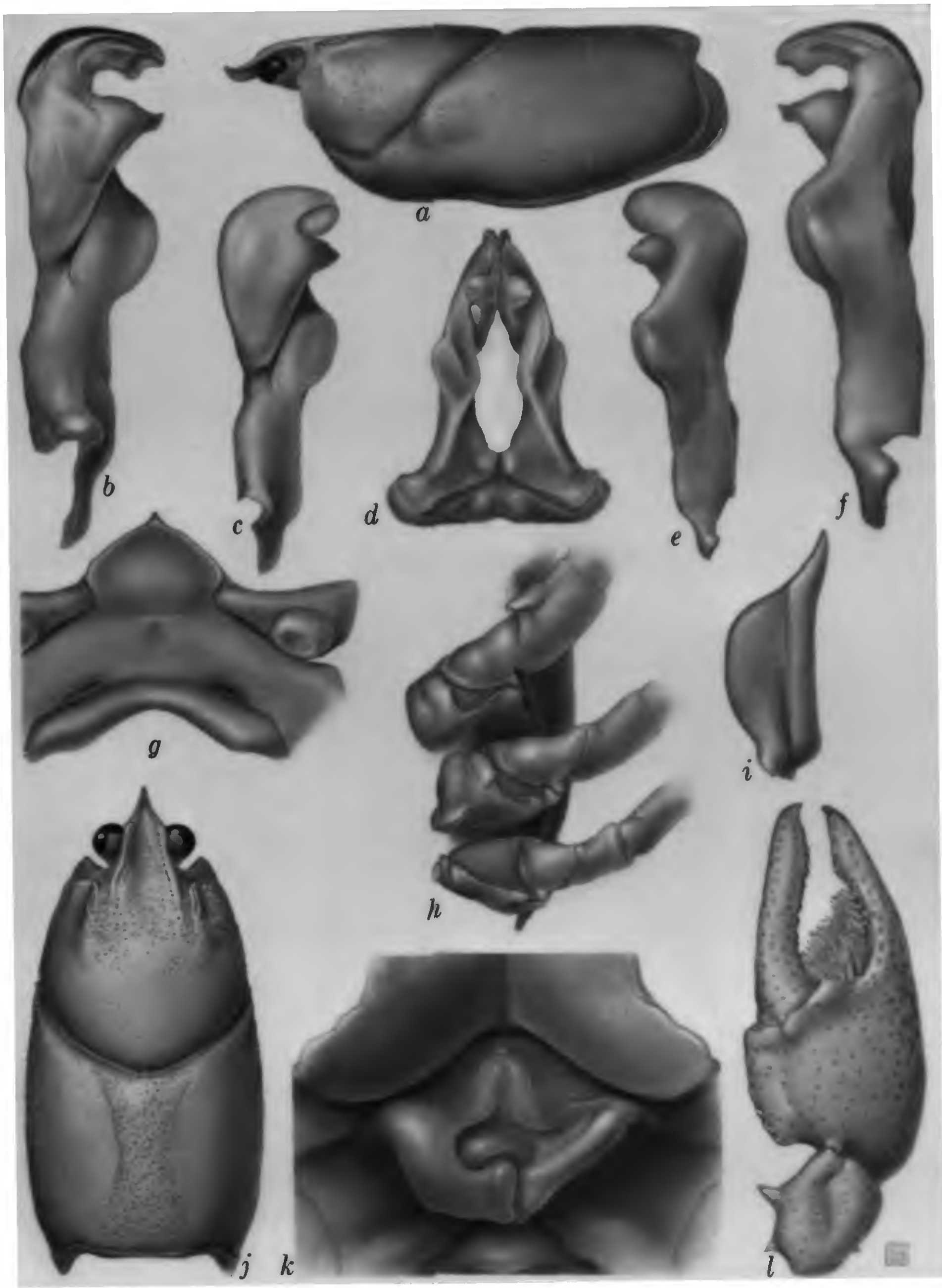


FIGURE 67.—*Cambarus (Hiaticambarus) manningi* (all from holotype except *c*, *e*, from morphotype, and *k*, from allotype): *a*, lateral view of carapace; *b*, *c*, mesial view of first pleopod; *d*, caudal view of first pleopods; *e*, *f*, lateral view of first pleopod; *g*, epistome; *h*, proximal podomeres of third, fourth, and fifth pereiopods; *i*, antennal scale; *j*, dorsal view of carapace; *k*, annulus ventralis; *l*, dorsal view of distal podomeres of cheliped.

across narrowest part, length 40 percent of total length of carapace (47.5 percent of postorbital carapace length). Rostrum with strongly convergent, thickened margins ending suddenly at base of acumen; latter gently upturned, reaching base of ultimate podomere of antennular peduncle; dorsal surface of rostrum deeply concave with prominent punctations, some coalescing in basal region, forming irregular transverse striae. Subrostral ridge rather strong and visible in dorsal aspect along entire length of rostrum, continuing onto acumen. Postorbital ridge short and deeply grooved dorsolaterally, terminating cephalically in acute corneous tubercle. Suborbital angle obtuse; branchiostegal spine very small, tuberculiform. Cervical spine represented by small, rounded tubercle scarcely larger than neighboring ones. Carapace punctate dorsally except for polished median gastric area, and granulate to tuberculate laterally; posterior orbital area with several rather large tubercles. Abdomen shorter than carapace (21.6 and 24.0 mm); pleura rather long, subangular caudoventrally and with sloping cephaloventral margins. Cephalic section of telson with 2 spines in each caudolateral corner, usual lateral incision deep and transverse suture clearly defined. Uropod with proximal podomere bearing acute mesial lobe, lateral lobe rounded; mesial ramus with well-defined submedian ridge bearing premarginal spine and spine present on distolateral extremity.

Cephalomedian lobe of epistome (Figure 67*g*) broadly subtriangular with weakly elevated (ventrally) margins, surface convex; main body with distinct fovea and arched epistomal zygoma, latter flanked anterolaterally by deep elongate pits. Ventral surface of proximal podomere of antennular peduncle with short, heavy, acute tubercles at base of distal third. Antennal peduncle with strong lateral spine on basis, remaining podomeres lacking spines; flagellum reaching second abdominal tergum; antennal scale (Figure 67*i*) about 2.8 times as long as wide, broadest at about midlength, distal spine very strong and reaching midlength of ultimate podomere of antennular peduncle. Ventral surface of ischium of third maxilliped with broad, longitudinal band of long, stiff setae mesially and with submarginal lateral row of smaller both stiff and plumose ones, few additional short plumose setae in area between; distolateral angle subacute but not produced.

Right chela (Figure 67*l*) 2.5 times as long as broad, mesial margin of palm occupying about one-third of its length. Mesial surface of palm without well-defined tubercles although with single row of 7 low elevations; dorsal and ventral surfaces with rather widely spaced large, deep punctations, lateral surface rounded with only slightest suggestion of costa. Fingers widely gaping and proximal half of opposable surface of fixed finger bearing conspicuous tufts of long plumose setae; neither finger with median longitudinal ridge on dorsal or ventral surface, both with conspicuous deep punctations; opposable margin of fixed finger with row of 13 small, rounded corneous tubercles (more proximal ones concealed among setal tufts) extending from base almost to distal seventh, single row of minute denticles present on level slightly ventral to tubercular row along distal fourth of finger, and corneous area immediately proximal to denticles with 1 prominent and 2 less well defined tuberculiform areas; opposable margin of dactyl also with row of 13 tubercles reaching level corresponding to that on fixed finger, minute denticles forming single row below tubercles along distal third, 2 additional tubercles present on lower level between fourth and sixth tubercles of long row. Lateral surface of fixed finger and mesial surface of dactyl punctate.

Carpus of cheliped with distinct oblique furrow dorsally flanked by setiferous punctations; mesial surface with single large spikelike tubercle; ventral surface punctate and bearing 2 tubercles on distal margin: 1 on lateral condyle and other situated mesioventrally. Merus with 1 (left with 2) premarginal tubercles dorsally; ventrolateral row of tubercles represented by 2 and ventromesial row consisting of 8, of which only distal member of each row spikelike; distolateral surface not produced, lacking spiniform tubercle. Ventromesial margin of ischium with only 2 tubercles.

Ischium of third pereiopod with simple hook (Figure 67*h*) extending proximally over basioischial articulation not opposed by tubercle on basis. Coxa of fourth pereiopod with caudomesial transverse ridgelike boss disposed vertically; that of fifth pereiopod devoid of boss but with ventral membrane sparsely setiferous.

First pleopods (Figure 67*b,d,f*) reaching coxae of third pereiopods, symmetrical, and with contiguous bases (see "Diagnosis" for description).

ALLOTYPIC FEMALE.—Excluding secondary sexual characters, differing from holotype in following respects: rostrum almost reaching distal end of ultimate podomere of antennular peduncle; suborbital angle rounded; branchiostegal spine virtually obsolete; cervical spine represented by single low tubercle; flagellum of antenna reaching tergum of third abdominal segment; abdomen much broader; proximal part of mesial margin of palm of chela with elevations more distinctly delimited, tuberculiform on right chela; opposable margin of fixed finger of chela with row of 12 tubercles and 1 well-defined tubercle on lower level immediately proximal to row of denticles; corresponding margin of dactyl also with row of 12 tubercles and single 1 on lower level between fourth and fifth tubercle of row; dorsal surface of merus of cheliped with single premarginal tubercle on right and left members, ventrolateral row represented by single, distal spikelike tubercle; ischium of left cheliped with ventromesial margin bearing only 1 tubercle. (See "Measurements.")

Annulus ventralis (Figure 67*k*) 1.4 times as long as broad, slightly movable, distinctly asymmetrical posteriorly with caudodextral wall more convex and slightly produced caudally along median line; cephalic and central area conspicuously less sclerotized than caudal part; cephalic area with caudally diverging ridges flanking trough leading to depressed central area; sinus originating under caudal end of dextral ridge, coursing caudodextrally, making hairpin turn, and extending cephalosinistrally just across median line, where turning sharply caudally to caudal margin of annulus: tongue thus directed caudodextrally. Postannular sclerite about half as wide as annulus and about 3 times as long. First pleopods reaching midlength of annulus when abdomen flexed.

MORPHOTYPIC MALE, FORM II.—Differing from holotype in following respects: rostrum reaching midlength of ultimate podomere of antennular peduncle; cephalic section of telson with 3 spines in caudodextral corner; opposable margin of fixed finger with row of 11 tubercles, that of dactyl with 12 and row of denticles extending farther proximally on both fingers, as far as seventh tubercle from base on dactyl; merus of right cheliped with 1 spine representing ventrolateral row and 6 in ventromesial row, that of left with 1 and 9, respectively; hook on ischium of third pereiopod much reduced, not reaching basioischial articulation. (See "Measurements.") First pleopod (Figure 67*c,e*) with neither terminal element corneous; central projection more inflated and disposed at right angle to shaft of appendage, its distal portion not being so strongly reflexed. Shaft with juvenile oblique suture.

COLOR NOTES (Figure 58*e*).—Dorsum of carapace largely dark brown to dark olive, fading ventrally; margins of rostrum and postorbital ridges bright orange to vermilion; dark brown reticulate pattern on mandibular adductor region. Hepatic area with broad, pale L-shaped cream splotch flanked by dark brown orbital and antennal areas anteriorly and reticulate mandibular adductor area and dark brown cervical groove posteriorly and ventrally; posteromedian part of gastric region very dark brown. Posterior thoracic region with almost black saddle, narrow dorsally and expanding ventrally, covering caudal flange. Terga of abdomen blue black except for narrow vermilion band along posterior margin of each, that of sixth segment sometimes paler bluish green, but if so, mottled in blue black; pleura white to cream anteriorly, bluish black posteriorly; pleuron of second segment with anterior vermilion spot. Anterior section of telson with pale transverse band anteriorly and broad band of sky blue across midlength, its posterior part and posterior section orange, suffused medianly with blue; entire telson edged with orange to vermilion. Uropods similarly margined; proximal two-thirds of mesial ramus sky blue fading distally to pale orange; proximal section of lateral ramus suffused with blue and distal section orange. Antennular and antennal peduncles dark olive to brown, flagella orange to orange brown. Third maxillipeds mostly pale blue to cream. Chelipeds pale turquoise from coxa to distal part of merus where becoming darker blue, and distal margin and articular knobs vermilion; carpus olive to brown dorsally, spines, distal margin, and articular knobs vermilion; propodus olive to dark brown with ridge opposite base, of dactyl and proximal articular knob vermilion; fingers dark olive to brown and with corneous tips. Remaining pereiopods vermilion at joints, otherwise blue from merus distally. Entire sternal area cream suffused with blue and some ridges and knobs orange to vermilion.

Measurements (mm)

	Holotype	*Allotype*	*Morphotype*
Carapace			
Height	9.9	11.2	9.0
Width	12.2	14.6	11.7
Entire length	24.0	28.0	23.3
Postorbital length	20.2	23.6	19.2
Areola			
Width	2.5	2.6	2.2
Length	9.6	10.6	9.1
Width	2.5	2.6	2.2
Length	9.6	10.6	9.1
Rostrum			
Width	3.5	4.2	3.4
Length	5.2	5.5	5.1
Chela			
Length of mesial margin of palm	7.5	8.1	6.0
Width of palm	11.2	10.0	8.5
Length of lateral margin	23.5	24.5	19.6
Length of dactyl	14.1	14.8	11.9
Abdomen			
Width	10.2	14.9	10.2
Length	21.6	26.8	20.3

TYPES.—The holotypic male, form I, allotypic female, and morphotypic male, form II (numbers 147911, 147912, and 147913, respectively), are deposited in the National Museum of Natural History, Smithsonian Institution, together with the paratypes comprising 7♂I, 28♂II, 36♀, 2j♂, 3j♀, and 1♀ with young.

TYPE-LOCALITY.—Little Cedar Creek (Coosa River basin) near school for deaf on outskirts of Cave Spring, Floyd County, Georgia. There the stream, some 7 meters wide and 0.3 meter deep, flows through a cleared, formerly cultivated area. *Acer* sp., *Alnus rugosa*, and *Juniperus* sp. are present along the banks. The water is clear and courses with a moderate current over a sandy clay bed littered with rocks in alternating pool and riffle areas. *Cambarus (H.) manningi* was found only in the riffles. Collected with it were *C. (D.) striatus* and *C. (P.) coosae*.

RANGE.—This crayfish is known only from the Coosa River basin in northwestern Georgia, southeastern Tennessee, and eastern Alabama, where it was found in the Ridge and Valley Province.

SPECIMENS EXAMINED.—I have examined 110 specimens from the following localities. GEORGIA. *Chattooga County*: (1) Armuchee Creek 7.1 airmi NNW of Armuchee near St Rte 200, 3♂II, 26 Jul 1974, O. S. Lancaster, J. E. McCaleb, A. E. Johnson, collectors. *Floyd County:* (2) type-locality, 5♂I, 29♂II, 29♀, 1♀ with young, 1 May 1967, Torgny Unestam, HHH; 2♂I, 6♀, 2j♂, 3j♀, 21 Oct 1976, T. A. English, Jr., HHH; (3) Cedar Creek at St Rte 100, 4.8 mi N of jct with St Rte 53, 1♀, 21 Oct 1976, TAE, HHH; (4) trib to Cedar Creek on US Hwy 41 near Cave Spring, 1♂I, 1♀, 13 Sep 1954, R. M. Bailey; (5) Armuchee Creek, 1♀, 6 Jul 1948, D. C. Scott. *Whitfield County:* (6) Conasauga River at St Rte 286, about 7 mi NE of Dalton at Murray Co line, 1♂I, 11 Oct 1969, E. T. Hall, Jr., HHH; (7) Mills Creek at unpaved road parallel to Tennessee line NE of Red Clay, 9♂I, 14♀, 1j♀, 23 Oct 1977, R. W. Bouchard, J. W. Bouchard. TENNESSEE. *Polk County:* (8) Conasauga River off US Hwy 411 at Easley Ford Bridge NW of Tennga, Georgia, 1♀, 17 Mar 1977, RWB, J. R. Weaver. (The type series is limited to specimens from localities 2–4).

Dr. Bouchard has informed me that he has examined specimens from three additional localities: ALABAMA. *Cherokee County:* (9) trib to Frog Creek off Co Rd 33 (Sec 15 SE, R 10E, T 12S), 1♂I, 10 Oct 1977, RWB, JRW. TENNESSEE. *Bradley County:* (10) Coahulla Creek at mouth of Tate Branch off St Rte 74, 1 specimen, 22 Oct 1969, D. A. Etnier, R. A. Stiles, and J. L. Wilson; (11) Mills Creek off Co Rd 4332 at unpaved road parallel to Georgia-Tennessee state line, 2♂II, 1♀, 1j♂, 16 Nov 1968, RWB, DAE.

VARIATIONS (Figure 68).—This crayfish exhibits few variations, perhaps the most obvious of

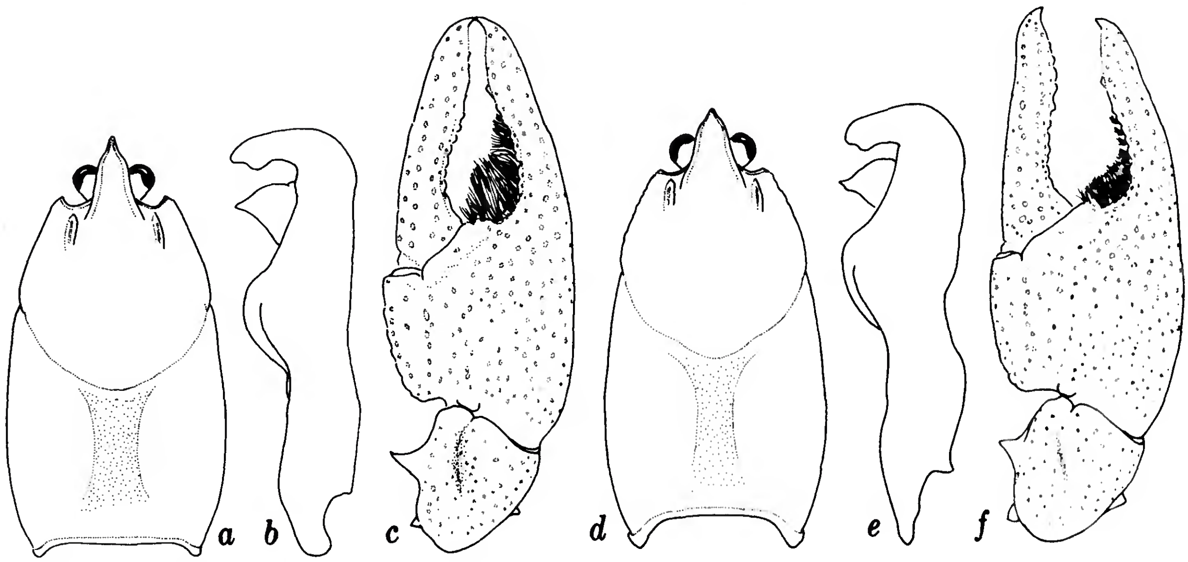


FIGURE 68.—*Cambarus (H.) manningi,* variations (*a, d,* dorsal view of carapace; *b, e,* lateral view of first pleopod of first form male; *c, f,* dorsal view of distal podomeres of cheliped of same): *a–c,* from type-locality; *d–f,* from Conasauga River at St Rte 286, Murray-Whitfield Co line.

which is in the suborbital angle; although consistently obtuse, it may be so broad as to appear almost obsolete. The areola varies from 3.1 to 4.6 times as long as wide and may have as few as six punctations across the narrowest part. Rarely is there more than one well-developed spine representing the ventrolateral row on the merus of the cheliped, but occasionally there are two, one of which, the more proximal, is much smaller than the other. The presence of a proximomesial tubercle on the carpus of the cheliped is unusual. Slight differences occur in the numbers of tubercles comprising the rows on the several podomeres of the cheliped but none exceeds the range that might be anticipated in better known species.

SIZE.—The largest specimen available is a female having a carapace length of 28.5 (postorbital carapace length 23.2) mm. The corresponding lengths of the largest and smallest males, form I, are 27.2 (23.1) and 17.2 (13.6) mm. Those lengths in the single female carrying young are 21.2 (17.5) mm.

LIFE HISTORY NOTES.—First form males have been collected in May, September, and October, and a female carrying young was obtained in May.

ECOLOGICAL NOTES.—All of the specimens for which data are available were taken from beneath rocks in riffle areas of streams which, except following heavy rains, are clear and flow with a moderate to swift current.

RELATIONSHIPS.—*Cambarus (H.) manningi* appears to have its closest affinities with *Cambarus (H.) longirostris,* from which it differs most conspicuously in its brilliant coloration. Its longer areola, constituting at least 45 percent of the postorbital carapace length, is with few exceptions unique in the subgenus. (See "Remarks" under "*Hiaticambarus.*")

GEORGIA CRAYFISH ASSOCIATES.—Occurring with *Cambarus (H.) manningi* were the following species (the number of times is indicated in parentheses): *C. (D.) striatus* (1), *C. (L.) acanthura* (1), *C. (P.) coosae* (6), and *Orconectes spinosus* (3).

ETYMOLOGY.—This crayfish is named in honor of my colleague, Raymond B. Manning, in token of my appreciation for the encouragement and invaluable assistance he has given me in my studies for some 15 years.

Cambarus (Hiaticambarus) speciosus, new species

FIGURES 22*g*, 58*f*, 65, 69, 212

Cambarus (Hiaticambarus) species H.—Hobbs, 1969a:106, 141, fig. 10.

In his review of the crayfishes of the genus *Cambarus*, Hobbs (1969a) noted the occurrence of this undescribed species in the Coosa River basin.

DIAGNOSIS.—Rostrum with convergent margins, usually tapering from base, thickened but devoid of marginal spines or tubercles. Postorbital ridge terminating cephalically in well-developed spine. Suborbital angle rounded to acute. Cervical spine strong. Areola 2.6 to 4.1 times as long as wide, comprising 30.3 to 35.4 percent of entire carapace length (40.0 to 44.6 percent of postorbital carapace length), and bearing 7 to 10 punctations across narrowest part. Chela with 1 well-defined row of 6 to 9 tubercles on mesial margin of palm and with or without 1 or 2 additional rows flanking it dorsolaterally; lateral half of dorsal surface of palm with crowded deep punctations, especially near base of fixed finger; fingers gaping, particularly in older males, and with conspicuous tuft of plumose setae protruding from proximal opposable part of fixed finger; lateral margin of fixed finger and distal third of palm strongly costate; both fingers with well-defined submedian longitudinal ridges dorsally; dactyl of first form male quite or almost as long as mesial margin of palm. Tubercle on basis of third pereiopod opposing hook on ischium. Pleura of second through fifth abdominal segments truncate or rounded ventrally with caudoventral angle. First pleopod with comparatively long terminal elements: corneous central projection tapering distally, recurved at approximately 120 degrees to main shaft of appendage, and lacking subapical notch; and mesial process, somewhat inflated, tapering, often to acute apex, directed caudally and slightly laterally at angle of about 90 degrees. Terga of abdomen largely greenish gray with narrow reddish transverse band on caudal margin and large tan median splotch on second through fifth, as well as with green spot just dorsal to pleura, latter lacking dark scalloped line along bases. Female with first pleopod present.

HOLOTYPIC MALE, FORM I.—Cephalothorax subovate in cross section, depressed (Figure 69*a,j*). Abdomen narrower than thorax (15.4 and 18.5 mm); greatest width of carapace distinctly greater than height at caudodorsal margin of cervical groove (18.5 and 13.5 mm). Areola 3.4 times as long as broad with crowded punctations, 7 to 9 across narrowest part; length of areola 34.5 percent of total length of carapace (42.2 percent of postorbital carapace length). Rostrum with somewhat thickened, elevated, tapering margins devoid of spines or tubercles, tip reaching base of distal podomere of antennular peduncle (tip abraded but distinctly upturned in other specimens); dorsal surface of rostrum concave with many punctations, rather sparse on and at base of indistinctly delimited acumen. Subrostral ridges well developed and evident in dorsal aspect to base of acumen. Suborbital angle acute. Postorbital ridges moderately prominent, grooved dorsolaterally and terminating cephalically in acute corneous spine. Branchiostegal spine represented by very low, inconspicuous tubercle. Cervical spine well developed. Carapace densely punctate dorsally except in gastric region, and distinctly sculptured over attachment of mandibular muscle; lateral surface strongly granulate except in dorsalmost hepatic region.

Abdomen slightly shorter than carapace (32.7 and 34.5 mm); pleura rounded to subtruncate ventrally with angular caudoventral extremities on second through fifth segments. Cephalic section of telson with 2 spines in caudodextral corner and 3 in caudosinistral; free margin of caudal section evenly rounded. Proximal podomere of uropod with both lobes terminating in corneous-tipped spine; mesial ramus with low submedian dorsal keel ending in small premarginal spine.

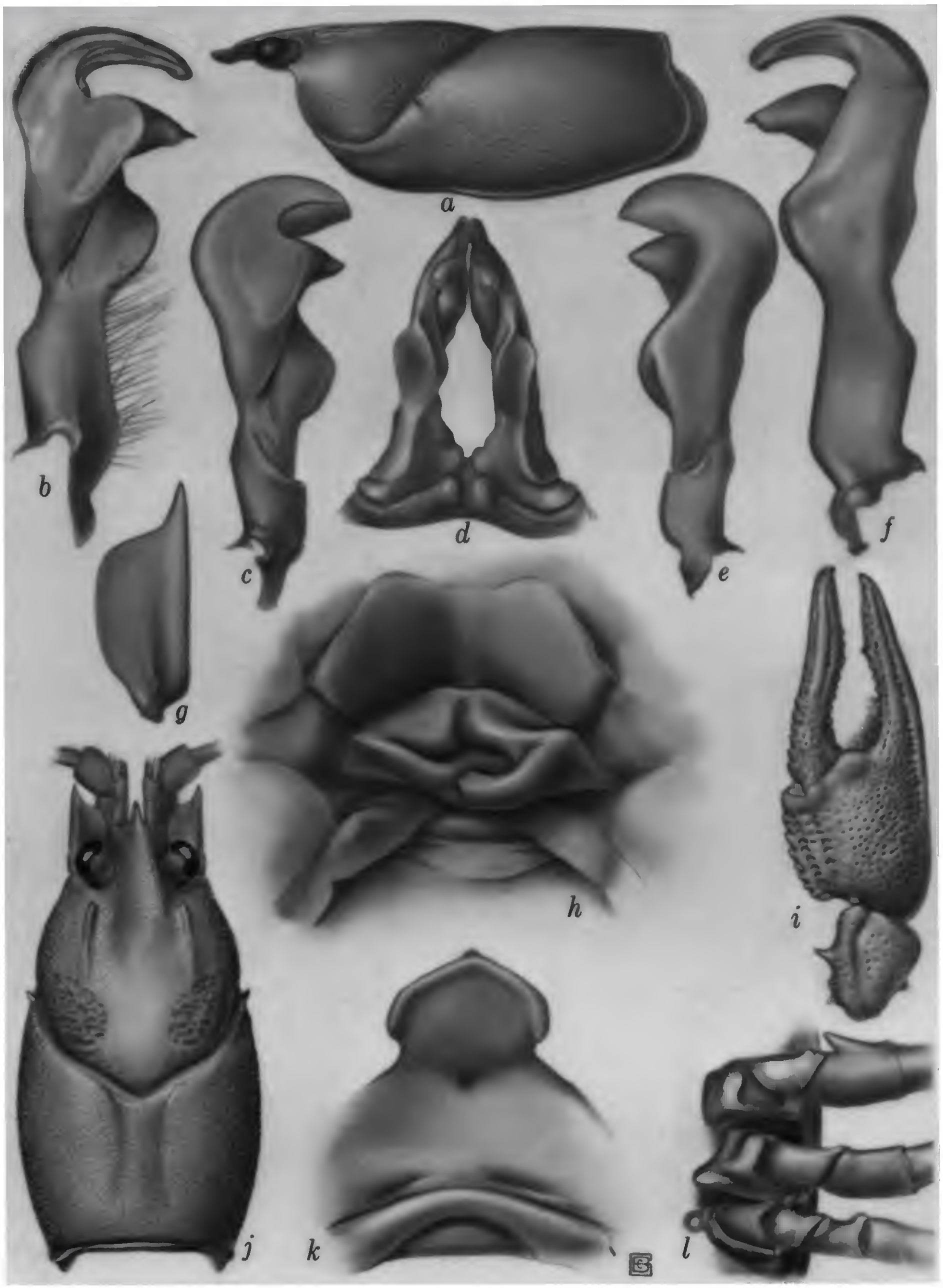


FIGURE 69.—*Cambarus (Hiaticambarus) speciosus* (all from holotype except *c*, *e*, from morphotype, and *h*, from allotype): *a*, lateral view of carapace; *b*, *c*, mesial view of first pleopod; *d*, caudal view of first pleopods; *e*, *f*, lateral view of first pleopod; *g*, antennal scale; *h*, annulus ventralis; *i*, dorsal view of distal podomeres of cheliped; *j*, dorsal view of carapace; *k*, epistome; *l*, proximal podomeres of third, fourth, and fifth pereiopods.

Cephalomedian lobe of epistome (Figure 69*k*) broadly rounded with small cephalomedian projection, margin somewhat thickened and elevated ventrally; main body with distinct median fovea and paired slitlike grooves immediately cephalic to arched epistomal zygoma. Ventral surface of proximal segment of antennule with small spine at base of distal third. Antenna broken, in other specimens reaching beyond caudal margin of telson; basis with distinct lateral spine and ischium with small spiniform tubercle. Antennal scale (Figure 69*g*) about 2.5 times as long as broad with mesial and lateral margins subparallel for some distance proximal and distal to midlength; strong distal spine reaching beyond midlength of ultimate podomere of antennular peduncle. Mesial half of ischium of third maxilliped with longitudinal band of punctations bearing long, stiff plumose setae; lateral half possessing submarginal row and widely spaced punctations bearing very short, small setae; distolateral extremity only slightly produced in short, acute corneous tip.

Right chela (Figure 69*i*) 2.4 times as long as broad and moderately depressed; mesial margin of palm with row of 8 tubercles subtended dorsally by row of 8 more squamous ones, 2 additional parallel shorter rows of smaller extremely depressed tubercles extending proximally from thickened rim immediately mesial to dorsal articular knob at base of dactyl; remainder of palm with prominent crowded, deep punctations and single tubercle ventrolateral to distal tubercle in mesialmost row. Both fingers with prominent dorsomedian longitudinal ridges and less well defined ventral ones, latter ridge on dactyl scarcely recognizable except by flanking rows of punctations. Fixed finger arched and with broad excavation along proximal three-fifths of opposable margin bearing row of 8 knoblike tubercles, row continuing with 5 additional smaller ones decreasing in size toward distal end of finger; prominent tubercle situated immediately ventral to ninth tubercle of row, at about base of distal two-fifths of finger; single row of minute denticles broken by tubercles along distal half of finger; lateral margin of finger and that of distal half of palm strongly costate and mesial two-fifths of ventral opposable surface with prominent tuft of plumose setae. Dactyl arched and opposable margin somewhat sinuous, bearing row of 12 tubercles along basal four-fifths, minute denticles as on fixed finger; mesial margin with row of 6 rather distinct tubercles along proximal two-fifths followed by others decreasing in size to beyond midlength of finger.

Carpus of cheliped longer than broad (11.6 and 8.4 mm) with moderately deep longitudinal furrow dorsally, flanked by punctations mesially and laterally; mesial surface with prominent, slightly procurved spiniform tubercle near midlength and small, rounded ones proximally slightly dorsodistal to proximomesial articular condyle; lateral surface punctate, and ventral surface with usual distal marginal tubercles (1 poorly developed on ventrolateral articular knob and other large and situated mesially) and 2 small ones, 1 proximal to mesiodistal tubercle and other ventral to procurved tubercle on mesial surface. Merus with 2 premarginal spines dorsally, mesial and lateral surfaces sparsely punctate, and ventral surface of right cheliped with ventromesial row of 12 tubercles and only 2 spikelike ones representing ventrolateral row, left cheliped with 13 and 3, respectively. Ischium with 5 small tubercles in ventromesial row.

Hook on ischium of third pereiopod only, hook (Figure 69*l*) overreaching basioischial articulation and opposed by tubercle on basis. Coxa of fourth pereiopod with prominent caudomesial boss, vertically disposed and somewhat flattened caudally. Boss on coxa of fifth pereiopod vestigial. First pleopods (Figure 69*b,d,f*) reaching coxae of third pereiopods, symmetrical, with gap between their bases (See "Diagnosis" for description.)

Allotypic Female.—Excluding secondary sexual characteristics, differing from holotype in following respects: apex of rostrum reaching distal end of antennular peduncle, and antennal scale extending slightly beyond it; branchiostegal spine well developed, acute with corneous tip; fingers of chela not gaping nearly so much as in holotype; mesial margin of palm of right chela with row of

9 tubercles; opposable margin of fixed finger with row of 8 tubercles, 9 on left; corresponding margin of dactyl with 10 and 11, respectively; mesial surface of carpus with single tubercle proximally, its ventral surface lacking small tubercles proximal to distal margin; ventromesial row of tubercles on merus of both chelipeds consisting of 10 and ventrolateral row represented by 2 tubercles. (See "Measurements.")

Annulus ventralis (Figure 69*h*) subspindle shaped, about twice as broad as long, and situated shallowly in sternum; cephalic half rather flattened but surface interrupted by median trough leading caudally into transverse depressed area bearing sinistrally directed tongue; sinus originating under caudosinistral wall of trough, coursing sinistrally and making hairpin curve to median line, there forming broad arc, crossing median line, returning caudosinistrally, and ending on caudal wall slightly dextral to median line. Postannular sclerite about 3 times as broad as long and about two-fifths as wide as annulus. First pleopod reaching midlength of annulus when abdomen flexed.

Morphotypic Male, Form II.—Differing from holotype in following respects: postorbital ridges and suborbital angle with extremities distinctly more acute; branchiostegal spine well developed; epistome more triangular; ischium of antenna with distinct spine ventrally; spine on antennal scale reaching distal extremity of antennular peduncle; gap between fingers of chela much narrower; left chela regenerated, possessing only 6 tubercles along mesial margin of palm; opposable margin of fixed finger of right chela with 11 tubercles, that of left with 14; corresponding margins of left chela with 12 and 15 tubercles; carpus of cheliped with 1 tubercle on proximomesial surface, spines on ventrodistal margin much more acute than in holotype, and ventral surface of right member devoid of either of 2 more proximal tubercles present in holotype; ventral surface of merus of both chelipeds with ventromesial row of 11 tubercles and only 2 representing lateral row; hook on ischium of third pereiopod much reduced, not reaching basioischial articulation, and opposing tubercle on basis slightly reduced; boss on coxa of fourth pereiopod also reduced, but clearly evident. (See "Measurements.") First pleopod (Figure 69*c,e*) with juvenile oblique suture, neither process corneous; mesial process, although subacute, much shorter but inflated as in holotype, its distal base contiguous in lateral aspect to base of central projection; latter, although tapering to acute apex, very broad; cephalodistal surface of appendage protruding in broad arc.

Color Notes (Figure 58*f*).—Basic color of carapace orange tan with greenish to brown markings. Marginal parts of rostrum, postorbital ridges, and cephalic gastric region reddish orange, concavity of rostrum very dark olive, almost black, and cephalic gastric region with paired diffuse dark splotches between caudal bases of postorbital ridges; mandibular adductor region with dark green reticulations, merging caudally with paired, broad greenish black markings immediately cephalic to and covering cervical groove, latter markings partially separated dorsomedianly by apex of triangular caudal extension from orange portion of gastric region, apex not reaching cervical groove; hepatic region with greenish cream oblique area extending from dark green reticulations cephaloventrally almost to margin of carapace; orbital and ventral hepatic regions dilute greenish black with pale tubercles; antennal and mandibular regions cream. Thoracic region pale orange tan with cephalic half suffused with green and with moderately broad saddle caudally; saddle, although broader laterally than dorsally, lacking horns. Abdomen with first abdominal tergum greenish black; remaining terga greenish gray except for narrow reddish transverse band on caudal margin of each, and large tan median splotch on second through fifth terga; lateral extremity of these terga with distinct dark green spot flanked laterally by greenish cream spot. Pleura of all abdominal segments greenish gray basally, fading quickly to cream. Telson and uropods olive with orange to cream ridges and tubercles; lateral margins of rami of uropods also orange to cream. Chela olive tan with dorsal surface of palm bearing greenish black, heavy reticulate pattern; ridge at base of dactyl mostly reddish orange with cream areas where thickest; fingers rather uniformly olive tan; carpus of cheliped mostly cream tan dorsally and laterally with very dark olive patch covering dorsal furrow, also dark olive mesially with tubercles orange cream; distal part of merus also dark brown to black with pale orange tan distal ridge and similarly colored subdistal tubercles dorsally. Remaining pereiopods pale tan to cream, sometimes with greenish markings along distal part of merus and on carpus and propodus.

Measurements (mm)

	Holotype	*Allotype*	*Morphotype*
Carapace			
Height	13.5	11.9	10.2
Width	18.5	16.3	14.3
Entire length	34.5	32.5	29.0
Postorbital length	28.2	25.8	23.1
Areola			
Width	3.5	3.3	2.6
Length	11.9	10.7	10.0
Rostrum			
Width	4.4	4.7	4.2
Length	8.1	8.2	7.5
Chela			
Length of mesial margin of palm	12.0	8.8	7.2
Width of palm	15.1	10.1	8.9
Length of lateral margin	36.9	24.5	21.6
Length of dactyl	23.5	14.9	14.2
Abdomen			
Width	15.5	15.9	12.9
Length	33.7	33.1	29.9

TYPES.—The holotypic male, form I, allotype, and morphotypic male, form II (numbers 146023, 146024, 146025, respectively), are deposited in the National Museum of Natural History, Smithsonian Institution. The paratypes, consisting of the specimens listed below, are deposited in the same institution.

TYPE-LOCALITY.—Talking Rock Creek at State Route 5, Pickens County, Georgia. There the stream is some 12 to 15 meters wide, from a few centimeters to more than a meter deep, clear to slightly cloudy, and flows swiftly over a rock- and gravel-littered sandy bottom. *Podostemum ceratophyllum* is abundant on the gravel bar along the north bank where the water is shallow and the current less rapid. At this locality, the stream is shaded by *Platanus occidentalis*, *Liriodendron tulipifera*, *Alnus rugosa*, and *Salix* sp. growing along the waterside.

RANGE.—This crayfish seems to be confined to a small segment of the Coosawattee River basin in Pickens, Gilmer, and Murray counties, Georgia. To what extent much of its range has been destroyed by the construction of Carters Dam and a smaller "reregulation dam," which impounded a sizable segment of the river and the lower section of Talking Rock Creek, is not known.

GEORGIA SPECIMENS EXAMINED.—I have examined 76 specimens from the following localities. *Gilmer County:* (1) Town Creek 8.3 mi S of Ellijay on St Rte 156, 2♂I, 1♀, 8 Sep 1945, HHH, collector; (2) Cartecay River SE of Ellijay on St Rte 52, 1♂II, 15 Aug 1970, F. J. Schwartz; (3) small stream 9.1 mi NW of Blaine on St Rte 146 just E of Murray Co line, 1♂I, 1♂II, 1j♀, 22 Oct 1972, G. B. Hobbs, HHH. *Murray County:* (4) stream 2.5 mi N of Coosawattee River on US Hwy 411, 1♂I, 16 Apr 1958, P. C. Holt, D. E. Norby; (5) Talking Rock Creek at St Rte 156, 1♂II, 1♀, 3 May 1967, Torgny Unestam, HHH. *Pickens County:* (6) type-locality, 3♂I, 4♂II, 3♀, 6j♂, 4j♀, 28 Apr 1967, TU, HHH; 2♂I, 2♀, 1j♂, 10 Oct 1969, K. R. Martin, HHH; (7) Talking Rock Creek at Talking Rock, 2♂II, 1♀, 1j♀, 8 Oct 1945, GBH, HHH; 1♀, date and collector unknown; (8) Talking Rock Creek 2.6 mi SE of Gilmer Co line on St Rte 156, 3♂I, 5♂II, 5♀, 22 Sep 1972, GBH, HHH; (9) Little Scarecorn Creek 1.1 mi SW of Blaine on St Rte 156, 3♂I, 3♂II, 2♀, 1j♀, 22 Sep 1972, GBH, HHH; (10) Ball Creek 1.7 mi SE of Gilmer Co line on St Rte 156, 2♂I, 1j♂, 3j♀, 1 ovig ♀, 28 Apr 1967, TU, HHH; 3♂II, 1♀, 2j♂, 1j♀, 22 Sep 1972, GBH, HHH.

VARIATIONS.—In some respects this is one of the most variable of the Georgia crayfishes, but the structure of the first pleopod of the first form male and the basic color pattern seem to be stable. The rostrum differs slightly in length, but its general conformation is virtually constant. One of the most conspicuous variations occurs in the suborbital angle, which varies from being acute to rounded, almost obsolete. The branchiostegal spine may be acute and well developed or reduced to a small tubercle. Marked differences occur in the cheliped with the mesial margin of the palm bearing a single row of six to nine tubercles, or there may be two well-defined rows with as many as eight tubercles in each, and the two rows equally well developed; in some specimens traces of a third row are present, and not infrequently the second row is represented by only two or three tubercles. On the merus of the cheliped, none to several tubercles may be present dorsomesially, and there may be no trace of a proximomesial tubercle or one or two may be present. The width of the gap between the fingers may be broad or narrow, and in some specimens, the arch in both fingers is as marked as that in most members of the subgenus *Hiaticambarus*, but the consistent, strongly developed, dorsal longitudinal ridges of the fingers and the marked lateral costa belie its being a typical member of the subgenus. Other differences are summarized in the descriptions of the allotype and morphotype, and the ranges of several proportions are presented in the "Diagnosis." (See "Measurements.")

SIZE.—The largest specimen is a female having a carapace length of 45.3 (postorbital carapace length 37.0) mm. The corresponding lengths of the smallest and largest first form males are 27.9 (22.2) and 42.3 (34.7) mm, respectively, and those of the single ovigerous female, 30.7 (24.0) mm.

LIFE HISTORY NOTES.—Among the limited material available, first form males are represented among collections made in April, September, and October, and the single ovigerous female was taken in April.

Seasonal Data

Sex/stage	*J*	*F*	*M*	*A*	*M*	*J*	*J*	*A*	*S*	*O*	*N*	*D*	*?*
♂I				6					8	3			
♂II				4	1			1	11	3			
♀				3	1				9	3			1
♂j				7					2	1			
♀j				7					2	2			
♀ ovig				1									

ECOLOGICAL NOTES.—*Cambarus (H.) speciosus* is a stream inhabitant, occurring most abundantly where clear or slightly cloudy water flows moderately to swiftly over a rock-littered substrate. All of the specimens collected by me were found beneath rocks or in beds of *Podostemum ceratophyllum*. It is unlikely that they would shun tree litter, but in the localities where I encountered this crayfish the stream beds had been scoured of most debris. It does not seem to be present in small headwater streams and has never been taken from burrows.

Perhaps in the absence of data to quantify the "swimming ability" of crayfishes, I am in error in believing that members of this species are among the fastest, if not the fastest, swimmers in the Georgia crayfish fauna.

RELATIONSHIPS.—Occasionally species are encountered that tend, more than most, to combine characteristics of two subgenera in such proportions as to make their assignment to either defendable. *Cambarus speciosus* is such a species and could be assigned to either *Hiaticambarus* or *Puncticambarus* with good reason. The two rows of tubercles along the mesial margin of the palm (the second row rather well developed in some individuals) of the chela, the sharply defined longitudinal ridges on the dorsal surface of the fingers of the chela, and the strongly costate lateral margin of the fixed finger and distal portion of the palm all point toward relatives assigned to the subgenus *Puncticambarus*. In contrast, the gaping fingers of the chela, the setal tuft protruding into the gap from the proximal opposable base of the fixed finger, the crowded deep punctations in the areola, the thickened margins of the rostrum (not so thick, however, as in most representatives of *Hiaticambarus*), and the dark bands cephalic to the cervical groove and caudal margin of the carapace all suggest a closer affinity with the members of *Hiaticambarus*. Its apparent closest relatives are *C. (P.) coosae*, *C. (P.) hiwasseensis*, *C. (P.) extraneus*, and *C. (P.) scotti* in the subgenus *Puncticambarus* and *C. (H.) fasciatus* and *C. (H.) girardianus* in the subgenus to which it is tentatively assigned. It differs from all members of both subgenera in lacking a subapical notch on the central projection of the first pleopod of the first form male.

Georgia Crayfish Associates.—Collected with *Cambarus (H.) speciosus* were the following species (the number of times they were found together is noted in parentheses): *Cambarus (D.) latimanus* (4), *C. (D.) striatus* (1), *C. (H.) coosawattae* (1), *C. (J.) conasaugaensis* (3), and *Procambarus (Pe.) spiculifer* (1).

Etymology.—From the Latin *speciosus* (beautiful), chosen because of the strikingly pleasing coloration of this crayfish.

Subgenus *Jugicambarus*

Subgenus *Cambarus* Erichson, 1846:97 [in part].—Fowler, 1912:341 [in part].

Subgenus *Bartonius* Ortmann, 1905a:97 [in part].

Subgenus *Jugicambarus* Hobbs, 1969a:106 [type-species: *Cambarus bartonii asperimanus* Faxon, 1914:391].—Bouchard, 1973a:105 [emendation].

Subgenus *Jugocambarus*.—D. G. Hart and C. W. Hart, 1974: 74 [erroneous spelling].

Diagnosis.—Body and eyes pigmented except

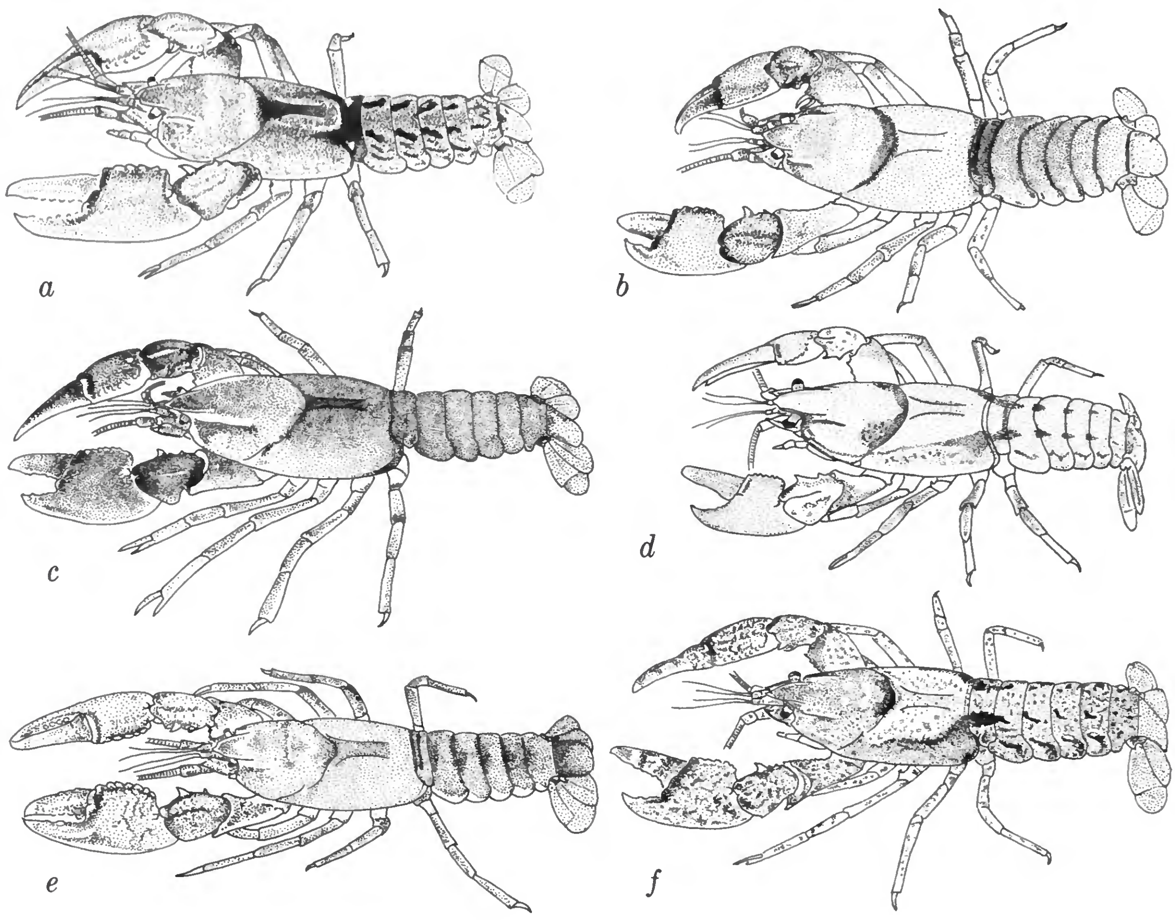


Figure 70.—Color patterns in members of subgenus *Jugicambarus*: *a*, *Cambarus (J.) asperimanus* from Big Creek at St Rte 28, Rabun Co; *b*, *C. (J.) conasaugaensis* from Conasauga Creek 3.2 mi E of Murray Co line on US Hwy 76, Gilmer Co; *c*, *C. (J.) nodosus* from 3.3 mi W of Vogel St Park on St Rte 180, Union Co; *d*, *C. (J.) distans* from Murphy Hollow Creek 2.1 mi S of Interstate Hwy 24 on Murphy Hollow Rd, Dade Co; *e*, *C. (J.) parvoculus* from tributary to Warren Creek 0.3 mi E of Alabama line, Dade Co; *f*, *C. (J.) unestami* from type-locality.

in troglobitic species. Antennal scale of latter less than twice as long as broad. Rostrum rarely with marginal spines or tubercles and with or without thickened margins. Postorbital and cervical spines present or absent, latter conspicuous only in troglobitic *C. (J.) setosus* (from Missouri). Suborbital angle present or absent. Branchiostegal spine small or absent. Areola broad to sublinear (3.8 to 29.0 times as long as wide), constituting 31.5 to 41.4 percent of entire length of carapace (in Georgia specimens, 38.2 to 48.8 percent of postorbital carapace length) and sparsely to densely punctate. Chela subrectangular, rather short except in troglobitic species, and somewhat depressed only in burrowing species; mesial surface of palm with single serrate or cristiform row of tubercles, occasionally with weak second row above and as many as 3 rows in troglobitic species; dorsal surface usually deeply pitted and both palm and fingers frequently bearing conspicuous setae; fingers never widely gaping and with well-defined longitudinal ridges dorsally; proximal opposable margin of dactyl never deeply concave; conspicuous tuft of setae never present at mesial base of fixed finger, lateral base never deeply impressed. Terminal elements of first pleopod of first form male consisting of (1) bladelike, usually tapering central projection, sometimes with subapical notch and recurved as little as 55 degrees to shaft but most often much more strongly curved and occasionally forming broad arc of almost 180 degrees; (2) subconical, usually long mesial process frequently extending farther caudally than central projection; and (3) caudal process, seldom conspicuous, usually reduced or absent. (Slightly modified from Hobbs, 1969a, and Bouchard, 1973a).

RANGE.—Discontinuous: from northeastern Oklahoma through the Ozark region into eastern Missouri, and from the western Highland Rim in Tennessee and Kentucky to the Allegheny Mountains in Pennsylvania and Virginia, and southward to South Carolina and northern Georgia. A single disjunct species occurs in subterranean waters in southwestern Georgia and the panhandle of Florida.

In Georgia, the six epigean species are distributed on the Appalachian Plateau, the Ridge and Valley, Blue Ridge, and in a small segment of the uppermost Piedmont provinces where they occur in the Tennessee, Hiwassee, Savannah, Chattahoochee, and Coosa watersheds. The single troglobitic species is known from a cave (in Eocene limestone) on the Tifton Upland in Decatur County.

SPECIES OCCURRING IN GEORGIA.—*Cambarus (J.) asperimanus, C. (J.) conasaugaensis, C. (J.) cryptodytes, C. (J.) distans, C. (J.) nodosus, C. (J.) parvoculus,* and *C. (J.) unestami.*

HABITAT.—In Georgia, the members of this subgenus occur primarily in the mountainous sections of the state, where they frequent small to moderately large streams with currents ranging from hardly more than a trickle to torrential rapids. All of these epigean species construct highly branching burrows, and at least one, *C. nodosus,* seldom enters open water. The albinistic *C. cryptodytes* is limited to subterranean waters in the southwestern part of the state.

Key to Georgia Members of Subgenus *Jugicambarus*

1. Albinistic, eyes without pigment or faceted cornea .... ***cryptodytes***
   Pigmented; eyes with pigment and faceted cornea 2
2. Mesial surface of palm of chela with 2 or more rows of tubercles 3
   Mesial surface of palm of chela with only 1 row of tubercles 4
3. Eyes small; suborbital angle obtuse; mesial process of first pleopod of male surpassing tip of central projection; caudal wall of annulus ventralis U-shaped .... ***nodosus***
   Eyes not distinctly small; suborbital angle subacute; mesial process of first

pleopod of male not surpassing tip of central projection; caudal wall of annulus ventralis broadly arched .... ***unestami***

4. Chela (especially fingers) provided with conspicuous tufts of stiff setae; central projection of first pleopod of first form male lacking subapical notch .... ***asperimanus***

   Chela usually lacking conspicuous tufts of long stiff setae; central projection of first pleopod of first form male with subapical notch 5

5. First pleopod of first form male with central projection bent but apex not reaching level proximal to distal margin of base of mesial process; annulus ventralis not strongly asymmetrical .... ***distans***

   First pleopod of first form male with central projection forming arc, apex reaching level distinctly proximal to distal margin of base of mesial process; annulus ventralis strongly asymmetrical 6

6. Suborbital angle acute; tip of central projection of first pleopod not reaching level of proximal base of mesial process; fingers of chelae never with conspicuous setal tufts .... ***parvoculus***

   Suborbital angle obsolete; tip of central projection of first pleopod reaching level of proximal base of mesial process; fingers of chelae sometimes with conspicuous setal tufts .... ***conasaugaensis***

Cambarus (Jugicambarus) asperimanus Faxon

FIGURES 24*b*, 70*a*, 71, 72, 213

Cambarus bartonii asperimanus Faxon, 1914:391, 424.—Hobbs and Shoup, 1947:142.—Hobbs, 1953c:20; 1969a:107; 1974a:16*.

Cambarus (Cambarus) bartoni asperimanus.—Ortmann, 1931: 107, 136–138.

Cambarus asperimanus.—Brimley, 1938:503.—Hobbs, 1953c: 20, 24, 27; 1959:897; 1966a:115; 1968b:K-14*, fig. 32e; 1976, fig. 1f.—Crawford, 1961:241; 1965:150.—Hobbs and Hobbs, 1962:41, 45.—Hobbs and Hart, 1966:51.—Hobbs and Walton, 1968:250.—Prins, 1968:458.—Bouchard, 1972:31, 49, 106.—Schuster, 1973:7–9.—Hart and Hart, 1974:44, 61, 101, 102.

Cambarus (Jugicambarus) asperimanus.—Hobbs, 1969a:107, 108, 139*, 142*, 143*, 144, figs. 1d, 13d, 14d, 18o; 1972b: 125, 145*, figs. 89e, i, 109d; 1974b:16*, fig. 57.—Bouchard, 1972:45, 47.

The above represents a complete bibliography of the species; although no specific Georgia records are included, references to the state are noted by asterisks.

DIAGNOSIS.—Body pigmented. Eyes small but well developed. Rostrum with thickened, converging margins lacking spines or tubercles. Areola 3.7 to 5.5 times as long as wide, comprising 33.3 to 37.7 percent of entire length of carapace (39.1 to 42.3 percent of postorbital carapace length), and bearing 2 to 4 punctations across narrowest part. Cervical spine represented by minute tubercle. Suborbital angle obsolete, cephalolateral margin of carapace broadly rounded. Postorbital ridge terminating cephalically without spine or tubercle. Antennal scale 2.2 to 2.5 times as long as wide, ususally broadest near midlength. Chela with single (usually stongly cristiform) row of 5 or 6 tubercles along mesial surface of palm, lateral margin of palm rounded; both fingers with well-defined longitudinal ridges dorsally, and fingers and distal part of palm provided with conspicuous tufts of long (in recently molted individuals) stiff setae. First pleopod of first form male with long, strongly reflexed central projection, its tip entire and directed caudoproximally, reaching midlength of base of mesial process; mesial process inflated basally and tapering to acute tip directed caudoproximally and somewhat laterally at angle of 90 to 110 degrees to main shaft of appendage and reaching caudally to or beyond tip of central projection. Annulus ventralis asymmetrical with inflated dextral or sinistral wall receiving tongue from less inflated opposite wall; sinus originating beneath inflated wall and forming broad arc ending on caudal surface near median line. First pleopod present in female.

COLOR NOTES (Figure 70*a*).—Carapace olive to orange brown with olive-cream mottlings. Rostral margins, postorbital ridges and cephalolateral margins of carapace olive cream; similarly, mandibular adductor regions, paired areas situated immediately caudomesially and abutting cervical groove, branchiocardiac groove, and small flecks on branchiostegites olive cream. Abdominal terga mostly light olive but tergum of first abdominal segment largely brown, and succeeding ones with 2 pairs of oblique dark brown splotches. Pleura with brown markings but margined in cream. Telson and uropods pale olive with dark ribs and transverse suture on lateral ramus of uropods brown. Antennular and antennal peduncles dark olive brown splotched with olive, flagella banded with same colors; antennal scale pale with deep olive lateral margin. Dorsal surface of cheliped dark olive to orange brown from mid-merus distally; larger tubercles and spines white, smaller ones cream; fingers red distally with brown corneous apices. Dorsal surface of remaining pereiopods pale olive proximally and dark olive brown from midlength of merus distally, darkest at extremities of merus and carpus. Ventral surface of pereiopods and sternal area pinkish cream; chelipeds more pink than cream.

TYPES.—Syntypes, USNM 47375 (2♂I).

TYPE-LOCALITY.—Flat Creek at Montreat, Buncombe County, North Carolina.

RANGE.—Mountains of North Carolina, South Carolina, and Georgia, in the headwaters of the French Broad, Little Tennessee, Catawba, Broad, Saluda, and Savannah rivers and in the Watauga Basin in Tennessee. In Georgia known only from the Blue Ridge and upper Piedmont provinces in the Savannah Basin.

GEORGIA SPECIMENS EXAMINED.—I have examined 11 specimens from the following localities. *Rabun County:* (1) stream near base of Rabun Bald, 2♂II, 13 May 1953, B. Martof, collector; (2) Tally Mill Creek 0.5 mi S of North Carolina line on St Rte 28, 1♂II, 1j♀, 16 Jun 1975, D. J. Peters, J. E. Pugh, HHH; (3) trib to Chattooga River 4.6 mi S of North Carolina line on St Rte 28, 2♀, 16 Jun 1975, DJP, JEP, HHH; (4) Gold Mine Creek about 9.5 airmi E of Clayton, 2♂II, 15 May 1954, BM; (5) Big Creek on St Rte 28, 1.6 mi S of North Carolina line, 1 ovig ♀, 26 Apr 1977, JEP, HHH. *Stephens County:* (6) Toccoa Falls, downstream less than 100 yards, 1♂I, 17 Jun 1972, DJP, JEP, HHH; (7) Cool Spring picnic area 7 mi NE of Toccoa, 1♂II, 16 Jul 1958, R. L. Hoffman.

VARIATIONS.—The few specimens from Georgia are remarkably uniform. The only conspicuous difference noted is the comparatively longer areola of the first form male, from Stephens County, that comprises 37.7 percent of the total carapace length (42.3 percent of the postorbital carapace length), whereas in the other localities the corresponding lengths range from 34.3 to 36.0 percent and 39.1 to 41.4 percent.

SIZE.—The largest specimen from Georgia is a second form male having a carapace length of 28.6 (postorbital carapace length 25.4) mm. Corresponding lengths of the only first form male are 27.6 and 24.1 mm; those of the single ovigerous female, 30.5 and 26.7 mm.

LIFE HISTORY NOTES.—The only first form male collected in the state was found in June. A female carrying eggs was taken in Georgia on 26 April 1977. Elsewhere first form males have been collected from May to October and ovigerous females in April, June, and December.

ECOLOGICAL NOTES.—Unfortunately altitudinal data are not available for most of the localities where this crayfish has been found, but some are situated above 1300 meters and most seem to be above 700. Within its range, it often occurs in streams at higher elevations than does *C. (C.) bartonii.* In a number of small cascading mountain brooks, it is the sole crayfish inhabitant. There it tunnels its way among rocks and gravel in the stream bed or less frequently seeks cover under a large rock in a pool. When sharing the stream with *C. (C.) bartonii,* the latter is usually largely restricted to pools, and *C. (J.) asperimanus* occupies tunnels in cascading areas. In streams tumbling over bedrock, it seems to be confined to those segments where rock debris, entrapped tree

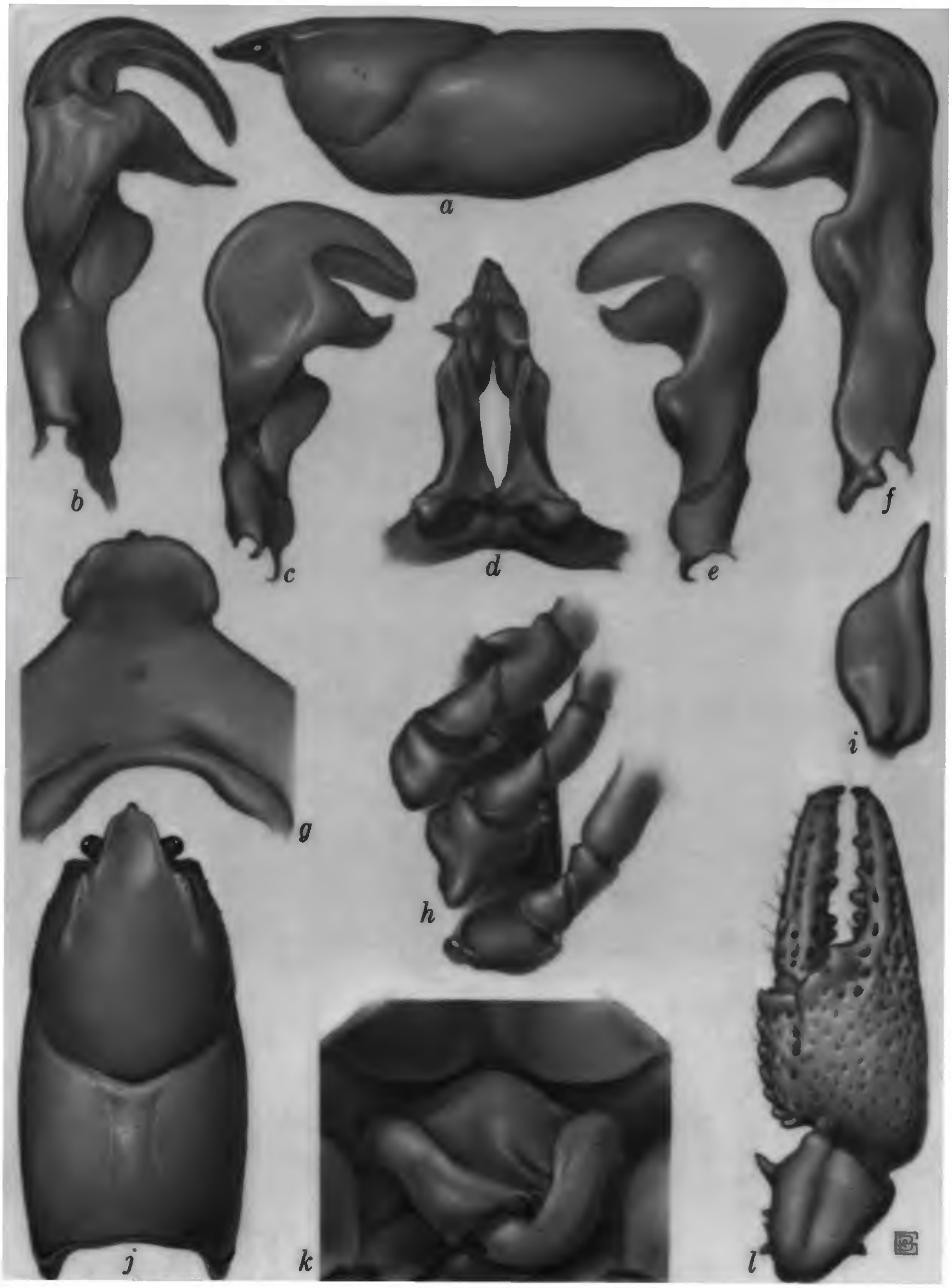


FIGURE 71.—*Cambarus (Jugicambarus) asperimanus* (all from syntypic male, form I, except *c, e*, from topotypic male, form II, and *k*, from topotypic female): *a*, lateral view of carapace; *b, c*, mesial view of first pleopod; *d*, caudal view of first pleopods; *e, f*, lateral view of first pleopod; *g*, epistome; *h*, basal podomeres of third, fourth, and fifth pereiopods; *i*, antennal scale; *j*, dorsal view of carapace; *k*, annulus ventralis; *l*, dorsal view of distal podomeres of cheliped.

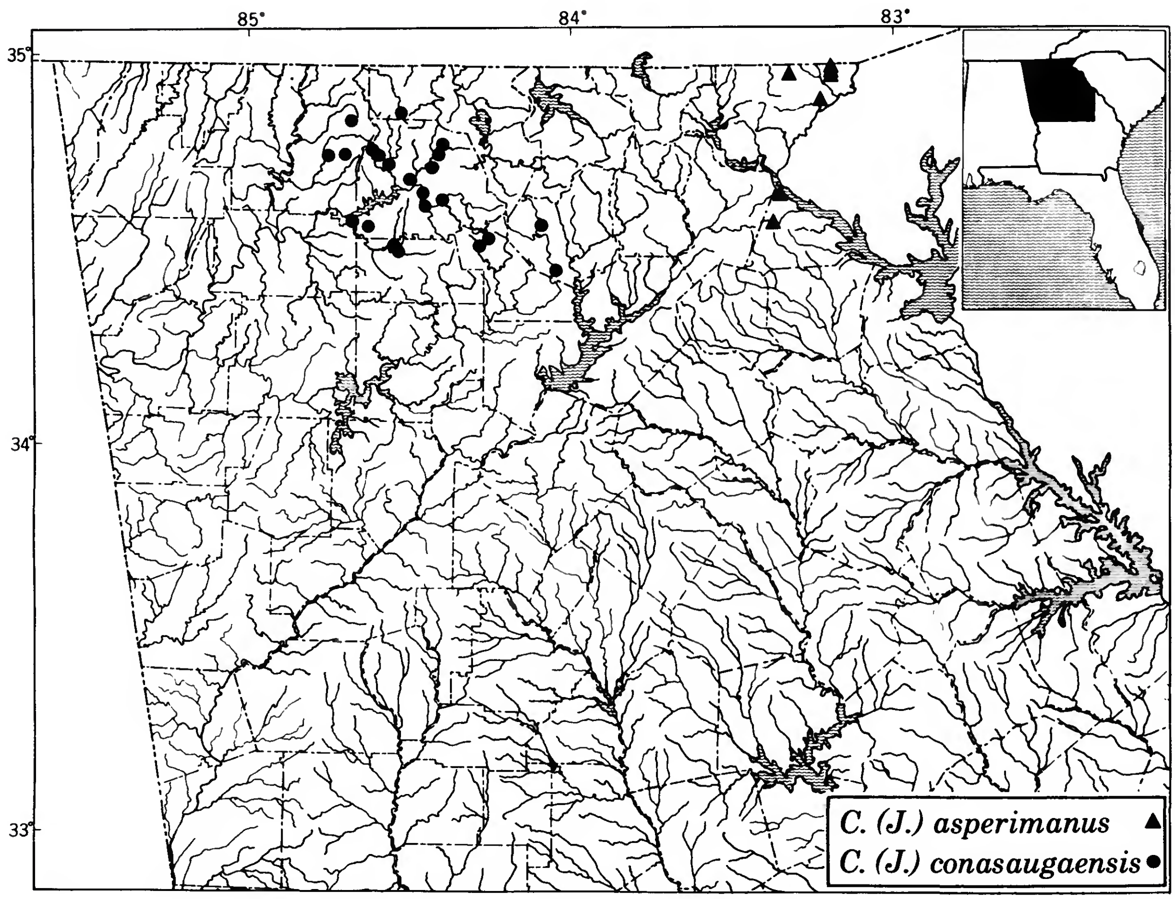


FIGURE 72.—Distribution of *Cambarus (J.) asperimanus* and *C. (J.) conasaugaensis* in Georgia.

litter, and gravel have accumulated, or in complex tunnels among rocks in adjacent seepage areas. In larger rock-littered streams, it occurs in riffles along with its congener, *C. (C.) bartonii.*

GEORGIA CRAYFISH ASSOCIATES.—*Cambarus (C.) bartonii* and *C. (P.) chaugaensis* are the only crayfishes that have been collected with *C. (J.) asperimanus* in Georgia; it was found with the latter in one and the former in three localities.

REMARKS.—Certainly this crayfish is not so rare in the state as indicated here, but I failed to find it in a number of localities in other parts of Rabun and Towns counties where I suspected it to be present. It should occur in the Savannah Basin in Habersham County, and additional localities will probably be found in Stephens County.

Cambarus (Jugicambarus) conasaugaensis Hobbs and Hobbs

FIGURES 24*c*,70*b*, 72, 73–76, 214

Cambarus conasaugaensis Hobbs and Hobbs, 1962:41–45, figs. 1–10.—Hobbs, 1966a:115; 1968b:K-15, fig. 12*b*.—Bouchard, 1972:31, 106.

Cambarus (Jugicambarus) conasaugaensis.—Hobbs, 1969a:107, 108, 142, 143, figs. 9, 19*c*; 1972b:123, 146, figs. 106*c*, 108*b*; 1974b:17, fig. 56.—Hobbs and Cooper, 1972:55.—Bouchard, 1972:46, 49.—Bouchard and Hobbs, 1976:12.

Cambarus conasougaensis Schuster, 1973:9 [erroneous spelling].

The above represents a complete bibliography of the species. The only reference to the occurrence of this crayfish beyond the political boundaries of Georgia is that of Bouchard (1972:49), who reported its presence in Tennessee; all other references are based on data from Georgia.

SUMMARY OF LITERATURE.—Following the description of this crayfish, which was based only on specimens from the type-locality, Hobbs (1968b, 1969a) noted its range in Georgia and included it in his key (1972b). In the same year, Bouchard treated it among the species occurring in Tennessee but gave no locality other than "Conasauga and Hiwassee River systems. . . ." Bouchard and Hobbs (1976) reported it as occurring in the "Blue Ridge province of Tennessee and Georgia." Thus the only precise occurrence for the species that has been recorded is the type-locality. The other references are based upon similarities to, or discussions of relationships with, other crayfishes.

DIAGNOSIS.—Body pigmented, eyes small but well developed. Rostrum with thickened converging margins lacking spines or tubercles. Areola 2.6 to 5.8 (in one specimen 7.1) times as long as wide and comprising 31.6 (in juveniles) to 37.6 percent of entire length of carapace (39.2 to 41.7 percent of postorbital carapace length), and bearing 2 to 4 punctations across narrowest part. Cervical spine represented by minute tubercle. Suborbital angle obsolete. Postorbital ridge terminating cephalically with or without low corneous tubercle. Antennal scale 2.2 to 2.4 times as long as broad, broadest near midlength. Chela with single row of 5 or 7 (usually 5 or 6) tubercles along mesial surface of palm; lateral margin of palm rounded, and both fingers with well-defined longitudinal ridges dorsally. First pleopod of first form male with long, strongly arched central projection, its subapically notched tip directed proximally, reaching distinctly proximal to distal base of mesial process; mesial process bulbiform basally, quickly becoming slender and tapering to apex directed caudoproximally and somewhat laterally at angle between 120 and 130 degrees to main shaft of appendage, reaching caudally almost or quite as far as central projection. Female with annulus ventralis strongly asymmetrical with dextral or sinistral wall highly inflated, receiving tongue from much more poorly developed opposite wall; sinus originating beneath inflated wall, extending across median line, and gently curving toward median line on caudal margin of annulus; first pleopod present.

COLOR NOTES (Figure 70*b*).—Ground color of carapace and abdomen olive green to reddish tan although dorsum of abdomen darker than that of carapace; cervical groove and posterior margin of carapace almost black or dark brown; hepatic area suffused with gray and midgastric region with rectangular or transverse dark splotch; postorbital ridges and rostral margins usually tan to pinkish orange; abdomen sometimes with broad, median longitudinal dark brown stripe composed of rectangular patches covering cephalic four-fifths of each tergum, caudal fifth lighter tan; caudal margins of terga always reddish brown; antennular and antennal peduncles pinkish tan mottled with brown, flagella reddish brown; antennal scale with dark gray or brown lateral margins; dorsal surface of podomeres distal to midlength of merus of cheliped mostly olive green; distal margin of merus, carpus, and propodus (at base of dactyl) suffused with black; basal podomeres, major tubercles, and ventral surface of cheliped cream to pinkish orange. Remaining pereiopods also pinkish orange basally with podomeres distal to ischium pale green dorsally, fading to pinkish orange ventrally. Uropods orange tan, distinctly paler than telson.

TYPES.—Holotype, allotype, and morphotype, USNM 107156, 107157, 107158 (♂I, ♀, ♂II); paratypes, USNM.

TYPE-LOCALITY.—Small cascading, but sluggish, tributary of Holly Creek (to Conasauga River), 2 miles east of Chatsworth, Murray County, Georgia, on U.S. Highway 76.

RANGE.—Blue Ridge, Ridge and Valley, and upper Piedmont provinces in headwater tributaries of the Conasauga, Coosawattee, and Etowah rivers (Coosa Basin) in Dawson, Fannin, Gilmer, Murray, Lumpkin, and Pickens counties,

FIGURE 73.—*Cambarus (Jugicambarus) conasaugaensis* from tributary of Ellijay River 5.4 mi NE of Ellijay on US Hwy 76, Gilmer Co (all from male, form I, except *c, e,* from male, form II, and *k,* from female): *a,* lateral view of carapace; *b, c,* mesial view of first pleopod; *d,* caudal view of first pleopods; *e, f,* lateral view of first pleopod; *g,* antennal scale; *h,* proximal podomeres of third, fourth, and fifth pereiopods; *i,* epistome; *j,* dorsal view of carapace; *k,* annulus ventralis; *l,* dorsal view of distal podomeres of cheliped.

Georgia, and in the Hiwassee Basin in Polk County, Tennessee.

SPECIMENS EXAMINED.—I have examined a total of 131 specimens from the following Georgia localities. *Dawson County:* (1) Amicalola Creek 2 mi E of St Rte 183 on St Rte 52, 1♂II, 1j♂, 4 May 1967, T. Unestam, HHH, collectors; (2) trib of Amicalola Creek 19 mi SE of Ellijay on St Rte 52, 2j♀, 4 May 1967, TU, HHH. *Fannin County:* (3) Watson Creek W of Higdon on St Rte 2, 1 ovig ♀, 4 Jun 1959, K. W. Simonds. *Gilmer County:* (4) Hell's Creek, trib to Carters Reservoir, on unnumbered road between St Rtes 5 and 156, 1♂II, 5♀, 1j♂, 4j♀, 28 Apr 1967, TU, HHH; (5) small stream 0.6 mi NW of Ellijay on US Hwy 76, 3♂II, 1♀, 1j♂, 2j♀, 1 ovig ♀, 16 Apr 1962, J. F. Fitzpatrick, Jr., HHH; (6) trib to Mountain Town Creek 8.3 mi NW of Ellijay on US Hwy 76, 1♂II, 1j♂, 1 ovig ♀, 16 Apr 1962, JFF, HHH; (7) Conasauga Creek 9.7 mi NW of Ellijay on US Hwy 76, 3♂II, 2♀, 1j♂, 1j♀, 16 Apr 1962, JFF, HHH; (8) seepage area and trib to Conasauga Creek 3.2 mi E of Murray Co line on US Hwy 76, 3♂I, 2♂II, 1♀, 1j♀, 21 Sep 1972, HHH; (9) stream SE of Ellijay on St Rte 52, 1♀, 15 Aug 1970, F. J. Schwartz; (10) Cartecay River 3.0 mi SE of Ellijay on St Rte 52, 1♂II, 1j♀, 22 Apr 1968, C. R. Gilbert; (11) stream 7.3 mi SW of Fannin Co line on US Hwy 76, 1♂I, 1♂II, 5♀, 1j♂, 16 Apr 1962, JFF, HHH; (12) small trib of Ellijay River 5.4 mi NE of river at Ellijay on US Hwy 76, 2♂I, 2♂II, 7♀, 4j♂, 1j♀, 10 Oct 1969, K. R. Martin, HHH; 2♂I, 2♂II, 4♀, 1j♂, 21 Sep 1972, HHH; (13) Rock Creek 8 mi NE of Ellijay on US Hwy 76, 1j♂, 1j♀, 28 Apr 1967, TU, HHH; (14) Cartecay River 6 mi SSE of Ellijay near Flint Hill Church, 1♂I, 23 Oct 1976, T. A. English, Jr., HHH. *Lumpkin County:* (15) stream 3 mi N of St Rte 52 just off Jones Creek Rd, 1♂I, 6♂II, 10♀, 4j♂, 4j♀, 12 Apr 1968, G. B. Hobbs, HHH; (16) Jones Creek NE of Nimblewill Church, 1j♀, 25 Mar 1978, B. A. Caldwell; (17) Etowah River at US Hwy 19, 1 mi W of Auraria, 1♂II, 1♀, 18 Jun 1975, D. J. Peters, J. E. Pugh, HHH; (18) Etowah River at Jay Bridge Rd, at first bridge upstream from St Rte 52, 1♂II, 25 Mar 1978, BAC. *Murray County:* (19) type-locality, 1♂I, 2♂II, 1♀, 12 Apr 1958, T. L. Johnson, HHH; (20) stream 5.8 mi NW of Gilmer Co line on US Hwy 76, 1♂I, 1♂II, 1♀, 2j♂, 3j♀, 16 Apr 1962, JFF, HHH; (21) trib to Talking Rock Creek on mountain along drive to Carters Dam from St Rte 156, 1♂II, 3 May 1967, TU, HHH; (22) 3.1 mi NW of Lake Conasauga on Elton Fork Rd off Holly Creek Rd, 1♀, date?, A. Grobman, R. Highton. *Pickens County:* (23) Ball Creek 2.4 mi NW of Blaine on St Rte 156, 1♂I, 1♂II, 22 Sep 1972, HHH; (24) Talking Rock Creek 1.7 mi SE of Gilmer Co line on St Rte 156, 1♀, 28 Apr 1967, TU, HHH. *Locality Uncertain:* 1♂I, 1♀.

A single collection was obtained from 0.6 mi E of T.V.A. Power Plant No. 3 on US Hwy 64, Polk County, Tennessee (1♂I, 1♂II, 1♀, 8 Jun 1959, KWS).

VARIATIONS (Figures 74, 75, 76*a–g*).—Perhaps most conspicuous among the variations noted in this species are the relative width and length of the areola that, to some degree, seem to be correlated with the size of the animal, that of smaller ones tending to be broader and shorter. Both the narrowest and longest areolae occur in specimens from the Coosawattee Basin northwest of Ellijay, Gilmer County. The ventral surface of the proximal podomere of the antennular peduncle may or may not have a small spine or tubercle; generally, among specimens from a single locality the spine is present or absent in all of them, but occasionally a lot is encountered in which most individuals possess the spine but one or two lack it. In the first pleopod of the first form male (Figure 76*a–g*), the tip of the central projection always reaches the level of at least the distal side of the base of the mesial process and in some

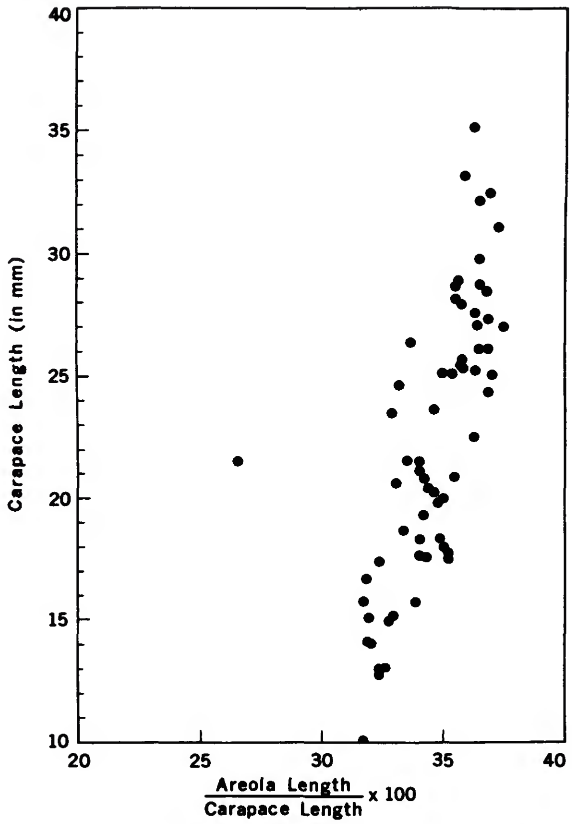


FIGURE 74.—*Cambarus (J.) conasaugaensis:* relationship between carapace length and ratio of areola length to carapace length.

specimens it reaches a level almost to the proximal side of it. Other differences may be noted in the illustrations cited. (See "Measurements.")

SIZE.—The largest specimen available is a female having a carapace length of 35.1 (postorbital carapace length 31.1) mm. Corresponding lengths of the largest and smallest first form males are 29.9 (26.3) and 19.8 (16.9) mm; those of the smallest ovigerous female, 28.4 (25.0) mm.

LIFE HISTORY NOTES.—Collections have been made from April to October (very few specimens are available from June through August), and first form males were found in April, June, September, and October. Ovigerous females were taken in April and June. The number of eggs carried by the three females from Georgia are as follows:

Carapace and postorbital carapace lengths (mm)	*Number of eggs*	*Diameter of eggs (mm)*
28.4 (25.0)	35	2.2–2.3
31.1 (27.5)	53	2.2–2.3
32.4 (28.6)	27	2.1–2.2

Well-developed cement glands were noted on a female collected in Gilmer County on 21 September 1972.

Seasonal Data (Georgia and Tennessee)

Sex/stage	*J*	*F*	*M*	*A*	*M*	*J*	*J*	*A*	*S*	*O*	*N*	*D*	*?*
♂I				4		1			6	3			1
♂II			1	19	2	2			5	2			
♀				26		2		1	5	7			2
♂j				12	1				1	4			
♀j				16	2				1	1			
♀ ovig			1	2		1							

ECOLOGICAL NOTES.—Three features stand out among others in all of the localities in which this crayfish has been collected: elevations above 400 meters, clear, cool water, and many rocks under which the animals might take cover. It has been found beneath rocks and in rather complex burrows in seepage areas, in small cascading mountain brooks, and in swiftly to moderately flowing streams ranging in width from less than one meter to approximately eight meters, at depths from a few to some 60 centimeters. In the larger streams it occurs with other crayfishes, but within its range it is the only species that has been collected from seepage areas where it constructs complex passageways among rock litter. Each burrow was provided with two or three openings to the surface, marked by poorly constructed, low chimneys. In some of the smaller streams, its runways reminded one of those constructued by *C. (J.) asperimanus* in cascading brooks. As pointed out in the paragraph devoted to the type-locality, there the stream, although cascading, was quite sluggish when the type series was collected. This crayfish seems to vicariate for *C. (J.) asperimanus* and *C. (C.) bartonii* that occur in mountain streams in the Savannah and Chattahoochee river basins.

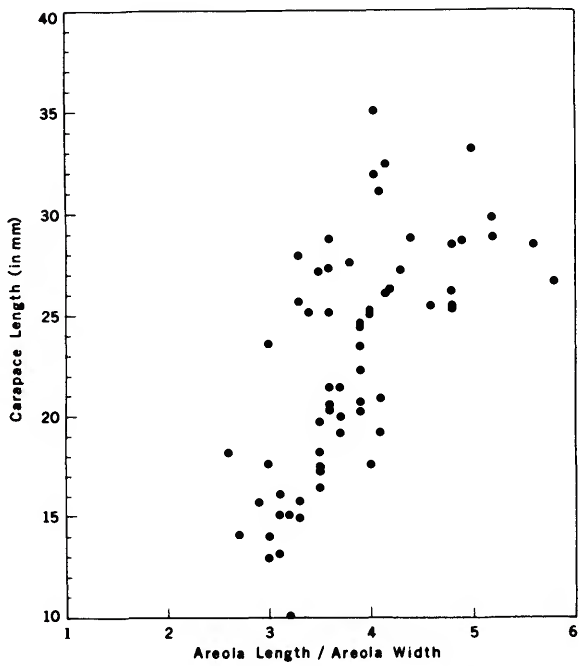


FIGURE 75.—*Cambarus (J.) conasaugaensis*: relationship between carapace length and ratio of areola length to areola width.

GEORGIA CRAYFISH ASSOCIATES.—*Cambarus (J.) conasaugaensis* has been collected with the following crayfishes (the number of times they have been found together is noted in parentheses): *Cambarus (C.) bartonii* (2), *C. (D.) latimanus* (13), *C. (D.) striatus* (3), *C. (H.) coosawattae* (11), *C. (H.) fasciatus* (5), *C. (H.) speciosus* (3), *C. (L.) acanthura* (1), and *Procambarus (Pe.) spiculifer* (2).

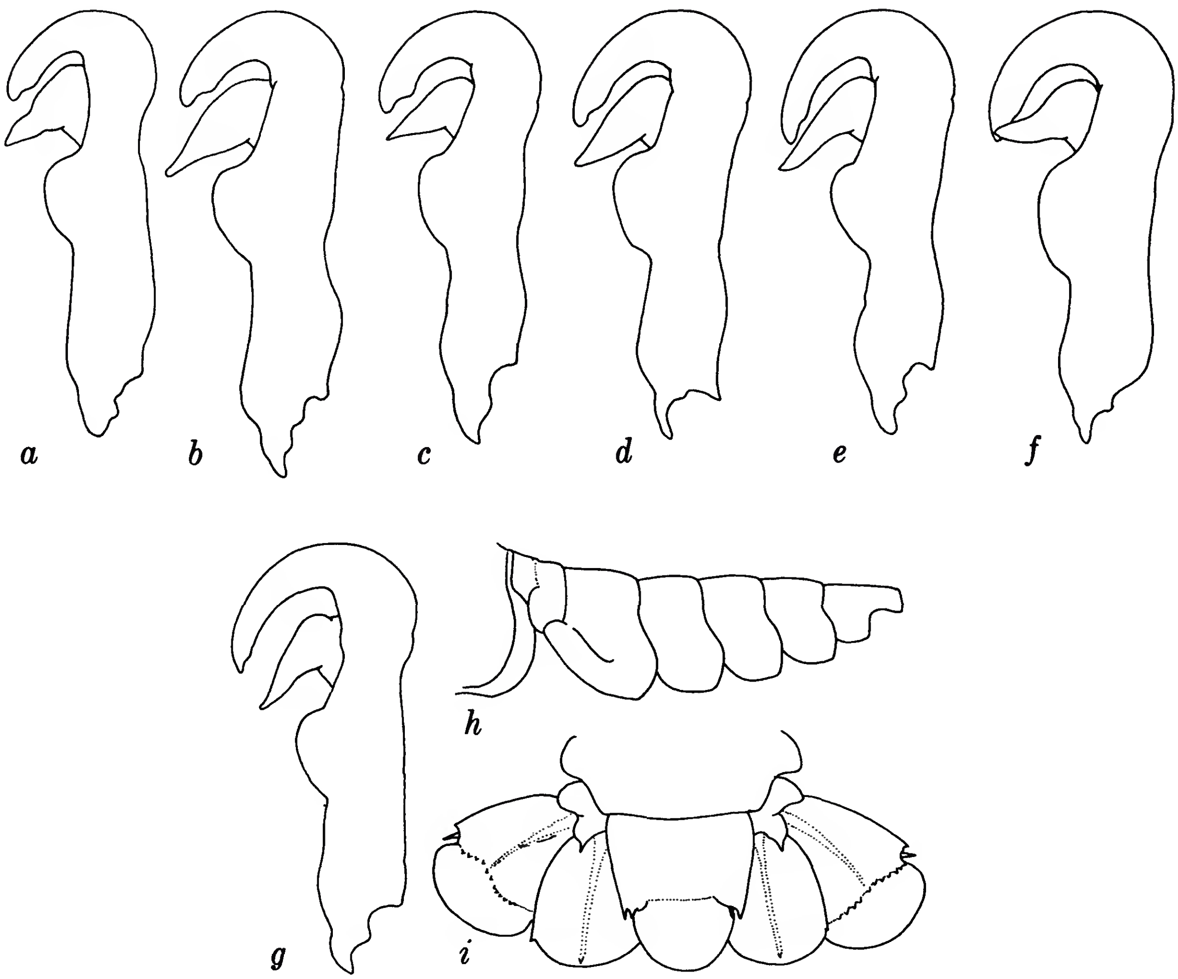


FIGURE 76.—*Cambarus (J.) conasaugaensis* (*a–g*, lateral view of left first pleopod of first form male). Conasauga Basin: *a*, Murray Co. Coosawattee Basin: *b*, Murray Co; *c*, Pickens Co; *d–f*, Gilmer Co. Etowah Basin: *g*, Lumpkin Co; *h*, lateral view of abdomen of holotype; *i*, dorsal view of telson and uropods of holotype.

Cambarus (Jugicambarus) cryptodytes Hobbs

FIGURES 24*e*, 77, 87, 215

Cambarus (Cambarus) cryptodytes Hobbs, 1941b:110, 112–114, figs. 2, 3, 7, 11, 13, 15, 18, 21, 24, 28, 29.

Cambarus cryptodytes.—Hobbs, 1942a:354; 1942b:9, 12, 21, 32, 156–158, 162–163, figs. 196–200; 1952c:689, 693; 1959: 895; 1971a:122*, fig. 18.—Pennak, 1953:458.—Pylka and Warren, 1958:334.—Hobbs and Hart, 1959:149.—Hobbs and Barr, 1960:13–16, 31, figs. 48–57.—Nicholas, 1960: 132.—Warren, 1961:2*, 6, 7*, 10.—Hobbs and Bedinger, 1964:9*.—Hobbs and Walton, 1968:251*.—Sutton and Relyea, 1971:58.—Holsinger and Peck, 1971:30*.—Hobbs and Means, 1972:393.—Caine, 1974b:ii, 3, 7, 12–15, 18, 20, 23, 25, 26, 33–36, 49–41, 43, 44, 47, 50, 55, 57, 62–63, 66, 69, figs. 2c, 4g, 5b; 1975:4280-B.—Hart and Hart, 1974:139*.—Means, 1977:45*, 51, fig. 5*.—Wharton, 1978:176*.

Cambarus (Jugicambarus) cryptodytes.—Hobbs, 1969a:107, 142*–144, 161*, figs. 9*, 19d; 1972b:122*, 146*, 154*, figs. 10e, 107b; 1974b:18*, fig. 64; 1975b:14*.—Hobbs and Barr, 1972:3*.—Hobbs and Cooper, 1972:49*, 55.—Holt, 1973a:246, 248*.—Hobbs III, 1975:276*.—Hobbs, Hobbs, and Daniel, 1977:11*, 21*, 27, 82, 83*, 151*, fig. 40.

cambarus cryptodytes.—Padgett, 1970:19*.
Crayfish.—Peck, 1974:31* [in part].

The above is believed to be a complete bibliography for the species. References to its occurrence in Georgia are indicated by asterisks.

SUMMARY OF LITERATURE PERTAINING TO GEORGIA.—The first record of the occurrence of this crayfish in Georgia was that of Warren (1961), who cited it from Climax Cave, Decatur County, the only known locality in the state. Prior to Caine's (1974b) study, little was known about this crayfish other than its range (see below), and except for opinions of its affinities, descriptions, and keys to aid in its identification, little other than new locality records are included among the above citations. Caine's study provides valuable comparative data on adaptations of this and six other crayfishes occurring in northern Florida to the rather diverse environments available to them. Among the "adaptive traits" considered are tolerance to temperature, stream velocity, and oxygen tensions, as well as preference of substrate, and differences in metabolism and behavior. A summary of all the known localities is included in Hobbs, Hobbs, and Daniel (1977:83). Means (1977) has included this crayfish among the assemblage of troglobites comprising the "Chattahoochee Fauna," which occurs in the "Marianna Lowlands-Dougherty Plain physiographic region" of the Florida panhandle and southwestern Georgia.

DIAGNOSIS.—Body without pigment, eyes small and lacking pigment and faceted cornea. Rostrum long and acuminate, margins not thickened and lacking spines or tubercles. Areola 6.0 to 9.8 times as long as wide and comprising 37.3 to 39.3 percent of total length of carapace (46.9 to 48.8 percent of postorbital carapace length), as little as 35.5 and 43.0, respectively, in juveniles under 20 mm carapace length, and bearing 3 or 4 punctations across narrowest part. Cervical spine usually not much larger than flanking tubercles (both branchiostegites and hepatic area with prominent tubercles, often spiniform ones on latter). Suborbital angle weak and obtuse or obsolete. Postorbital ridge terminating in spine or tubercle. Antennal scale slightly less than twice as long as broad, broadest short distance distal to midlength. Chela with 1 or 2 rows of tubercles along mesial margin of palm (8 to 11 in mesialmost row); entire palm tuberculate except for part of dorsolateral surface, lateral margin of palm and proximal half of fixed finger and mesial margin of dactyl subserrate. First pleopod of first form male with very short, broad central projection bearing conspicuous subapical notch and directed at 90-degree angle to main shaft of appendage; mesial process not conspicuously inflated basally, tapering from base and extending much farther caudally than central projection. Female with annulus ventralis only slightly asymmetrical with usually deep, slightly oblique cephalomedian groove, swollen caudal wall, and rather small tongue, latter directed dextrally or sinistrally; sinus, either vaguely S- or C-shaped, terminating on caudal wall at or near median line; first pleopods vestigial, almost tuberculiform.

COLOR NOTES.—This crayfish is albinistic, lacking any pigment, thus translucent to white.

TYPES.—Holotype, allotype, and "morphotype," USNM 79339, 79340, 79343 (♂I, ♀, ♂II); paratypes, MCZ, USNM.

TYPE-LOCALITY.—Well on farm of R. W. Williams, 2 miles south of Graceville, Jackson County, Florida.

RANGE.—Known only from several caves in Jackson County, Florida, and Climax Cave, Decatur County, Georgia.

GEORGIA SPECIMENS EXAMINED.—I have examined a total of 22 specimens from the following locality. *Decatur County*: Climax Cave, 3 mi N of Climax, 1♂I, 1♀, Oct 1956, P. C. Drummond, collector; 1♀, 1j♂, 1j♀, 28 Oct 1961, R. D. Warren; 1j♂, 3j♀, 13 Oct 1963, RDW; 2♀, 2j♂, 9j♀, 13 Aug 1965, S. B. Peck.

VARIATIONS.—With such an array of tubercles on the carapace and chelipeds, it is not surprising that there is considerable variation in both numbers and their distribution. In some of the smaller individuals, the tubercles of the hepatic region of the carapace are distinctly spiniform, and, in others, those in the same region are hardly dis-

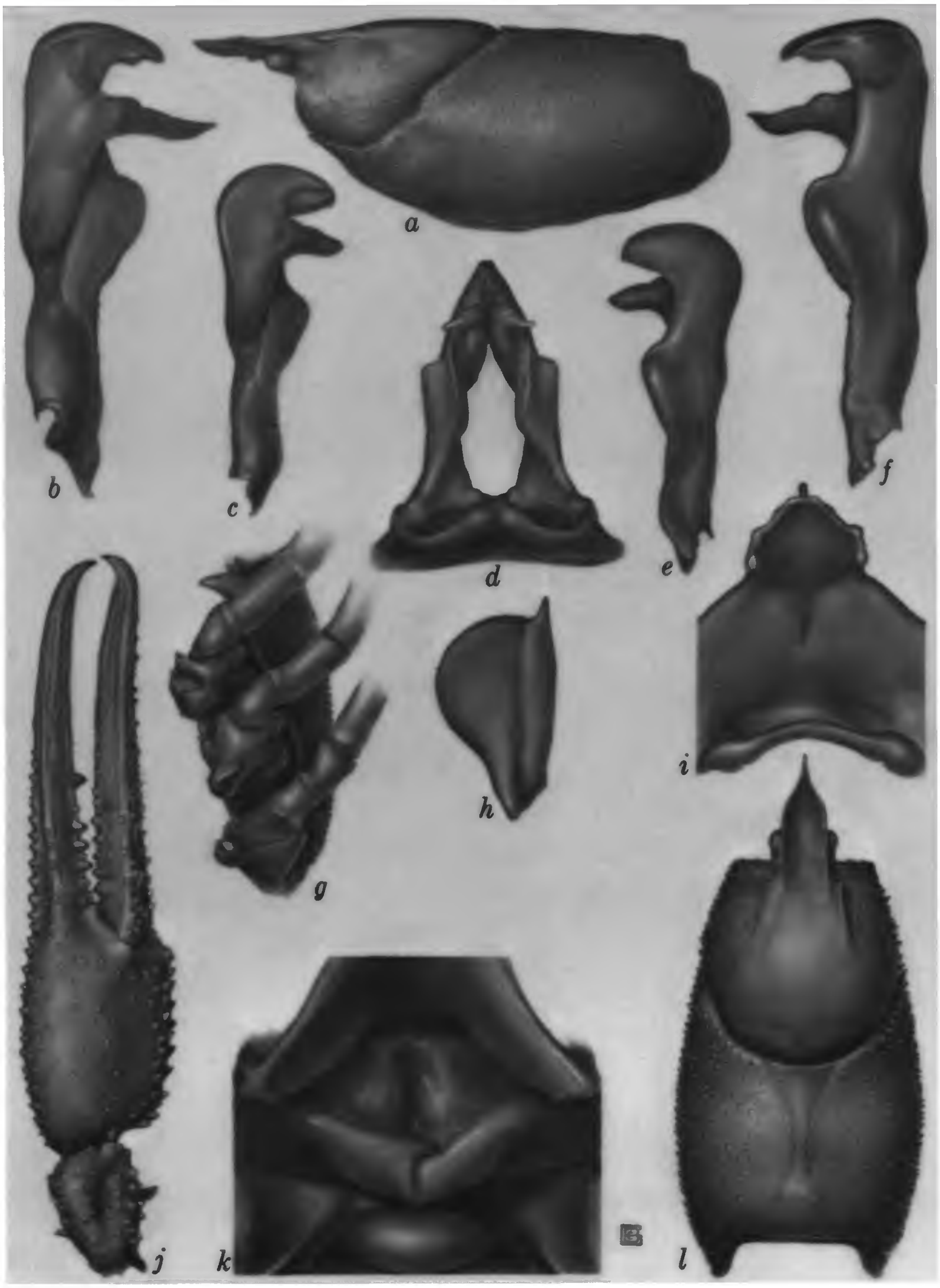


FIGURE 77.—*Cambarus (Jugicambarus) cryptodytes* from Climax Cave, Decatur Co (all from male, form I, except *c*, *e*, from male, form II, and *k*, from female): *a*, lateral view of carapace; *b*, *c*, mesial view of first pleopod; *d*, caudal view of first pleopods; *e*, *f*, lateral view of first pleopod; *g*, proximal podomeres of third, fourth, and fifth pereiopods; *h*, antennal scale; *i*, epistome; *j*, dorsal view of distal podomeres of cheliped; *k*, annulus ventralis; *l*, dorsal view of carapace.

cernible; the cervical spines may be long and conspicuous or barely noticeable. Specimens from Climax Cave do seem to have more strongly developed tubercles (in greater numbers) than do those from Florida. The mesial margin of the palm of some of the chelae have the tubercles arranged in a clearly defined row; in others they are irregularly dispersed, and the number comprising most of the sublinear series cannot be accurately counted.

SIZE.—The largest specimen available is the first form male, which has a carapace length of 26.3 (postorbital carapace length of 20.9) mm. The corresponding lengths of the largest female are 26.1 (21.1) mm.

LIFE HISTORY NOTES.—First form males have been collected in September (in Florida) and October (in Climax Cave). No ovigerous females or those carrying young have been observed.

ECOLOGICAL NOTES.—This crayfish has been found only in subterranean habitats. Mr. R. W. Williams obtained the type specimens by using a bucket dipped into an open well. I have not collected representatives of the species and none of those who have obtained crayfishes have recorded descriptions of the habitat except for one of the localities, Gerard's Cave, in Jackson County, Florida. Pylka and Warren (1958:334) indicated that three pools were present when they visited the cave, two of about 1.3 meters in diameter and a third "extends under the wall of the cave and appears to be rather deep." Issuing from the latter was a small, swiftly flowing stream that disappeared beneath the opposite wall of the cave. The clear water had a pH of 6 and a temperature of 67.5°F (19.7°C), and the bottoms of the pools were covered with a layer of fine silt.

Sutton and Relyea (1971:58) stated that this crayfish "is the only known predator of *Haideotriton* [*wallacei*, a troglobitic salamander]."

GEORGIA CRAYFISH ASSOCIATES.—None.

Cambarus (Jugicambarus) distans Rhoades

FIGURES 24*h*, 70*d*, 78, 79, 216

Cambarus distans Rhoades, 1944:136–139, 141, fig. 9a–f.
Cambarus diistans.—Rhoades, 1944:139 [erroneous spelling].
Cambarus (Jugicambarus) distans.—Hobbs, 1969a:107, 108, 142, figs. 9, 19e; 1972b:123, 146, figs. 106a, 107d; 1974b: 18, fig. 53.—Bouchard, 1976a:573–575; 1976b:585–587, 589, 593.

The above list of references is not a complete bibliography of the species but includes all synonyms, and references to illustrations and to summary articles. No previous records of its occurrence in Georgia have been recorded.

DIAGNOSIS.—Body pigmented, eyes well developed. Rostrum with margins somewhat thickened and lacking marginal spines or tubercles. Areola 4.3 (in juveniles) to 5.7 (rarely) times as long as wide and comprising 33.9 (in juveniles) to 37.3 percent of entire length of carapace (40.0 to 44.1 percent of postorbital carapace length), and bearing 2 to 4 punctations across narrowest part. Cervical spine represented by small tubercle, latter sometimes flanked by 1 or 2 additional ones. Suborbital angle obtuse (sometimes acute in juveniles). Postorbital ridge ending cephalically in rounded, elevated terminus but lacking distinct tubercle. Antennal scale 2.0 to 2.5 times as long as broad, broadest at or slightly distal to midlength. Chela with single row of 7 to 9 (usually 7) tubercles along mesial margin of palm; distolateral margin of palm weakly costate; both fingers with well-defined longitudinal ridges dorsally. First pleopod of first form male with long distally notched central projection bent at approximately 120 degrees to shaft of appendage, its tip not reaching level proximal to distal base of mesial process; mesial process somewhat inflated, tapering to weakly emarginate tip directed caudoproximally and somewhat laterally at angle of about 120 degrees to main shaft of appendage and reaching caudally as far as central projection. Female with annulus ventralis comparatively symmetrical; central depression broad with tilted S-shaped sinus originating on dextral side of depression and ending on caudal wall of annulus near median line; first pleopod present.

COLOR NOTES (Figure 70*d*).—Carapace olive tan with gray brown transverse band immediately cephalic to cervical groove and along posterior flank of reticulate mandibular adductor region; similarly colored line coursing along lat-

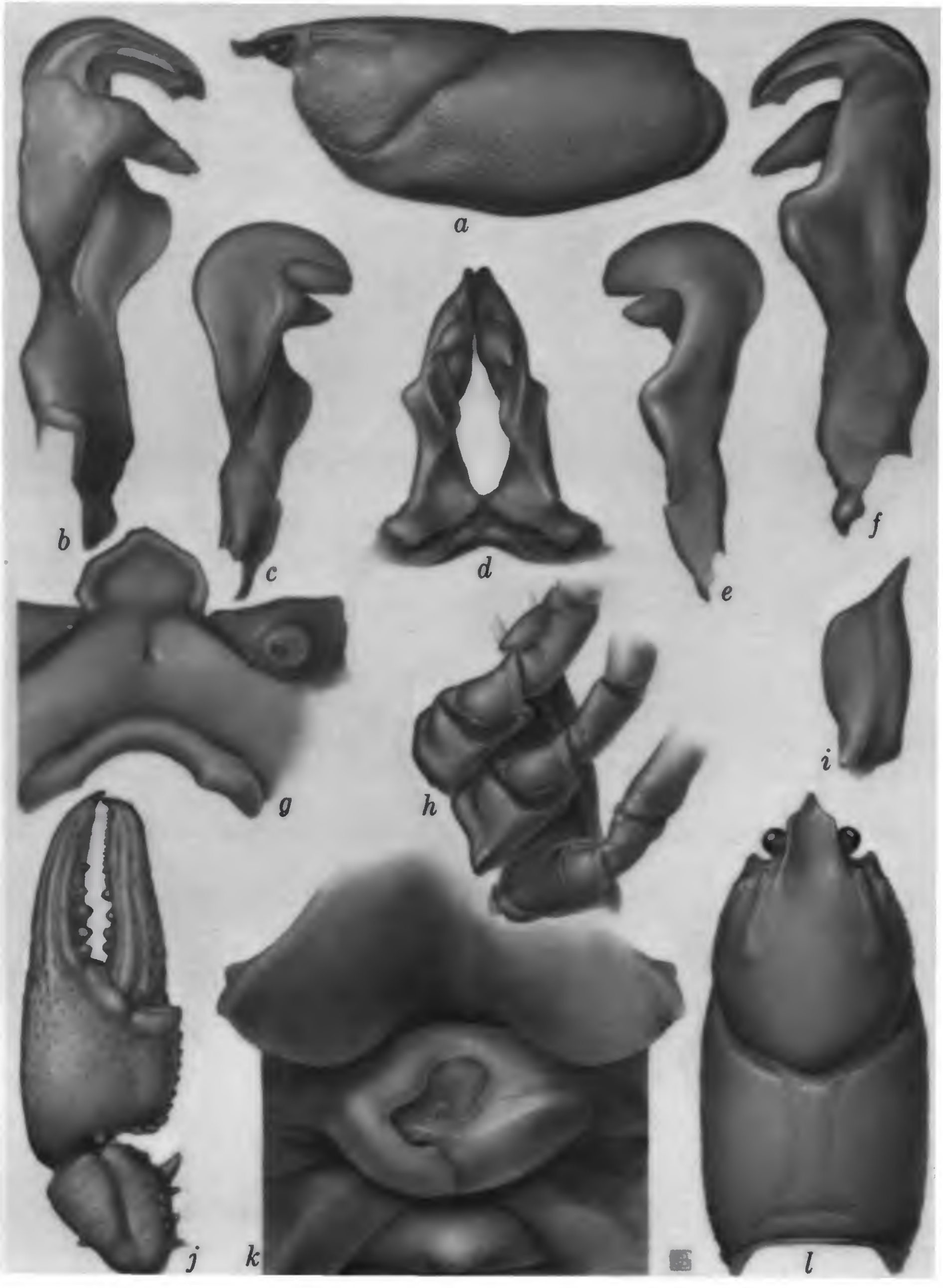


FIGURE 78.—*Cambarus (Jugicambarus) distans* from tributary to Murphy Hollow Creek 2.1 mi S of Interstate Hwy 24 on Murphy Hollow Creek Rd, Dade Co (all from male, form I, except *c*, *e*, from male, form II, and *k*, from female): *a*, lateral view of carapace; *b*, *c*, mesial view of first pleopod; *d*, caudal view of first pleopods; *e*, *f*, lateral view of first pleopod; *g*, epistome; *h*, proximal podomeres of third, fourth, and fifth pereiopods; *i*, antennal scale; *j*, dorsal view of distal podomeres of cheliped; *k*, annulus ventralis; *l*, dorsal view of carapace.

eral margin of postorbital ridge. Dark rostral ridges flanked by pale tan to cream; hepatic and cervical tubercles also tan to cream. Thoracic region with irregular gray brown horns of saddle, bar totally lacking; branchiostegal region below horns mottled. Abdomen with paired dorsolateral linear series of maculations on anterior part of first through fifth abdominal segments, spots decreasing in size caudally, those on first segment joined by narrow transverse band along caudal margin; bases of pleura with broad V-shaped markings on second through fifth segments, markings on first and sixth segments more nearly straight. Telson with cephalic section and marginal area of caudal section mottled. Uropods with lateral halves of both rami distinctly mottled, mesial halves less so. Chela olive tan dorsally with dark band on proximal side of ridge on propodus opposite base of dactyl and along lateral costa; tips of fingers and tubercles on palm orange tan; tubercles on opposable margins of fingers almost cream. Carpus and distal part of merus olive tan with dark markings and pale tubercles. Peduncles of antennule and antenna mottled, flagella banded almost black on pale tan. Antennal scale mostly pale but with lateral margin and distolateral spine dark. Remaining pereiopods greenish dorsally from distal part of ischium to dactyl, joints flanked proximally by orange tan markings. Venter and third maxillipeds pinkish cream.

TYPES.—Holotype, allotype, and "morphotype," USNM 81327, 81329, 81328 (♂I, ♀, ♂II); paratypes, CM, USNM, RR.

TYPE-LOCALITY.—"Cumberland River and small tributary, just above Cumberland Falls, McCreary County, Kentucky."

RANGE.—According to Bouchard (1976b:593), this crayfish occurs in the Kentucky, Cumberland, and Tennessee river drainages in Kentucky and Tennessee southward to the Emory drainage. He also reported it from Town and South Sauty creeks on Sand Mountain in Alabama. The new localities cited below for Georgia are also situated on Sand Mountain in the Appalachian Plateau Province sector of the Tennessee River basin.

GEORGIA SPECIMENS EXAMINED.—I have examined a total of 17 specimens from the following localities. *Dade County*: (1) Murphy Hollow Creek about 1 mi S of Interstate Hwy 24 on Murphy Hollow Creek Rd, 3j♂, 2j♀, 23 Apr 1968, E. T. Hall, Jr., HHH, collectors; (2) spring run trib to Murphy Hollow Creek, 2.1 mi S of Interstate Hwy 24 on Murphy Hollow Creek Rd, 6♂II, 2♀, 1j♂, 3j♀, 24 Oct 1975, T. A. English, Jr., HHH. (See "Life History Notes.")

VARIATIONS.—All of the specimens known from Georgia were collected in the two nearby localities on Murphy Hollow Creek, and few differences worthy of note have been observed among them. The most obvious involves the number of tubercles along the mesial margin of the palm of the chela that, as pointed out in the "Diagnosis," ranges from seven to nine (the maximum illustrated in Figure 78*j*). The antennal scale is also variable in shape, the distomesial margin strongly inclined as in Figure 78*i* or almost transverse.

A comparison of the Georgia specimens with the primary types alone would convince one that the specimens from Sand Ridge are far from being typical of *Cambarus (J.) distans* (see the illustrations cited in Rhoades, 1944, fig. 9*a–f*, and Hobbs, 1974b, fig. 53). The first pleopod of the male differs strikingly in that the central projection of the holotype is much shorter and less strongly recurved, the mesial process of that appendage is more robust basally, less evenly tapering, and directed at about 90 degrees to the shaft of the appendage; also the rostral margins are more tapering, and the areola is more densely punctate; conspicuous differences also exist in the annuli ventrales. Because the variations that occur in the species, particularly in specimens occurring in the Tennessee drainage, have never been analyzed in detail, and because of the apparent affinity of these Georgia crayfish to the Tennessee material, the Georgia specimens are tentatively assigned to *Cambarus (J.) distans*, but the possibility exists that a separate taxon should be proposed to receive them.

SIZE.—The largest specimen available from Georgia is a first form male having a carapace length of 32.4 mm (postorbital carapace length, 27.9 mm). The corresponding lengths of the other first form male are 30.5 (29.3) mm.

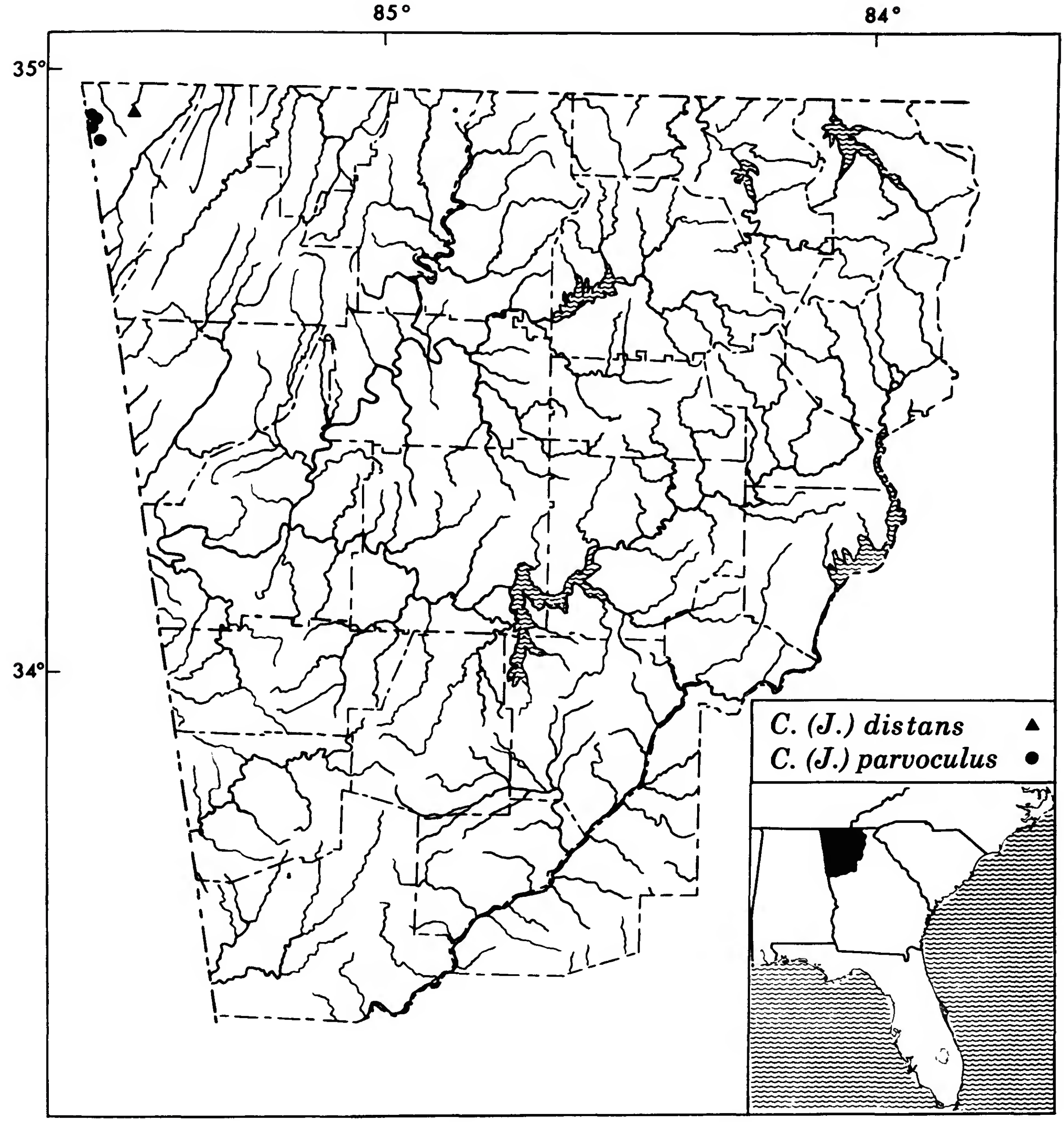


FIGURE 79.—Distribution of *Cambarus (J.) distans* and *C. (J.) parvoculus* in Georgia.

LIFE HISTORY NOTES.—Only a single collection containing adults of this crayfish is available from Georgia. When they were obtained, neither first form males, ovigerous females, nor females carrying young were found. However, two males maintained alive in the laboratory molted to first form, one in October 1975 shortly after having been collected, the other on 22 October 1976.

Ecological Notes.—The first Georgia specimens obtained that are assigned to this species were juveniles that were collected in a swiftly flowing stream with a cobblestone bed. No other macroscopic living organisms were observed in the stream at the time, and when the same locality was visited in October some seven years later, the stream bed was dry, thus indicating the temporary nature of the creek and explaining the depauperate fauna observed there in 1968. In 1975, in at least one dry area of the stream bed, the water was obviously flowing beneath the dry cobblestones, but nowhere along the bed were we able to find crayfishes.

In the small spring tributary to the same stream, the water flows over a short cascade before meandering over a sandy boggy stretch. There, where local human inhabitants obtain water from a trough leading from the cascades, much litter (ranging from boards and discarded clothes to plastic and glass containers) is entrapped along the shallow water course. The crayfish were found among the debris in this clear, cool water.

Georgia Crayfish Associates.—No other crayfish has been obtained in the streams frequented by this species.

Cambarus (Jugicambarus) nodosus Bouchard and Hobbs

Figures 24*d*, 70*c*, 80, 81, 217

Cambarus carolinus.—Holt, 1968b:32.
Cambarus (Jugicambarus) nodosus Bouchard and Hobbs, 1976: 8–14, fig. 3.

The above references are all that exist for the species.

Diagnosis.—Body pigmented, eyes small but well developed. Rostrum with thickened, converging or subparallel margins lacking spines or tubercles. Areola 5 to 12.5 times as long as broad and comprising 34.6 to 41.4 percent of entire length of carapace (38.2 to 44.1 percent of postorbital carapace length) and bearing 2 to 4 punctations across narrowest part. Cervical spine represented by small tubercle. Suborbital angle well developed, obtuse. Postorbital ridge terminating cephalically without spine or tubercle. Antennal scale approximately 2.5 times as long as broad, broadest at about midlength. Chela with 2 rows of tubercles, mesialmost of 6 or 7 forming subserrate row along mesial margin of palm; more lateral of 2 rows usually irregular; additional tubercles scattered over dorsomesial half of palm; lateral surface of propodus weakly costate and both fingers with well-defined longitudinal ridges dorsally. First pleopod of first form male with central projection long, bladelike, tapering, bearing subapical notch, and recurved at about 110 degrees to main shaft of appendage; mesial process also long and directed at about 110 degree angle to shaft of appendage, somewhat inflated basally and tapering to subacute tip, latter extending slightly beyond apex of central projection; caudal knob, if present, rudimentary. Female with annulus ventralis asymmetrical, hinged across midlength, with much inflated dextral or sinistral wall receiving tongue from opposite side; cephalomedian trough curved toward swollen side; sinus originating beneath inflated wall, extending across median line, and gently recurving almost to median line; first pleopod present. (Modified from Bouchard and Hobbs, 1976:8–9.)

Color Notes (Figure 70*c*).—(Based on specimens from Towns and Union counties, Georgia.) Dorsum of carapace rather uniformly olive tan, fading ventrally to pale tan. Rostral margins, postorbital ridges, and cephalolateral margins of carapace orange tan. Abdomen, telson, and uropods olive tan, slightly darker than dorsum of carapace. Antennular and antennal peduncle olive tan with pale orange tan ring on distal extremity of each podomere; flagella olive tan. Cheliped olive tan dorsally from midlength of merus over dorsal surface of palm but with vermilion tubercles; distal portion (occasionally almost all) of both fingers and ventral, mesial, and lateral surfaces from ischium distally also vermilion; ventral surface of cheliped orange basally, becoming vermilion on fingers; articular membranes pinkish cream. Remaining pereiopods orange tan proximally, suffused with olive on distal half of merus and becoming pale green over propodus and

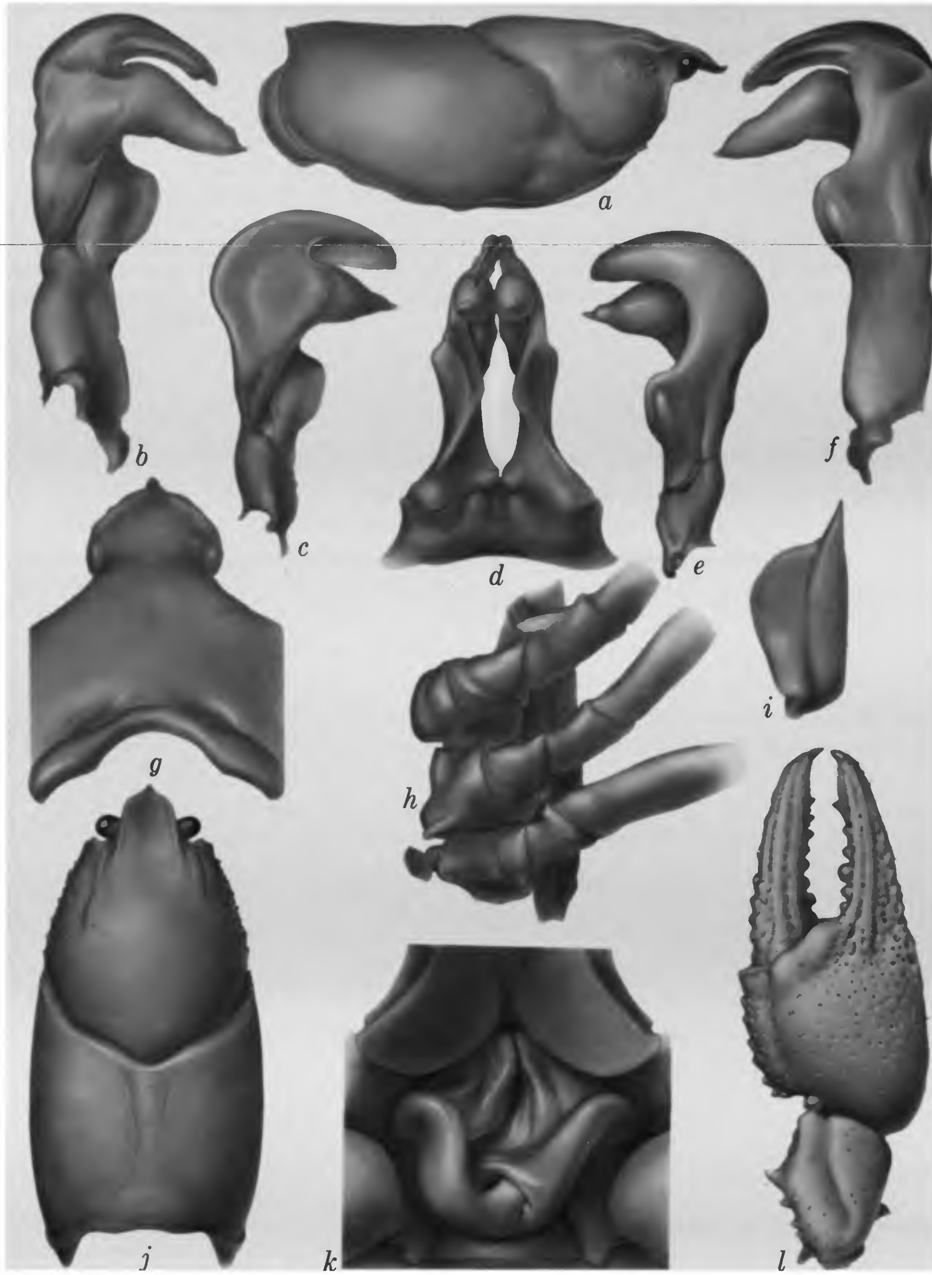


FIGURE 80.—*Cambarus (Jugicambarus) nodosus* (all from holotype except *b*, *f*, from paratopotypic first form male from Union Co, Georgia, *c*, *e*, from morphotype, and *k*, from allotype): *a*, lateral view of carapace; *b*, *c*, mesial view of first pleopod; *d*, caudal view of first pleopods; *e*, *f*, lateral view of first pleopod; *g*, epistome; *h*, proximal podomeres of third, fourth, and fifth pereiopods; *i*, antennal scale; *j*, dorsal view of carapace; *k*, annulus ventralis; *l*, dorsal view of distal podomeres of cheliped. (From Bouchard and Hobbs, 1976.)

dactyl. Ventral surface of third maxilliped, sternum, and ventral surface of proximal podomeres of pereiopods pinkish cream.

TYPES.—Holotype, allotype, and morphotype, USNM 146756, 146757, 146758 (♂I, ♀, ♂II); paratypes, USNM, RWB.

TYPE-LOCALITY.—A small, unnamed tributary of North Potato Creek (Hiwassee River system) between 0.7 and 0.9 mile west of the Tennessee–North Carolina line on U.S. Highway 64, Polk County, Tennessee.

RANGE.—Headwater areas of tributaries to the Hiwassee, Savannah, and Chattahoochee rivers, in Polk County, Tennessee, and in the Blue Ridge and upper Piedmont provinces in Lumpkin, Rabun, Towns, and White counties, Georgia.

GEORGIA SPECIMENS EXAMINED.—I have examined 45 specimens from the following localities. *Lumpkin County*: (1) 3.6 mi S of Union Co line on US Hwy 19, and 0.4 mi W in DeSoto Falls camping area, 1♂II, 3j♂, 2j♀, 17 Jun 1975, D. J. Peters, J. E. Pugh, HHH, collectors. *Rabun County*: (2) 2 mi E of Clayton just S of US Hwy 76, 1♀, 25 Apr 1967, Torgny Unestam, HHH. *Towns County*: (3) bog in headwaters of Tallulah River, N of Tate City, 2♂I, 2♀, 11 Apr 1967, C. H. Wharton, F. K. Parrish; 1♂I, 7 Jun 1967, CHW; 1♀, 23 Jun 1967, CHW; 1♂II, 1♀, 6 Jul 1967, CHW; (4) roadside seepage area on Forest Rd 70 at edge of Tate City, 2♀, 1j♂, 2 ovig ♀, 1♀ with young, 16 Jun 1975, DJP, JEP, HHH; (5) roadside ditch 5 mi S of jct of US Hwy 76 on St Rte 17, 2♀, 1 ovig ♀, 1♀ with young, 17 Jun 1975, DJP, JEP, HHH. *Union County*: (6) seepage area 3.6 mi W of US Hwy 19 on St Rte 180 (top of mountain W of Vogel State Park), 1j♀, 27 Apr 1967, TU, HHH; 1♂II, 3♀, 1j♂, 17 Jun 1975, DJP, JEP, HHH; (7) stream 0.5 mi N of Vogel State Park on US Hwy 19, 1♂I, 5 Nov 1958, K. W. Simonds. *White County*: (8)

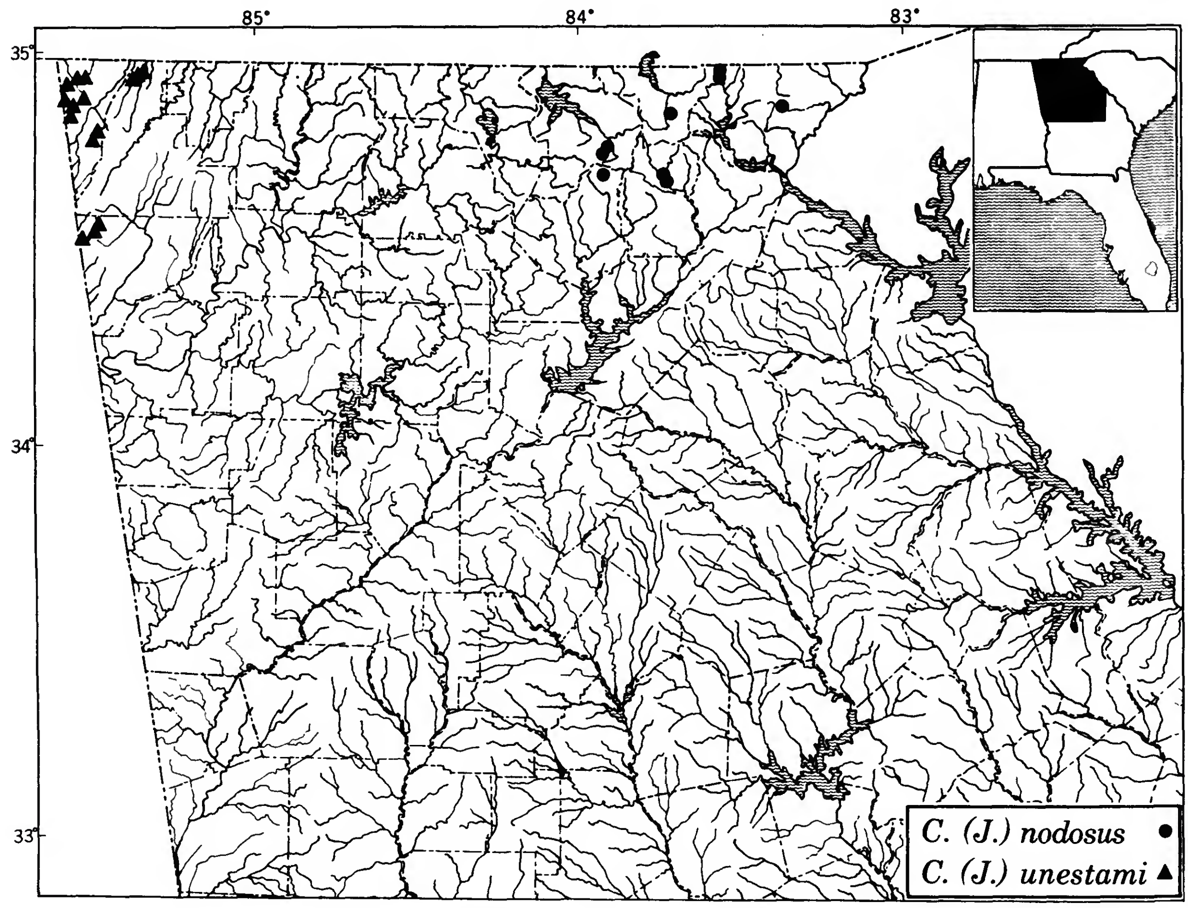


FIGURE 81.—Distribution of *Cambarus (J.) nodosus* and *C. (J.) unestami* in Georgia.

seepage area across road from Spoil Cane Creek, 9.1 mi S of Towns Co line on St Rte 17, 2♂II, 3♀, 2j♂, 2j♀, 1 ovig ♀, 17 Jun 1975, DJP, JEP, HHH; (9) Chattahoochee River at Helen, 3j♀, 26 Jul 1940, George Kleiser. (Except for locality 9, all were reported by Bouchard and Hobbs, 1976:13.)

VARIATIONS.—Despite the striking contrast in color between the Tennessee and Georgia specimens of this crayfish described by Bouchard and Hobbs (1976:8), all of the specimens from Georgia are remarkably uniform. Some individuals maintained in the laboratory acquired a lighter more reddish carapace than when first removed from their burrows, and thus there developed a greater contrast with the darker abdomen. Some of the specimens possess a small median carina on the rostrum; rostral margins are rather suddenly contracted in occasional individuals so that the acumen is triangular; in others, the margins are broadly rounded and the acumen is by no means distinct. There is no evidence, however, that these types are restricted to a drainage basin or to a limited area. Considerable individual variation occurs in the mesial contour of the lamellar part of the antennal scale; some even possess short subserrate areas, but other specimens collected in the same locality lack such embellishments. As pointed out by Bouchard and Hobbs, all except one of the specimens from the Chattahoochee Basin have broader areolae than do virtually all of those from the Hiwassee and Savannah basins (see the accompanying tabulation). Most of the specimens from the Chattahoochee and Toccoa (southwestern tributary to the Hiwassee River) basins also have proportionately shorter areolae than do those from the Hiwassee and Savannah drainage systems. None of the other variations noted are other than minor ones and they are not typical of any of the local populations sampled.

In the tabulation, the ratios of areola length (AL) to carapace length (CL) and to postorbital carapace length (POCL) are expressed as percentages. The relationship of areola length to areola width (AW) is expressed directly as a ratio. Averages are in parentheses following the ranges for the ratios.

River basin	*Number of specimens*	*AL/CL × 100*	*AL/POCL × 100*	*AL/AW*
Savannah	11	37.5–41.4 (39.3)	42.0–46.5 (44.2)	9.1–11.5 (10.6)
Hiwassee	5	38.0–39.1 (38.4)	42.4–43.6 (43.0)	7.6–10.4 (9.3)
Combined average		(39.1)	(43.9)	(10.4)
Chattahoochee	9	34.6–39.0 (37.0)	38.7–44.2 (41.6)	5.2–7.4 (6.0)
Toccoa	6	33.9–37.1 (35.9)	39.1–41.8 (40.4)	6.2–7.8 (7.1)
Combined average		(36.6)	(41.1)	(6.4)

SIZE.—The largest specimen collected in Georgia is a female having a carapace length of 32.1 (postorbital carapace length 28.7) mm. Corresponding lengths of the smallest and largest first form male are 26.9 (24.0) mm and 31.7 (28.3) mm, and those of the smallest female with eggs or young are 26.6 (23.6) mm.

LIFE HISTORY NOTES.—First form males have been collected in Georgia in April, June, and November, and females with eggs and one with young in June.

The number of eggs and/or young carried by the seven females from Georgia are as follows (the low numbers suggest that most of the eggs and/or young were lost before the specimens were collected):

Carapace and postorbital carapace lengths (mm)	*Number of eggs, young*	*Diameter of eggs (mm)*
26.6 (23.6)	22y	-
28.1 (26.0)	2e	2.0
29.4 (25.0)	14e, 11y	2.0–2.1
30.2 (26.8)	12e	1.9–2.0
30.8 (27.5)	11e	1.6–1.8
31.1 (27.8)	28e	1.9–2.0
32.1 (28.5)	1e	2.0

ECOLOGICAL NOTES.—Only one adult and three juveniles of the Georgia specimens of this species have been taken from open water. Simonds collected a first form male from a stream just north of Vogel State Park in November. The remaining 41 specimens were dug from complex burrows or were obtained in buried cans used as small rodent traps set in a sphagnum bog in the headwaters of the Tallulah River. All of those collected by me were dug from burrows in seepage areas or in very wet ditches. The burrows always have at least two openings to the surface and, in addition to the horizontal, blindly ending galleries, one or two passages leading downward. In seepage areas where the water table is at the surface, the burrows are shallow but more highly branching than in localities where the water table drops well below the surface during dry seasons. Where large rocks occur in moist or wet areas, the crayfish construct several passages downward to a large, flooded central excavation beneath the rock. Chimneys are usually poorly developed and are often situated several centimeters from the open or plugged mouths of the tunnels.

Georgia Crayfish Associates.—No other crayfish has been dug from burrows adjacent to those of *C. (J.) nodosus*, but from streams in the immediate vicinity of the burrows, the following species have been found (the number of times is noted in parentheses): *Cambarus (C.) bartonii* (7), *C. (H.) longirostris* (1), *C. (P.) hiwasseensis* (1), and *C. (P.) parrishi* (2).

Cambarus (Jugicambarus) parvoculus Hobbs and Shoup

Figures 24*g*, 70*e*, 79, 82, 218

Cambarus parvoculus Hobbs and Shoup, 1947:142-145, figs. 12-22.—Hobbs, 1953c:20, 27; 1955b:332; 1959:897; 1968a:268; 1968b:K-15.—Holt, 1965:12; 1968b:12, 20.—Hobbs and Hart, 1966:44.—Hobbs and Walton, 1968: 238.—Bouchard, 1972:4, 31, 36, 39, 43, 50, 53, 68, 71, 73, 86, 107; 1976a:573-575; 1976b:585.—Hart and Hart, 1974:37, 38, 59.

Cambarus (Jugicambarus) parvoculus.—Hobbs, 1969a:107, 108, 142, figs. 9, 19i; 1972b:123, 147, figs. 106b, 108a; 1974b: 19, 93, fig. 55.—Hobbs and Cooper, 1972:55.—Bouchard, 1972:26, 46, 53-54; 1976b:594.—Hobbs and Bouchard, 1973:49.—Hobbs and Walton, 1975:9, 12; 1977:602, 606.—Bouchard and Hobbs, 1976:12.

The above is a complete bibliography of the species, but no record of its occurrence in Georgia is included in any of the articles. Bouchard (1976b:594) stated that "this species also may occur in Georgia."

Diagnosis.—Body pigmented, eyes small but well developed. Rostrum with thickened, converging margins lacking spines or tubercles. Areola 5.7 to 9.7 (as little as 4.5 in juveniles) times as long as wide and comprising 37.1 to 40.2 (as little as 35.0 in juveniles) percent of entire length of carapace (42.8 to 46.3 percent of postorbital carapace length) and bearing 2 to 4 punctation across narrowest part. Cervical spine represented by small tubercle. Suborbital angle acute. Postorbital ridge terminating cephalically in small blunt tubercle. Antennal scale approximately 2.4 times as long as broad, widest slightly distal to midlength. Chela with single row of 5 to 8 (usually 6) tubercles along mesial surface of palm; lateral margin of palm rounded (very weakly costate at base of fixed finger) and both fingers with well-defined longitudinal ridges dorsally. First pleopod of first form male with long, strongly arched central projection, its subapically notched tip directed caudoproximally, and reaching slightly proximal to distal margin of mesial process; mesial process swollen basally, gently tapering to subacute tip directed caudoproximally at angle of 140-150 degrees to main shaft of appendage and reaching caudally as far as, occasionally beyond, central projection. Female with annulus ventralis usually strongly asymmetrical with dextrally or sinistrally oriented tongue disappearing beneath inflated wall; sinus in form of tilted S and ending near median line on caudal declivity of annulus; first pleopod present.

Color Notes (Figure 70*e*).—Carapace without conspicuous markings, dark olive to purplish brown dorsally (darkest areas in cephalic gastric region and on dorsolateral part of branchiostegite), fading ventrally to pinkish tan. Abdomen also largely concolorous (dark olive to brown) but with cephalic half of each abdominal tergum darker than remainder of segment; pleura pale grayish tan anteroventrally; color of telson same as that of 5 posterior abdominal terga; uropods with mesial halves and distal section of lateral ramus somewhat paler. Peduncles and flagella of antennule and antenna mostly olive or purplish brown, former with tan markings on dorsodistal part of distal 2 podomeres and flagella with tan

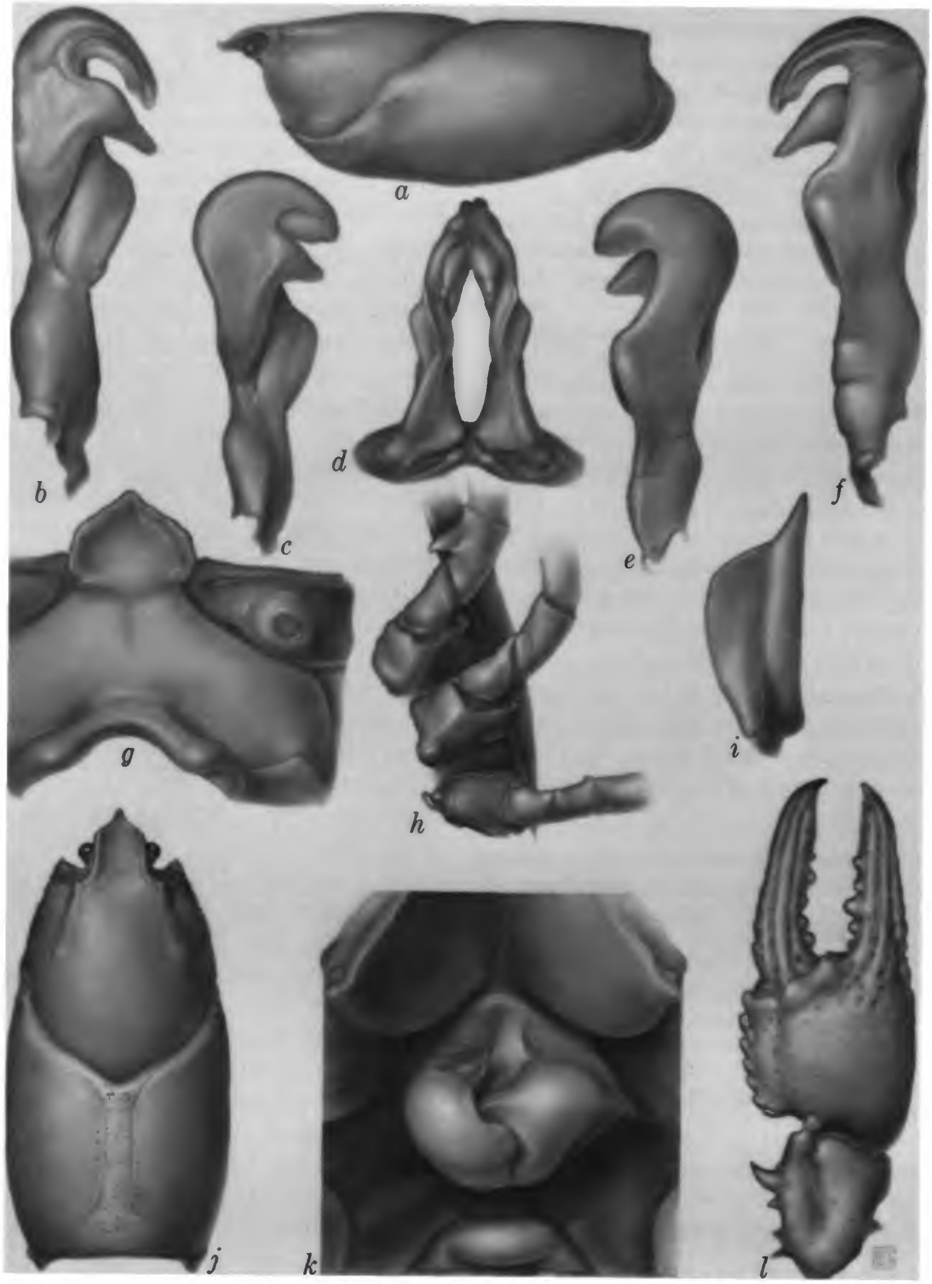


FIGURE 82.—*Cambarus (Jugicambarus) parvoculus* from tributary to Warren Creek 0.3 mi E of Alabama line on unnumbered road, 1.0 mi N of St Rte 301, Dade Co (all from male, form I, except *c*, *e*, from male, form II, and *k*, from female): *a*, lateral view of carapace; *b*, *c*, mesial view of first pleopod; *d*, caudal view of first pleopods; *e*, *f*, lateral view of first pleopod; *g*, epistome; *h*, proximal podomeres of third, fourth, and fifth pereiopods; *i*, antennal scale; *j*, dorsal view of carapace; *k*, annulus ventralis; *l*, dorsal view of distal podomeres of cheliped.

articular rings. Antennal scale with dark lateral margin, lamellar area pale. Chela reddish to olive brown with cream to reddish tan lateral margin and tubercles; fingers olive, fading distally to pale tan area proximal to corneous tip; distal part of merus and carpus also reddish to olive brown with pinkish cream to orange tubercles. Remaining pereiopods similarly colored from merus distally. Sternal area and third maxillipeds bluish cream.

TYPES.—Holotype, allotype, and "morphotype," USNM 82259 (♂I, ♀, ♂II); paratypes, USNM, MCZ, TU.

TYPE-LOCALITY.—Tributary to Big Hurricane Creek in southwestern part of Fentress County, Tennessee.

RANGE.—Largely restricted to the Cumberland Plateau section of the Appalachian Plateau Province, ranging through the Cumberland River basin from Overton, Fentress, and Putnam counties, Tennessee, and Bell County, Kentucky, to headwaters of the Kentucky River in Letcher County, Kentucky; and in the Tennessee Basin in Lee County, Virginia, southward along the plateau to the northwestern part of Dade County, Georgia.

GEORGIA SPECIMENS EXAMINED.—I have examined 69 specimens from the following localities. *Dade County*: (1) trib to Warren Creek 0.3 mi E of Alabama line on unnumbered road, 1 mi N of St Rte 301, 2♂I, 7♂II, 10♀, 10j♂, 17j♀, 23 Oct 1975, T. A. English, Jr., HHH, collectors; (2) trib to Warren Creek 0.8 mi E of Alabama line on unnumbered road, 0.4 mi N of St Rte 301, 6j♂, 5j♀, 23 Oct 1975, TAE, HHH; (3) creek at Alabama line about 1.5 mi S of St Rte 301, 3♀, 3j♂, 23 Oct 1975, TAE, HHH; (4) Higdon Creek about 2.0 mi W of Stephensville on St Rte 143, 2♀, 2j♂, 2j♀, 23 Oct 1975, TAE, HHH.

VARIATIONS.—In most of the adult specimens from Georgia, the ratio of the areola length to carapace length is slightly greater than in specimens from the type-locality, exhibiting a range of 37.8 to 40.2 percent (43.1 to 46.3 percent of postorbital carapace length). The ratio of the length of the areola to its width is quite variable in the Georgia specimens, ranging from 6.4 to 9.7; that of specimens from Warren Creek is 6.4 to 7.6 times as long as broad, whereas in those from localities 3 and 4 (see above), the ratio is 7.2 to 9.7. Except for one specimen with regenerated chelae, all have a single row of tubercles along the mesial margin of the palm; rarely, one or two tubercles are present dorsolateral to the mesial row. The rostra are highly variable, but apparently as much variation exists in the rostra of juveniles and adults in localities outside of the state.

SIZE.—The largest specimen from Georgia is a female, which has a carapace length of 31.9 (postorbital carapace length 28.4) mm. The two first form males have corresponding lengths of 28.9 (25.6) and 30.0 (26.4) mm.

LIFE HISTORY NOTES.—There are no data for Georgia except that two first form males were collected in October. No ovigerous females or ones carrying young have been found. In other parts of the range, first form males have been collected in April, September, and November, and ovigerous females were obtained in April and May.

ECOLOGICAL NOTES.—In the Georgia localities, the streams were clear, swift, and ranged in width from 0.6 to 7 meters, and in the collecting areas they were no deeper than 0.6 meter. The stream beds consisted of bedrock, sand, or gravel with rock litter.

In Kentucky, Tennessee, and Virginia, this crayfish has been found in a wide variety of streams ranging from small rills flowing from seepage areas and springs to swift streams, some larger than those in the Georgia localities. In all of the places in which I have found it, the stream bed was littered with rocks. Bouchard (1976b: 594) summarized the habitat of this crayfish as "pool areas of small to medium sized streams, under rocks and in leaf litter."

GEORGIA CRAYFISH ASSOCIATES.—It has been found in three localities in areas of streams inhabited by *Cambarus (J.) unestami*.

Cambarus (Jugicambarus) unestami Hobbs and Hall

FIGURES 24*f*, 70*f*, 81, 83, 219

Cambarus (Depressicambarus) unestami Hobbs and Hall, 1969: 287–293*, figs. 13–24.—Hobbs, 1972b:113, 147*, figs. 92f, 100a, 101b.—Bouchard, 1976a:574*, 575; 1976b:594–595*.

Cambarus unestami.—Bouchard, 1973a:105; 1976b:585, 586.

Cambarus (Puncticambarus) unestami.—Bouchard, 1973a:105 [by implication, lapsus for *Depressicambarus*].

Cambarus (Jugicambarus) unestami.—Bouchard, 1972:45, 54*, 92, 107; 1973a: 105 [by implication].—Hobbs, 1974b:19–20*, fig. 54.—Hobbs and Walton, 1977:602.

The above is a complete bibliography for the species. Following the original description, however, the only contributions worthy of note are Bouchard's modification of the definition of the subgenus *Jugicambarus* to encompass this crayfish, and a new locality record in De Kalb County, Alabama (Hobbs and Walton, 1977). The following diagnosis of the species is only slightly modified from Hobbs and Hall, 1969:287.

DIAGNOSIS.—Body pigmented, eyes moderately large and well developed. Rostrum with convergent margins devoid of marginal spines or tubercles. Areola 3.4 to 6.0 times as long as broad, comprising 32.6 to 37.8 percent of entire length of carapace (40.9 to 45.2 percent of postorbital carapace length), and bearing 3 to 6 punctations across narrowest part. Lateral surface of carapace lacking cervical spines or prominent tubercles. Suborbital angle prominent and subacute. Postorbital ridge short and rounded, with or without small cephalic tubercle. Antennal scale approximately 2.2 times as long as broad. Chela with at least 2 rows of tubercles on mesial surface of palm, mesialmost consisting of 6 to 9 (rarely more than 7), sometimes additional ones situated dorsolateral to rows; lateral margin of chela costate along at least half its length and both fingers with well-defined longitudinal ridge dorsally. First pleopod of first form male with corneous central projection recurved at approximately 125 degrees to main shaft, not markedly tapering distally, with distinct subapical notch, and extending caudally beyond tip of mesial process; mesial process inflated, directed caudolaterally and somewhat proximally, and terminating in simple tip. Female with annulus ventralis somewhat asymmetrical with either dextral or sinistral wall elevated and with ridge extending transversely from opposite wall forming tongue disappearing beneath elevated wall; first pleopod present.

COLOR NOTES (Figure 70*f*).—

Ground color of carapace and abdomen brownish black dorsally fading ventrally to olive green and flecked with irregular brownish black splotches. Postorbital ridges brownish black. Lateral surface of carapace bearing brownish black "horn" originating in hepatic area and increasing in width caudally along branchiostegite at caudal margin of which almost reaching level of branchiocardiac groove. Terga of abdomen with dorsolateral linearly arranged series of oblique brownish black bars, similar series at bases of pleura. Telson and uropod with brownish black spots. Antennules and antennae dark brown. Chela brown with brownish black splotches on all podomeres distal to ischium [tubercles cream, and fingers with scarlet tips]. Podomeres distal to ischium of remaining pereiopods olive green with brownish black spots. Basal podomeres of all pereiopods and sternum cream (Hobbs and Hall, 1969:287).

Lighter individuals predominantly green or tan, bearing essentially same markings noted above.

TYPES.—Holotype, allotype, and morphotype, USNM 129863, 129864, 129865 (♂I, ♀, ♂II); paratypes, USNM.

TYPE-LOCALITY.—Daniel Creek (tributary of Lookout Creek), 2.5 miles west of Walker County line on State Route 143, Dade County, Georgia.

RANGE.—Tributaries of Chattanooga, Cole City, Lookout, and Long Island creeks (Tennessee River basin) in Walker and Dade counties, Georgia, and Jackson County, Alabama. This crayfish has also been collected from tributaries of the Little River (Chattooga-Coosa Basin) in the northwestern part of Chattooga County. These localities lie within the Appalachian Plateau and along the northwestern edge of the Ridge and Valley provinces.

GEORGIA SPECIMENS EXAMINED.—I have examined 157 specimens from the following localities. *Chattooga County:* (1) Gilreath Creek near Mt. Olive Church, 1♂II, 1j♂, 21 Jun 1977, B. A. Caldwell, G. Q. Tuggle, collectors; (2) Gilreath Creek about 80 m upstream from confluence with Gamble Branch, 1♂II, 20 Jun 1977, BAC, GQT; (3) East Fork of Little River 1.85 mi upstream from Alabama St line, 2j♂, 21 Jun 1977, BAC, GQT; (4) East Fork of Little River downstream from St Rte 48, 1j♂, 22 Jun 1977, BAC, GQT. *Dade County:* (5) type-locality, 1♂I, 6♂II, 2♀, 5j♂, 1j♀, 1 ovig ♀, 2 May 1967, Torgny Unestam, HHH; 1♂I, 9♂II, 9♀, 18j♂, 16j♀, 1 ovig ♀, 23 Apr 1968, E. T. Hall, Jr., HHH; (6) Bear Creek at St Rte 157, 1.8 mi N of St Rte 143, 1♂II, 3j♀, 22 Oct 1975, T. A. English, Jr., HHH; (7) trib to Warren Creek 0.8 mi E of Alabama St line on unnumbered rd, 0.4 mi N of St Rte 301, 1♂II, 4♀, 8j♂, 11j♀, 23 Oct 1975, TAE, HHH;

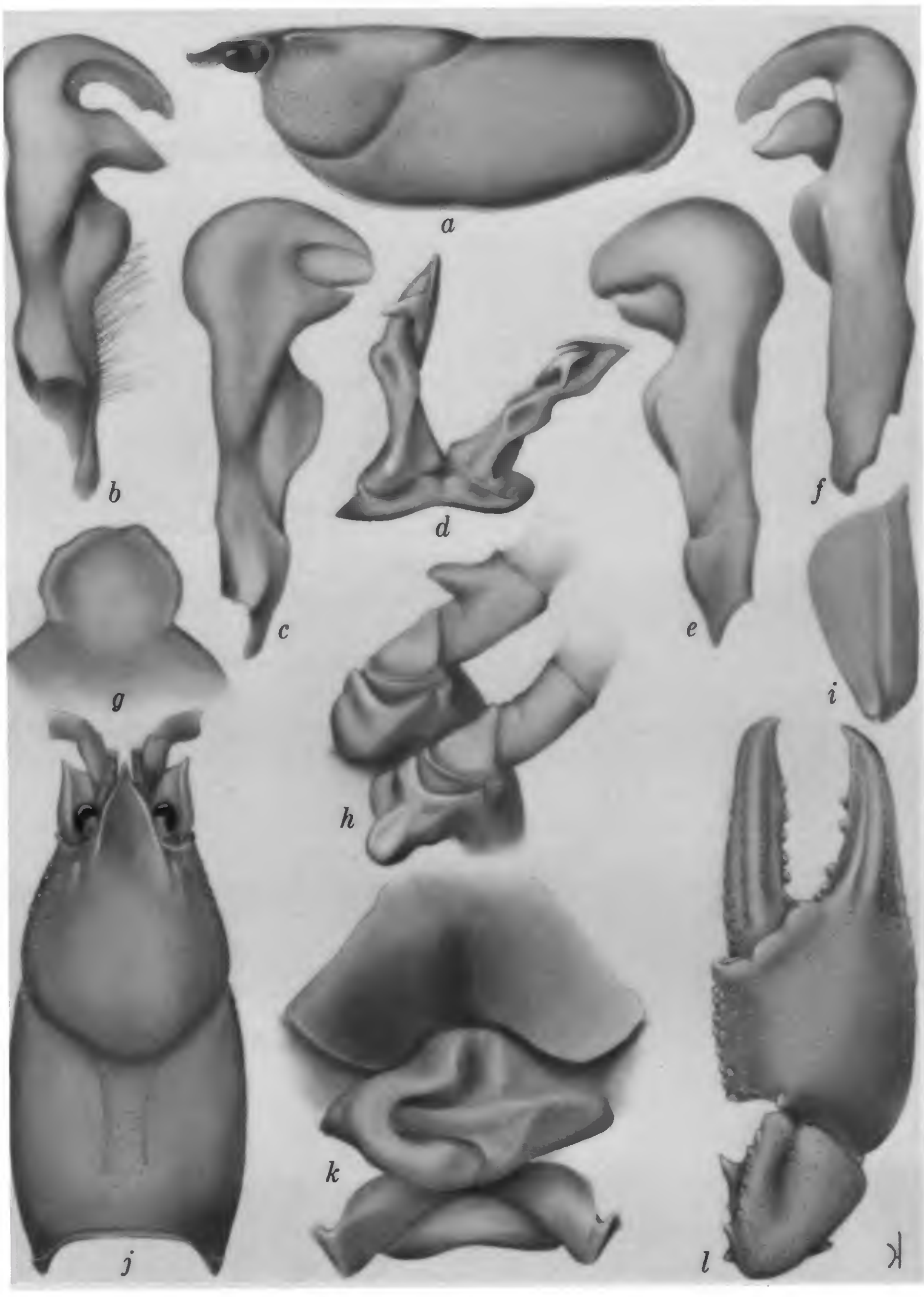


FIGURE 83.—*Cambarus (Jugicambarus) unestami* (all from holotype except *b, f,* from paratopotypic first form male, *c, e,* from morphotype, and *k,* from allotype): *a,* lateral view of carapace; *b, c,* mesial view of first pleopod; *d,* caudal view of first pleopods, left member deformed; *e, f,* lateral view of first pleopod; *g,* epistome; *h,* proximal podomeres of third and fourth pereiopods; *i,* antennal scale; *j,* dorsal view of carapace; *k,* annulus ventralis; *l,* dorsal view of distal podomeres of cheliped. (From Hobbs and Hall, 1969; relabeled.)

(8) creek at Alabama St line about 1.5 mi S of St Rte 301, 1♂I, 2♂II, 2♀, 1j♀, 23 Oct 1975, TAE, HHH; (9) Higdon Creek about 2 mi W of Stephensville on St Rte 143, 2♂I, 1♂II, 3♀, 1j♂, 1j♀, 23 Oct 1975, TAE, HHH; (10) Higdon Creek on St Rte 143, 0.7 mi E of Alabama St line, 4j♂, 1j♀, 23 Apr 1968, ETH, HHH; (11) McBriar Branch immediately S of Cole City area, 1♂I, 9♂II, 10♀, 3j♂, 3j♀, 23 Oct 1975, TAE, HHH; (12) trib to Tatum Gulf 1.3 mi W of Rte S2213, 1j♂, 2j♀, 23 Oct 1975, TAE, HHH; (13) Tatum Gulf on N side of Cole City area, 1♀, 1j♂, 1j♀, 23 Oct 1975, TAE, HHH. *Walker County:* (14) Rock Creek about 1.5 airmi NNW of Eagle Cliff, 1j♂, 4 Nov 1976, ETH, M. W. Walker; (15) Rock Creek about 2 mi N of Eagle Cliff, 1j♀, 3 Nov 1976, ETH, MWW; (16) Rock Creek at old St Rte 193, 3♂I, 5♂II, 6♀, 2j♂, 2j♀, 7 Nov 1971, R. W. Bouchard, J. W. Bouchard. (The latter record was furnished by Raymond W. Bouchard; I have not seen these crayfish.)

Variations.—The adult specimens that I have examined are quite uniform except for slight differences in the shape of the rostrum and number and position of tubercles on the cheliped. Few variations exceed the limits pointed out in the original description of the species, and those considered to be of importance are noted in the above "Diagnosis." The only local variation observed is the proportionately narrower areola (5.2 to 6.0 times as long as broad) in specimens from the tributary to Warren Creek at the Alabama State line. From an adjacent tributary, approximately one mile to the northwest, the areola of the single adult (male) is only 3.9 times as long as broad. Among adult specimens from the other localities, the ratio of the length to the width of the areola is rarely as much as 4.8.

Size.—The largest specimen available is the ovigerous allotypic female, which has a carapace length of 40.4 (postorbital carapace length 34.0) mm; the corresponding lengths of the smallest and largest first form males and of the smaller ovigerous female are 26.9 (21.9) mm, 31.3 (24.9) mm, and 32.5 (27.2) mm, respectively.

Life History Notes.—First form males have been collected in April, May, October, and November, and the two ovigerous females were found in April and May. The allotype with a carapace length of 40.4 (postorbital carapace length 34.0) mm was carrying 194 eggs, each about 2.5 mm in diameter, and the other female, with corresponding lengths of 32.5 (27.2) mm, bore 124 eggs of approximately the same diameter.

Seasonal Data

Sex/stage	*J*	*F*	*M*	*A*	*M*	*J*	*J*	*A*	*S*	*O*	*N*	*D*
♂I				1	1					4	3	
♂II		1		9	6	2				14	5	
♀				9	2					17	6	
♂j		1		22	5	2				14	3	
♀j				17	1					25	3	
♀ ovig				1	1							

Ecological Notes.—Insofar as is known this crayfish is confined to streams on Lookout and Sand mountains at altitudes of approximately 333 to 500 meters. There the crayfish frequent the clear, moderately to swiftly flowing streams coursing over bedrock or rock-littered sandy bottoms, where they find cover under rocks or in entrapped tree litter. All of the specimens available have been taken from such streams, and in at least one of the smaller creeks, *C. (J.) unestami* seemed to be the only crayfish inhabitant.

Georgia Crayfish Associates.—The only crayfishes with which it was collected are *Cambarus (D.) striatus* once, *C. (J.) parvoculus* three times, and *Procambarus (O.) lophotus* once.

Subgenus *Lacunicambarus*

Subgenus *Bartonius* Ortmann, 1905a:97 [in part].

Subgenus *Cambarus* Fowler, 1912:341 [in part; not Erichson, 1846:97].

Subgenus *Lacunicambarus* Hobbs, 1969a:110 [type-species: *Cambarus diogenes* Girard, 1852:88].

Diagnosis.—Eyes large, pigmented. Rostrum usually without marginal spines or tubercles. Postorbital and cervical spines absent. Suborbital angle prominent and often acute to subacute. Branchiostegal spine reduced or absent. Areola ranging from about 28 times as long as broad to obliterated and constituting 36.9 to 45 percent of total length of carapace (43.5 to 50.6 percent of postorbital carapace length), never bearing more than 2 punctations in narrowest part. Chela moderately robust with palm approximately one-half to two-thirds as long as dactyl; mesial surface of palm with 2 or more (usually several) rows of tubercles; dorsal surface tuberculate mesially,

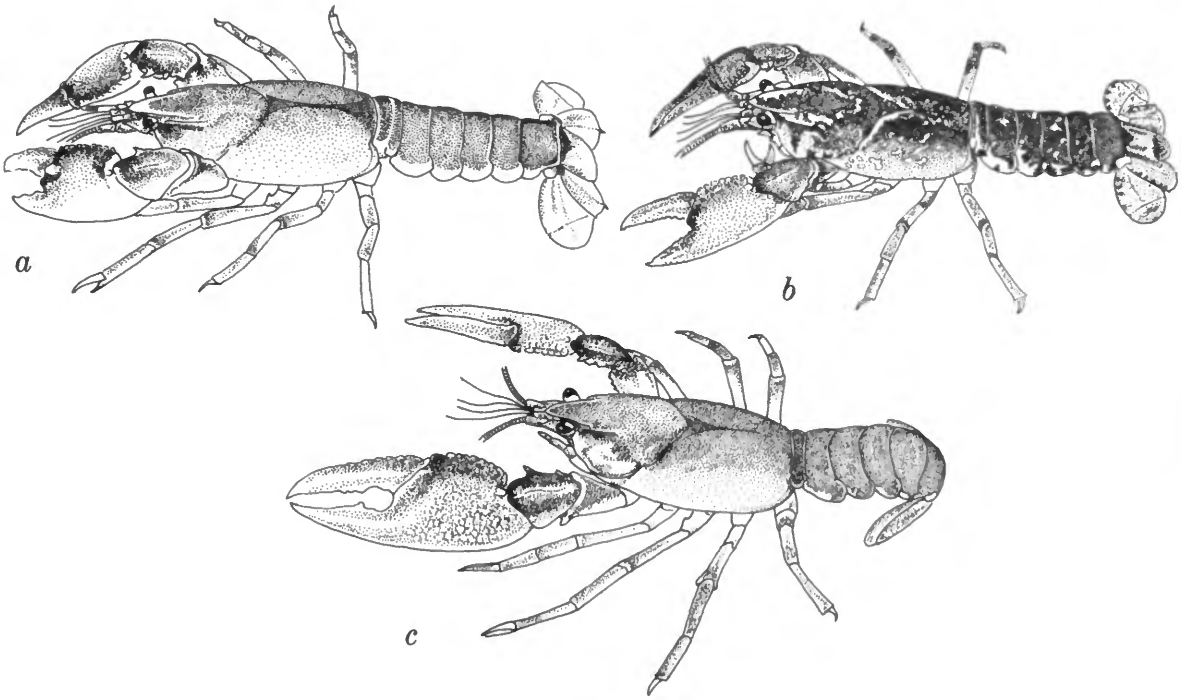


FIGURE 84.—Color patterns in members of subgenus *Lacunicambarus*: *a*, *Cambarus (L.) acanthura* from 1.0 mi NE of Chatsworth, Murray Co; *b*, *C. (L.) diogenes diogenes* from along Pataula Creek at US Hwy 82, Quitman Co; *c*, *C. (L.) diogenes diogenes* from along Muckalee Creek at St Rte 118, Lee Co.

punctate laterally; fingers gaping, sometimes rather robust, and with well-developed longitudinal ridges dorsally; proximal opposable margin of dactyl distinctly concave; moderately conspicuous tuft of setae sometimes present at mesial base of fixed finger, lateral base seldom deeply impressed. First form male with hook on ischium of third pereiopod not opposed by tubercle on basis; first pleopod with terminal elements short, bent caudally at angle of approximately 90 degrees: (1) central projection not tapering distally, usually broadly rounded (rarely with subapical notch); (2) mesial process weakly to moderately (rarely strongly) inflated; and (3) caudal knob rudimentary or absent. Female with annulus ventral is subsymmetrical, slightly movable; first peopod present and reaching cephalically beyond caudal margin of annulus.

RANGE.—"Very widespread east of the Rockies and south of the Great Lakes, except peninsular Florida and the Alleghenies, not reported northeast of New Jersey in the East and east of western Pennsylvania in the Mississippi drainage system" (Hobbs, 1974b:20).

SPECIES OCCURRING IN GEORGIA.—*Cambarus (L.) acanthura* and *C. (L.) diogenes diogenes*.

HABITAT.—The members of the subgenus *Lacunicambarus* are primary burrowers, living along water courses or in seepage areas, damp meadows, or swamps. As is true of the galleries of most burrowing species, those tunnel systems constructed in areas where the water table remains close to the surface are more highly branched than are those excavated in localities where the groundwater level drops one to several meters below the surface. During the spring, first form males and ovigerous females are sometimes found in the open water of ponds or streams, and the young that hatch in the spring may remain in such bodies of water for several months.

Key to Georgia Members of Subgenus *Lacunicambarus*

Mesial ramus of uropod with distomedian spine projecting beyond margin of ramus .... ***acanthura***
Mesial ramus of uropod with distomedian spine not reaching distal margin of ramus .... ***diogenes diogenes***

Cambarus (Lacunicambarus) acanthura, new species

FIGURES 25*g*, 84*a*, 85–87, 220

Cambarus (Lacunicambarus) species J.—Hobbs, 1969a:110, 146*, 148, fig. 11.
Cambarus diogenes subsp.—Anonymous, 1970b:221*.—Hart and Hart, 1974:44*, 134*.
Cambarus d. diogenes.—Bouchard, 1972:35.
Cambarus (Lacunicambarus) sp.—Bouchard and Hobbs, 1976: 13.

The above references to Georgia are indicated by asterisks.

REVIEW OF LITERATURE.—This crayfish was first mentioned by Hobbs (1969a) in his summary of the distribution and phylogeny of the genus *Cambarus*, in which he indicated its presence in the Coosa Basin in Alabama and Georgia. The Georgia records cited by Anonymous (1970b) and Hart and Hart (1974) were based on my tentative identifications. The former cited the crayfish from the Little Tallapoosa River at U.S. Highway 78, Carroll County, and the latter from two localities: 1.8 miles north of Calhoun on State Route 41, Gordon County, where it served as host to the entocytherid ostracod, *Cymocythere cyma* (Hobbs and Walton, 1960a), and 9.7 miles north of Rome, Floyd County, as host to *Uncinocythere simondsi*. Its association with *C. (D.) cymatilis* was pointed out by Bouchard (1972) and with *C. (J.) nodosus* by Bouchard and Hobbs (1976).

DIAGNOSIS.—Rostrum without marginal spines or tubercles and lacking median carina. Carapace without cervical spine or prominent tubercle. Areola 28 to about 75 times as long as broad, constituting, in adults, 36.9 to 43.9 (average 39.5) percent of entire length of carapace (43.5 to 51.0, average 46.4, percent of postorbital carapace length), and never with more than 2 punctations in narrowest part. Antennal scale little more than 2.5 times as long as wide, widest proximal to midlength. Palm of chela with several rows of tubercles, mesialmost row consisting of 6 to 9. Mesial ramus of uropod with prominent distomedian spine overreaching distal margin. First pleopod slightly convex cephalically, terminating in short, nontapering, distally rounded central projection and comparatively slender mesial process, both directed caudally at angle only slightly greater than 90 degrees. Female with annulus ventralis subcircular in outline and rather deeply embedded in sternum; first pleopod reaching about midlength of annulus.

HOLOTYPIC MALE, FORM I.—Body subovate, compressed (Figure 85*a,j*). Abdomen narrower than cephalothorax (12.7 and 16.4 mm); maximum width of carapace greater than depth at caudodorsal margin of cervical groove (16.4 and 14.5 mm). Areola about 49 times as long as broad with 2 punctations in narrowest part; length 41.6 percent of total length of carapace (48.5 percent of postorbital carapace length). Rostrum with convergent thickened margins; acumen not distinctly delimited basally, its upturned tip reaching base of ultimate podomere of antennular peduncle; upper surface of rostrum concave with relatively few punctations other than usual submarginal ones. Subrostral ridge weak but evident in dorsal aspect along basal two-thirds of rostrum. Postorbital ridge rather prominent, grooved dorsolaterally, and ending cephalically without spine or corneous tubercle. Suborbital angle very prominent although rounded apically; branchiostegal spine absent. Cervical spine represented by very small tubercle only slightly larger than granules on branchiostegites and in hepatic region. Carapace punctate dorsally and granulate laterally. Abdomen subequal in length to carapace, pleura (Figure 86*a*) short, subtruncate, rounded caudoventrally. Cephalic section of telson with 2 spines

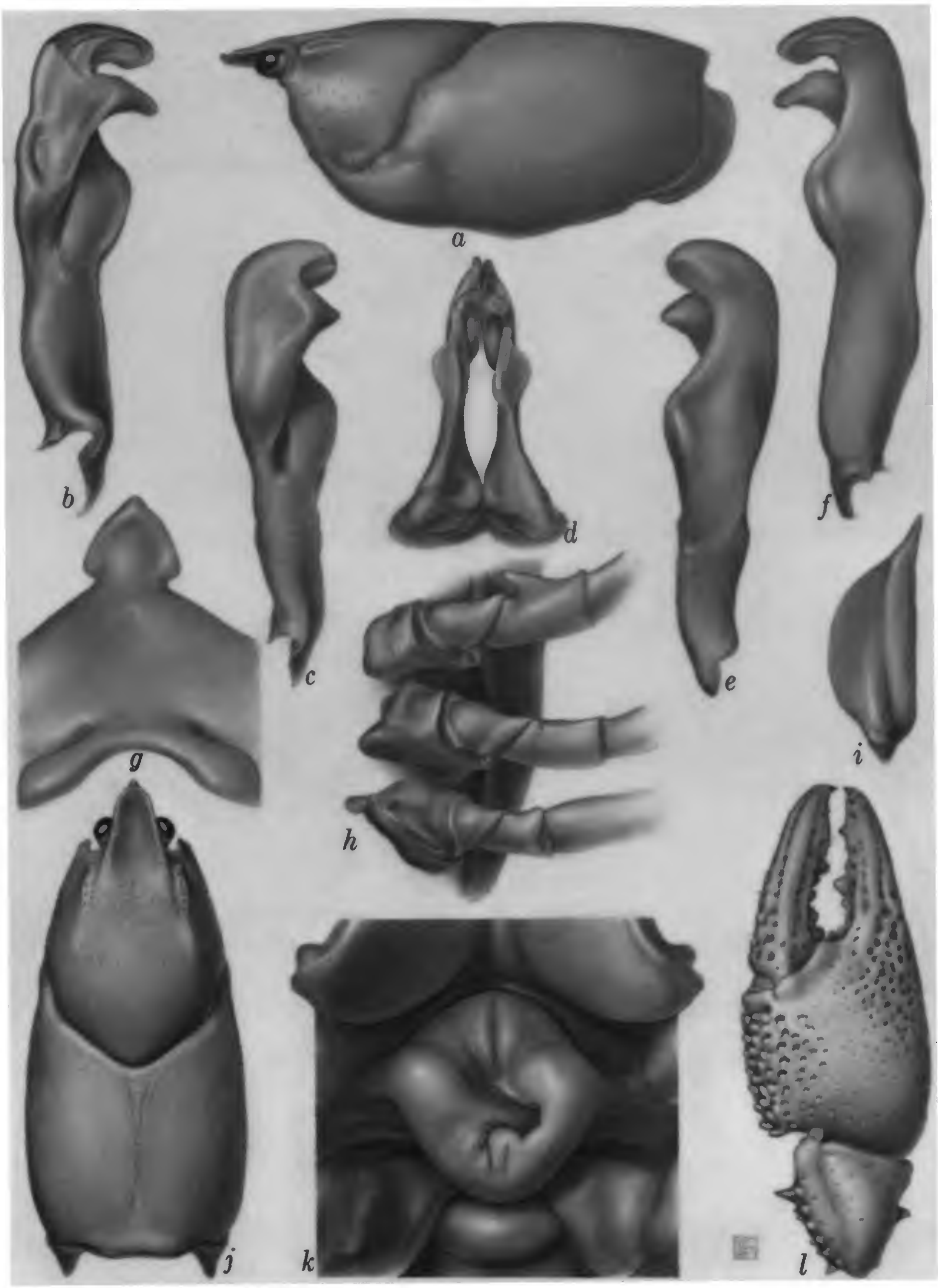


FIGURE 85.—*Cambarus (Lacunicambarus) acanthura* (all from holotype except *c*, *e*, from morphotype, and *k*, from allotype): *a*, lateral view of carapace; *b*, *c*, mesial view of first pleopod; *d*, caudal view of first pleopods; *e*, *f*, lateral view of first pleopod; *g*, epistome; *h*, basal podomeres of third, fourth, and fifth pereiopods; *i*, antennal scale; j, dorsal view of carapace; *k*, annulus ventralis; *l*, dorsal view of distal podomeres of cheliped.

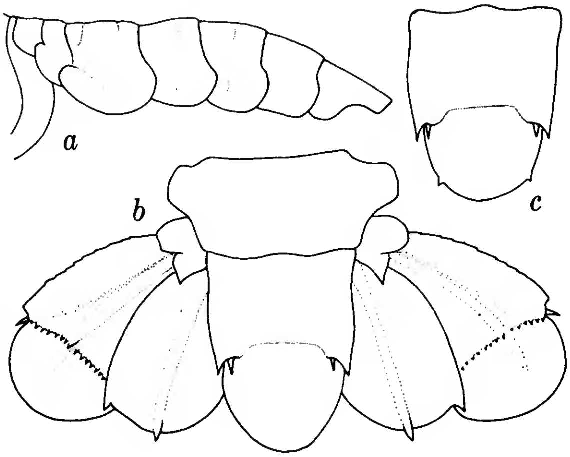


FIGURE 86.—*Cambarus (L.) acanthura*: (*a*, *b*, from holotype; *c*, from allotype): *a*, lateral view of abdomen; *b*, dorsal view of caudal region of abdomen; *c*, dorsal view of telson.

in each caudolateral corner. Proximal podomere of uropod (Figure 86*b*) with caudal spine on mesial lobe; mesial ramus of uropod with prominent median rib ending distally in strong distomedian spine overreaching rounded margin of ramus, laterodistal spine of ramus also strong.

Cephalomedian lobe of epistome (Figure 85*g*) narrow and subtriangular with margins somewhat thickened, ventral surface arched ventrally; main body with small, shallow fovea; epistomal zygoma arched. Ventral surface of proximal podomere of antennular peduncle with small acute spine at base of distal third. Antennal peduncle without spines; flagellum reaching fourth abdominal tergum; antennal scale (Figure 85*i*) 2.7 times as long as broad, broadest proximal to midlength, mesial border forming simple arc; distal spine strong, reaching distal extremity of antennular peduncle. Mesial half of ventral surface of ischium of third maxilliped studded with irregular rows of long, stiff setae; submarginal lateral row on podomere consisting of much smaller flexible ones; distolateral angle not acute.

Right chela (Figure 85*l*) slightly more than twice as long as broad, and mesial margin of palm occupying about two-fifths of its length. Mesial surface of palm with 2 clearly defined rows of tubercles and 1 or 2 additional less regular rows, mesialmost composed of 8 (left with 9) tubercles, and adjacent one of 6 (left with 7): dorsomesial half of palm with additional tubercles arranged sublinearly, and dorsolateral half punctate, punctations deep and larger in vicinity of dorsolateral base of fixed finger: lateral surface of palm and fixed finger not costate; ventral surface of palm punctate, with small corneous tubercle on articular rim opposite base of dactyl. Both fingers of chela with well defined submedian tubercle dorsally and ventrally; opposable margin of fixed finger with row of 6 tubercles (fourth from base largest) along proximal two-thirds of finger and additional large one on lower level at base of distal fourth. Opposable margin of dactyl with row of 7 tubercles (first and fifth from base larger) along proximal four-fifths; single row of minute denticles extending distally from fourth tubercle on both fingers, interrupted by more distal members of tubercular rows; mesial surface of dactyl with tubercles basally giving way to punctations distally.

Carpus of cheliped with distinct furrow dorsally; dorsomesial surface with row of 6 (left with more irregular row of 9) low, rounded tubercles; dorsolateral surface punctate; mesial surface with 1 large spiniform tubercle and 6 or 8 additional ones; ventral surface with usual 2 distal marginal tubercles and small more proximal one mesially. Merus with 2 premarginal tubercles dorsally, ventrolateral row of 4 (left with 5) tubercles, and ventromesial one of 9 (left with 10); podomere otherwise smooth to sparsely punctate. Mesial margin of ischium with row of 3 (left with 4) small tubercles. Ischium of third pereiopod with simple hook extending proximally over basioischial articulation (Figure 85*h*), not opposed by tubercle on basis. Coxa of fourth pereiopod with vertically disposed caudomesial boss; that of fifth pereiopod lacking boss, its ventral membrane bearing oblique row of small sclerites armed with stiff setae.

First pleopod (Figure 85*b*,*d*,*f*) reaching coxa of third pereiopod, slightly arched cephalically; central projection short, not tapering, lacking subapical notch, and broadly rounded apically; mesial process somewhat finger-like, tapering, and directed essentially caudolaterally, but arched laterally with tip directed caudally. Both terminal elements bent caudally at angle slightly greater than 90 degrees; caudal knob absent.

Allotypic Female.—Excluding secondary sexual characters, differing from holotype in following respects: rostrum with more nearly subparallel, nonthickened margins contracted sharply at base of acumen; apex of latter not quite reaching base of ultimate podomere of antennular peduncle; spine on antennal scale reaching only to base of ultimate podomere of antennular peduncle; caudal section of telson (Figure 86*c*) with subsymmetrically arranged pair of marginal spines; opposable margin of dactyl of chela with row of 8 tubercles; dorsomesial surface of carpus of cheliped with row of 7 tubercles; remaining podomeres with numbers and arrangements of tubercles within range of variation exhibited by holotype. (See "Measurements.")

Annulus ventralis (Figure 85*k*) deeply embedded in V-shaped sternum, subcircular in outline, with narrow median longitudinal furrow in cephalic half ending in central depression; tongue extending caudosinistrally across caudal side of depression, disappearing beneath thickened caudosinistral wall; sinus S-shaped and tilted sinistrally at almost 90 degrees, ending on caudal wall slightly dextral to median line. Postannular sclerite, partly hidden by caudomesial part of annulus, ovate, almost twice as broad as long, and approximately four-fifths as wide as annulus. First pleopod reaching midlength of annulus when abdomen flexed.

Morphotypic Male, Form II.—In addition to usual contrast in secondary sexual characters, differing from holotype in following respects; rostrum angular at base of acumen; apex of latter and spine on antennal scale both reaching base of ultimate podomere of antennular peduncle; branchiostegal spine represented by very small tubercle; median spine on mesial ramus of uropod more acute, and caudal section of telson with pair of marginal spines similar to those in allotype; mesial margin of palm of left chela with row of 7 tubercles; merus of chela with ventrolateral and ventromesial rows of tubercles consisting of 3 and 11 on right chela and 4 and 12 on left, respectively; mesial margin of ischium with only 2 minute tubercles. (See "Measurements.")

First pleopod (Figure 85*c*,*e*) with juvenile oblique suture in basal half; central projection noncorneous and not bent quite so strongly caudally; neither it nor mesial process so long as in holotype.

Color Notes (Figure 84*a*).—Carapace dark reddish brown dorsally, fading ventrally, with ventral area of branchiostegite pale bluish cream. Rostral margin and cephalic part of postorbital ridge bright red to reddish orange, and cephalic half of rostrum more red than brown. Color of abdominal terga same as dorsum of carapace with caudal margin of each tergum bearing narrow, red transverse band; pleura pale cream with pinkish suffusion. Telson and uropods pale tan with median ridges on rami of latter dark reddish brown; cephalic section of telson with triangular dark reddish brown patch at base and narrow, lateral marginal bands of similar color. Antennular peduncle cream tan, mottled with brown; flagella tan. Antennal scale tan with dark reddish brown lateral margin; peduncle and flagellum mostly brown. Cheliped basically pale yellowish tan overlain by reddish brown to black in following areas: dorsodistal region of merus, dorsal surface of carpus, dorsomesial half of palm of chela, ridge at base of dactyl, proximodorsal and proximomesial part of dactyl, and proximodorsal part of fixed finger. Tubercles in dark areas cream to light tan; ridges and distal portions of fingers of chela bright red; articular knobs on chela also frequently bright red. Remaining pereiopods basically tan with dorsal portion of distal region of merus, dorsal part of carpus, and proximal part of propodus with reddish brown suffusion.

Types.—The holotypic male, form I, allotypic female, and morphotypic male, form II, are deposited in the National Museum of Natural History, Smithsonian Institution, numbers 129758, 146601, and 146602, respectively, as are the par-

Measurements (mm)

	Holotype	*Allotype*	*Morphotype*
Carapace			
Height	14.5	12.0	11.7
Width	16.4	14.5	12.8
Entire length	35.0	31.4	27.2
Postorbital length	30.1	27.0	22.8
Areola			
Width	0.3	0.3	0.3
Length	14.6	12.1	10.6
Rostrum			
Width	4.8	3.7	3.7
Length	6.0	5.6	5.1
Chela			
Length of mesial margin of palm	10.3	8.7	7.8
Width of palm	12.9	11.1	9.9
Length of lateral margin	27.0	23.0	19.9
Length of dactyl	16.1	14.1	11.6
Abdomen			
Width	12.7	14.2	10.4
Length	34.9	33.8	27.3

atypes consisting of 5♂I, 5♂II, 9♀, 4j♂, 2j♀, 5 ovigerous ♀, and 2♀ with young.

Type-Locality.—Field on west side of Holly Creek (farm of Homer Robinson) about one mile northeast of Chatsworth, Murray County, Georgia. At the time the holotype was collected, the field had not been recently plowed, and the eroded chimneys of a number of burrows were evident. The soil consisted of a sandy clay, and the water table in the comparatively simple burrow was situated at a depth of about one meter. Specimens of both *C. (L.) acanthura* and *C. (D.) cymatilis* were dug from burrows some distance from the creek. Nearby, closer to the stream, a specimen of *C. (D.) striatus* was also obtained from a burrow.

Range.—The range of this crayfish encompasses the Tennessee Basin in Alabama, northwestern Georgia, and presumably in southeastern Tennessee, although I have seen no specimens from the latter; it occurs also in the Coosa Basin from its headwaters in Georgia to Chilton County, Alabama, and in headwater areas of the Black Warrior River in Blount and Tuscaloosa counties, Alabama. In the Chattahoochee watershed, it reaches as far south as Russell County, Alabama.

In Georgia (Figure 87), *C. (L.) acanthura* appears to be concentrated in the Ridge and Valley, Blue Ridge, and upper Piedmont provinces, where it occurs in the watersheds of Chattanooga and South Chickamauga creeks and the Hiwassee River (all in the Tennessee Basin) and in the Chattooga, Conasauga, Coosawattee, and lower Etowah drainage systems in the Coosa Basin. It has also been found in the Tallapoosa watershed in Carroll County and in the Chattahoochee and Ocmulgee basins in De Kalb and Walton counties.

Specimens Examined.—I have examined a total of 249 specimens from Alabama (35) and Georgia (213) of which there are 6♂I, 9♂II, 13♀, 5 ovigerous ♀, 2♀ with young, 112 j♂ and 103 j♀. The counties and number of localities in each are as follows (the localities from which the type specimens were collected are noted in brackets). ALABAMA: *Blount* (1); *Calhoun* (2); *Cherokee* (1); *Chilton* (1) [trib to Waxahatchee Creek 1.5 mi S of Shelby Co line on US Hwy 31, 3♀, 1♀ with young, 25 Apr 1970, K. R. Martin, HHH]; *Lauderdale* (1); *Limestone* (1); *Shelby* (2); *St. Clair* (3) [trib of Big Canoe Creek 12.5 mi SE of Oneonta on US Hwy 31, 1♂I, 1♂II, 1♀ ovig, 28 Apr 1970, B. R. Ford, P. L. Holcomb, HHH; 4.1 mi E of Blount Co line on US Hwy 341, 1♂II, 2j♂, 1j♀, 1 May 1968, HHH]; and *Tuscaloosa* (1). GEORGIA: *Bartow* (1); *Carroll* (1); *Catoosa* (2); *Chattooga* (2); *De Kalb* (2) [Lullwater Biol Field Sta near NE city limits of Atlanta, 1♂II, 23 May 1969, J. L. Boyce, HHH]; *Fannin* (2); *Floyd* (7); *Gilmer* (2) [Hells Creek to Carters Reservoir between St Rtes 5 and 145, 1♀ ovig, 28 Apr 1967, Torgny Unestam, HHH]; *Gordon* (2) [1.8 mi N of Calhoun on St Rte 41, 1♂I, 1♀, 2j♂, 12 Apr 1958, T. L. Johnson, HHH]; *Murray* (8) [type-locality, 1♂I, 25 Apr 1968, E. T. Hall, Jr., HHH; near W city limits of Chatsworth off Chestnut Street, 1♂I, 4 Apr 1973, C. S. Dunn; mountain branch to Conasauga River near Chatsworth, 3♂II, Dec 1937, Charles Harris]; *Polk* (2) [Euharlee Creek at Rockmart, 1♀ with young, 1 May 1967, HHH]; *Walton* (2) [Near Shiloh Baptist Church about 3.5 mi NE of Loganville on St Rte 8, 1♂I, 1♀, 24 May 1969, H. E. Hale, HHH; 3 mi W and about 1 mi N of Between, off US Hwy 78, 1♀, 24 May 1969, HEH, HHH]; *Whitfield* (10). A few of the Georgia localities are so close to others that they could not be included in Figure 87.

Variations.—While a number of variations have been noted, none are associated with a restricted part of the range of the species. Chief

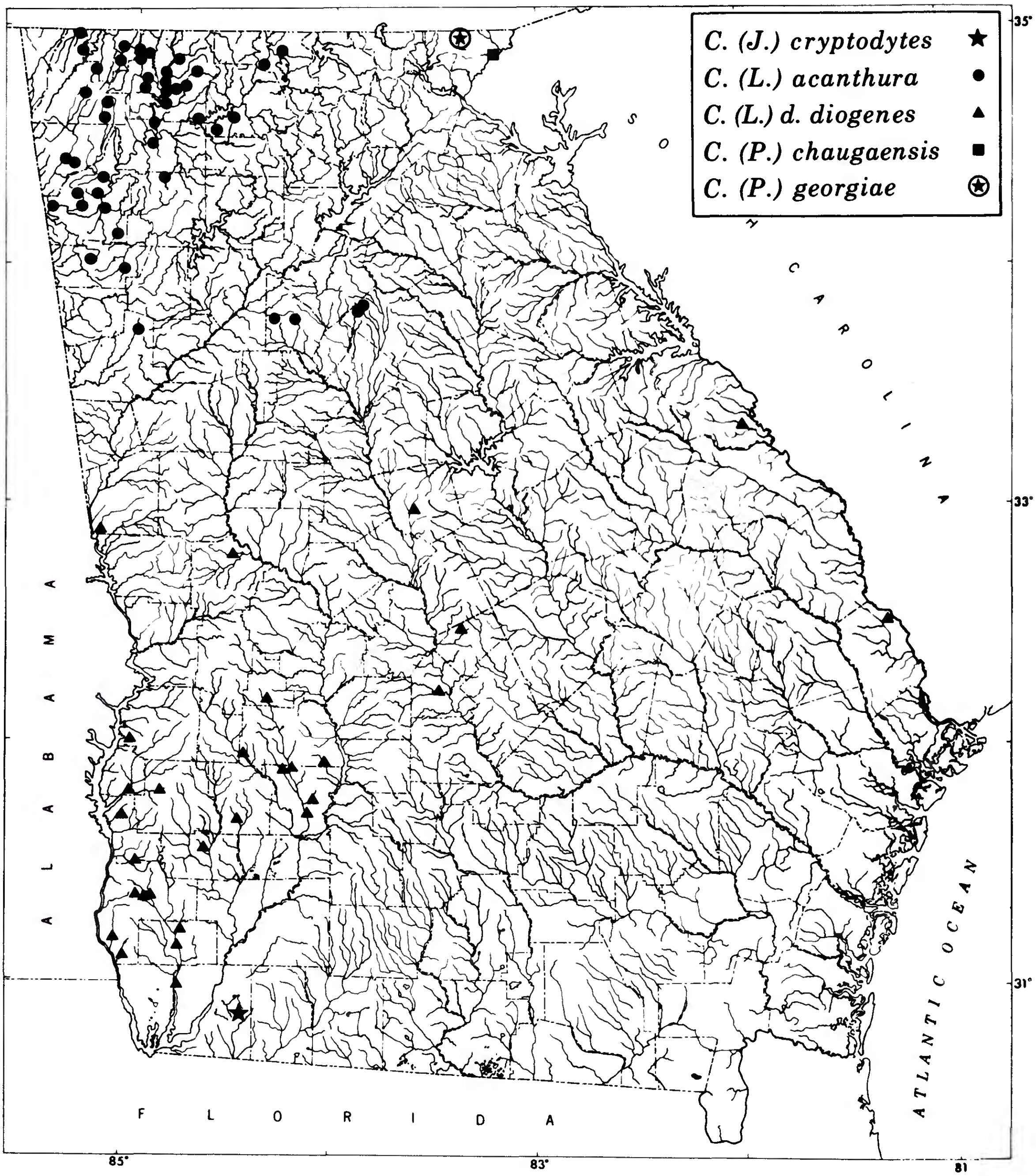


FIGURE 87.—Distribution of *Cambarus (J.) cryptodytes*, *C. (L.) acanthura*, *C. (L.) diogenes diogenes*, *C. (P.) chaugaensis*, and *C. (P.) georgiae* in Georgia.

among them are differences in the relative lengths of the areola and rostrum, which are reflected in the proportions cited in the "Diagnosis." In addition, the rostral margins vary from being strongly convergent to almost subparallel, the latter condition being particularly conspicuous in the young, which also bear marginal spines at the base of the acumen. The development of the spines on the uropods and telson seems, at least in part, to be dependent upon the stage in the molting cycle. More recently molted individuals have longer spines, but the spines on the caudal section of the telson exemplified by the allotype (Figure 86*c*) and morphotype are by no means common. Differences in tubercle counts vary little, except in regenerated appendages, from the range encompassed by the primary types. The first pleopods of the male are remarkably uniform, and the chief differences noted in the annulus ventralis involve the cephalomedian furrow that is hardly discernible in some specimens.

SIZE.—The largest specimen available is an ovigerous female, the carpace length of which is 39.2 (postorbital carapace length, 34.2) mm. The corresponding lengths of the largest first form male are 37.2 (32.0), of the smallest first form male 26.8 (22.6), and of the smallest ovigerous female 29.6 (24.7) mm.

LIFE HISTORY NOTES.—First form males have been collected in April and May, females with eggs in April, and females with young in April and May. While some of the eggs were lost from the females before they were preserved, the numbers cited here furnish at least an estimate of the number produced by five females from Alabama and Georgia.

Carapace and postorbital carapace lengths (mm)	*Number of eggs*	*Diameter of eggs (mm)*
39.2 (34.2)	41	2.4–2.5
36.7 (31.1)	305	2.2–2.3
34.7 (29.7)	89	2.0–2.1
33.7 (29.0)	222	2.2–2.3
29.6 (24.7)	117	2.3–2.4

A female with corresponding lengths of 35.2 (30.1) mm, probably carrying most of her young (250), was collected in Chilton County, Alabama, on 25 April 1970. Another that had lost most of her young was found in Polk County, Georgia, on 1 May 1967. Both of these and the ovigerous females were collected in streams rather than from burrows. Thus it is probable that following ovulation, the females leave their burrows and migrate to a stream where they remain until the young leave them. Young individuals are abundant in the streams from June to October. Unfortunately, almost no data are available on the species from November through March, but it is suspected that the young desert the open water and burrow before the onset of winter, remaining, for the most part, in the burrows until attaining sexual maturity. Extrapolating from what is known about some other crayfishes, the adult males probably enter the burrows of the female during the breeding season but leave before the female lays her eggs.

Seasonal Data (Alabama and Georgia)

Sex/stage	*J*	*F*	*M*	*A*	*M*	*J*	*J*	*A*	*S*	*O*	*N*	*D*
♂I				5	1							
♂II				1	2			1	2			3
♀				7	4			1	1			
♂j				10	3	21	14	22	23	18	1	
♀j		1		7	1	20	18	20	22	13		
♀ ovig				5								
♀ with young				1	1							

ECOLOGICAL NOTES.—On the basis of our limited knowledge of this species, its habits resemble in most respects those of its close relative, *Cambarus (L.) d. diogenes*. The young, as indicated above, remain in open water for several months, but by spring (probably by early winter) they are no longer in the streams and dwell in comparatively simple burrows, consisting usually of a subvertical passageway that descends below the water table and is connected to the surface by two or three tunnels leading from the main vertical passage. These openings are sometimes marked by neatly constructed chimneys but appear more frequently, probably due to erosion by rains, as irregular heaps of earth that may or may not be plugged. The only adults to be collected from open water have been ovigerous females and those carrying young. If all females return to streams when they become ovigerous (which I deem unlikely), then at least some of them accomplish migrations of distances of as much as a mile, for burrows are not confined to areas adjacent to a stream, and presumably the young crayfish also migrate for comparable distances!

RELATIONSHIPS.—*Cambarus (L.) acanthura* has more in common both morphologically and ecologically with *Cambarus (L.) d. diogenes* than with any other crayfish. It differs from the latter species, however, in possessing, even in the very young, a distomedian spine overreaching the margin of the mesial ramus of the uropod; furthermore, it differs from most members of *C. (L.) d. diogenes* in possessing an areola that is not obliterated along part of its length, and the chela is more nearly quadrangular with massive rather than tapering fingers. Its reddish brown carapace and abdomen and dark markings on the tan chelipeds differ rather strikingly from most of the color patterns observed in the latter species. Another closely allied species (perhaps a variant of *C. (L.) d. diogenes*) is an undescribed form occurring in the Tennessee Basin. The only specimens that I have examined were collected 7.2 miles southeast of Newport on U. S. Highway 25, Cocke County, Tennessee. Whereas the chela of this crayfish resembles that of *C. (L.) acanthura*, its areola is distinctly broader and the median spine on the mesial ramus of the uropod is premarginal.

CRAYFISH ASSOCIATES.—Only two species have been collected from burrows adjacent to those of *Cambarus (L.) acanthura*—*C. (D.) cymatilis* and *C. (D.) striatus*. Collected with it in the streams, however, are most of the stream-dwelling species occurring within its range. In Alabama, it was found with *C. (D.) latimanus*, *C. (D.) obstipus*, *C. (D.) striatus*, *C. (H.)* sp., *C. (P.) coosae*, *C. (P.) scotti*, *Fallicambarus (C.) fodiens* (Cottle, 1863:217), *Faxonella clypeata*, *Orconectes erichsonianus*, *O. spinosus*, *O. virilis* (Hagen, 1870:63), *Procambarus (O.) acutus acutus*, *P. (O.) lewisi* Hobbs and Walton, 1959:39, *P. (O.) lophotus*, and *P. (O.) verrucosus* Hobbs, 1952a:212. In Georgia, it was associated with the following species (the number of times they were found together is noted in parentheses): *Cambarus (C.) howardi* (1), *C. (D.) cymatilis* (2), *C. (D.) latimanus* (10), *C. (D.) striatus* (9), *C. (H.) coosawattae* (1), *C. (H.) fasciatus* (1), *C. (H.) girardianus* (1), *C. (H.) manningi* (1), *C. (J.) conasaugaensis* (1), *C. (P.) coosae* (9), *C. (P.) extraneus* (1), *Orconectes erichsonianus* (1), *O. spinosus* (8), *Procambarus (O.) lophotus* (3), *P. (Pe.) raneyi* (1), and *Procambarus (Pe.) spiculifer* (6).

ETYMOLOGY.—From the Greek *akantha* (thorn) plus *ura* (tail), so named because of the long spines on the mesial rami of the uropods, a character that serves to distinguish this crayfish from fellow members of the subgenus *Lacunicambarus*.

Cambarus (Lacunicambarus) diogenes diogenes Girard

FIGURES 25*h*, 84*b,c*, 87, 88, 221

Astacus fossor Rafinesque, 1817:42. [Name suppressed by International Commission on Zoological Nomenclature, Opinion 522, 1958.]

Cambarus diogenes Girard, 1852:88.

Cambarus nebrascensis Girard, 1852:91. [Location of types (if extant) unknown. Type-locality, Fort Pierre, Nebraska (now in Stanley County, South Dakota).]

Cambarus Diogenes.—Hagen, 1870:6.

Cambarus Nebrascensis.—Hagen, 1870:8.

Cambarus obesus Hagen, 1870:81, pl. 1: figs. 39–42, pl. 3: fig. 163, pl. 9. [Syntypes, MCZ 195 (2♂I, ♀), 165 (♀), 3361 (♂I), 229 (♂I), 3363 (♂); MHNP (2 dry); Saint Petersburg Museum, U.S.S.R. 9(♀), lost. Type-locality, Lawn Ridge, Illinois.]

Cambarus Diogenenes.—Abbott, 1873:83 [erroneous spelling].

Cambarus Diogenes Diogenes.—Faxon, 1884:144 [by implication].

Cambarus diogenes diogenes.—Hay, 1899b:959 [by implication].—Hobbs, 1942b:166*; 1969b:343*.—Hobbs and Hart, 1959:169*, 188*, 189*.—Hart, 1959:198*, 204*.—Marlow, 1960:229*.—Hobbs III, 1970:182*.—Hart and Hart, 1974:96*, 101*, 129*.

S[ambarus] diogenes.—Steele, 1902:11 [erroneous spelling].

Cambarus (Bartonius) diogenes.—Ortmann, 1905a:120.

Bartonius diogenes.—Williamson, 1907:749 [*Bartonius* intended as a subgeneric name].

Cambarus (Cambarus) diogenes.—Fowler, 1912:341, 348.

Cambarus (Lacunicambarus) diogenes diogenes.—Hobbs, 1969a: 110, figs. 2c, 11*, 13i, 14i, 20a; 1972b:127*, 146*, 154*, figs. 89n, 90d, 92a, 110a; 1974b:20, fig. 69.

Camabarus diogenes.—Huner, 1977:12 [erroneous spelling].

Cambarus (Lacunicambarus) diogenes.—Bouchard, 1978:39 [in part].

The above by no means constitutes an exhaustive list of references but is believed to include all synonyms and records of the species' presence in Georgia; those citations referring to the state are marked with asterisks.

SUMMARY OF LITERATURE PERTAINING TO GEORGIA.—The first record of the occurrence of this species in the state was that of Hobbs (1942b), who noted observations on its habitat in Early County. Its occurrence in Decatur and Early counties was reported by Hobbs and Hart (1959: 169), and they included additional observations on its habitat (pp. 188–189). In the same year, Hart (1959:198) indicated that in the Decatur locality, it was the host of the ostracod, *Entocythere geophila* Hart (1959) [= *Geocythere geophila*], and in Early County (p. 204) it was found to be a host of *Entocythere equicurva* Hoff (1944) [= *Uncinocythere equicurva*]. Hobbs III (1970:182) reported that in Randolph County this crayfish harbored members of *Hartocythere torreya* (Hart, 1959). Hobbs (1969a, 1974b) cited no specific localities but noted the occurrence of the species in the state. The most recent records of the presence of *C. (L.) d. diogenes* in Georgia are those of Hart and Hart (1974), who included the localities cited above.

DIAGNOSIS.—Rostrum without marginal spines or tubercles and lacking median carina. Carapace without cervical spine or prominent tubercle. Areola linear or obliterated, constituting in adults 39.0 to 42.4 (average 39.8) percent of entire length of carapace (46.1 to 49.8, average 47.7, percent of postorbital carapace length), and with room for no punctations in narrowest part. Antennal scale approximately 3 times as long as wide, broadest at about midlength. Mesial surface of palm of chela with 2 or 3 rows of tubercles, mesialmost consisting of 5 to 7. Mesial ramus of uropod with distomedian spine never reaching distal margin. First pleopod of male with convexity near midlength of cephalic surface, terminating in short, nontapering, distally rounded central projection and comparatively slender mesial process, both directed caudally at angle only slightly greater than 90 degrees. Female with annulus ventralis subquadrangular, usually longer than broad, and rather deeply embedded in sternum; first pleopod reaching about midlength of annulus.

COLOR NOTES.—Two color patterns are recorded here, one of a specimen from the Flint River basin in Lee County, Georgia, which is comparatively concolorous and rather typical of the species along the eastern side of the Appalachians. The other is based on a specimen from the Chattahoochee Basin in Quitman County, which, while unusual in this watershed, occurs more frequently in Alabama and resembles others that have been found in Mississippi and Tennessee.

Concolorous Pattern (Figure 84*c*): Basic color of carapace olive to forest green dorsally, fading ventrally on hepatic and branchiostegal regions to pale green or greenish blue. Rostral margins, postorbital ridges, and knobs at caudal extremities of latter scarlet. Abdomen similarly basically dark green with caudal portion of terga margined in red. Antennular and antennal peduncles very dark green, flagella tan to olive; antennal scale with dark lateral margin, otherwise greenish or tan. Cheliped with dorsal surface of distal half of merus, carpus, and lateral half of palmar area of propodus largely dark green; however, distal part of all 3 podomeres, mesial part of palmar area of propodus, and dactyl suffused with very dark purplish red, latter totally replacing green on parts of fingers, from near midlength almost to end of fixed finger and virtually all of dactyl; distal part of fingers bright red with orange to brown corneous tips; distal articular knobs and dorsodistal margin of merus, major procurved spine on mesial surface of carpus, proximal articular knob at base of propodus, and ridge on latter at base of dactyl scarlet to reddish orange. Remaining pereiopods with merus through dactyl green dorsally, fading to pale bluish green ventrally, and distal margins of ischium, merus, carpus, and propodus scarlet to reddish orange. (Occasional specimens are more tan than olive, and in them the chela tends to be basically tan rather than green, and the red coloration is more dilute.)

FIGURE 88.—*Cambarus (Lacunicambarus) diogenes diogenes* from along Muckalee Creek at St Rte 118, Lee Co (all from male, form I, except *c*, *e*, from male, form II, and *k*, from female): *a*, lateral view of carapace; *b*, *c*, mesial view of first pleopod; *d*, caudal view of first pleopods; *e*, *f*, lateral view of first pleopod; *g*, epistome; *h*, proximal podomeres of third, fourth, and fifth pereiopods; *i*, antennal scale; *j*, dorsal view of carapace; *k*, annulus ventralis; *l*, dorsal view of distal podomeres of cheliped.

Speckled Pattern (Figure 84*b*): Basic color of dorsum of carapace dark olive green, fading to pale green ventrally, and marked with irregular olive cream splotches of various sizes and shapes. Rostral margins and postorbital ridges reddish orange, coloration of latter bleeding into adjacent light markings extending caudomesially over midgastric region. Caudolateral margins of cervical groove marked by yellowish sublinear splotches, curving and becoming more reticulate caudomesially along branchiocardiac grooves; cephalic areolar triangle with pair of small yellow spots. Abdomen also dark olive with small irregular pale olive cream flecks. In other features resembling concolorous green phase described above.

TYPES.—Not known to be extant except for questionable paratype (♀) in the Academy of Natural Sciences of Philadelphia.

TYPE-LOCALITY.—Vicinity of Washington, D.C.

RANGE.—As indicated by Hobbs (1974b:20), "this is a species complex and needs considerable attention." It is "very widespread east of the Rockies and south of the Great Lakes, except in [southeastern Georgia,] peninsular Florida and the Alleghenies; not reported northeast of New Jersey in the East and east of western Pennsylvania [and western Tennessee] in the Mississippi drainage system."

In Georgia, except for three localities in the lower Piedmont Province, this crayfish appears to be confined to the Coastal Plain Province. There all except one of the known localities lie in the Dougherty Plain and Fall Line Hills, where its range encompasses segments of the Flint-Chattahoochee and Ocmulgee basins. In the former basin, it has crossed the fall line, penetrating the lower Piedmont Province in Troup and Talbot counties, and in the Ocmulgee Basin into Jones County. The single locality in the Barrier Island Sequence District occurs in the Savannah Basin. Otherwise, its apparent absence seaward from the Tifton Upland is, for the most part, probably real.

GEORGIA SPECIMENS EXAMINED.—I have examined a total of 61 specimens from the following localities. *Bleckley County:* (1) 1.9 mi S of Twiggs Co line on US Hwy 129, 1♀, 2 Apr 1966, E. T. Hall, Jr., HHH, collectors. *Calhoun County:* (2) trib to Ichawaynochaway Creek 3 mi N of Morgan on St Rte 41, 1♂I, 28 Jan 1972, J. S. Ramsey. *Clay County:* (3) along trib to Lake George 6.9 mi N of St Rte 37 on Rte 39, 2j♀, 26 Jun 1975, D. J. Peters, J. E. Pugh, HHH. *Decatur County* (4) along Spring Creek 4.8 mi E of Iron City on US Hwy 84 (Hobbs and Hart, 1959:169), 1♂II, 4j♂, 2j♀, 1 Sep 1955, C. W. Hart, Jr., HHH; 1♂II, 25 Jun 1975, DJP, JEP, HHH. *Early County:* (5) along Baptist Branch in Blakely (Hobbs, 1942b:166), 2♀, 24 Jul 1936, HHH; (6) 0.7 mi E of Blakely on St Rte 62 (Hobbs and Hart, 1959:169), 1j♂, 2 Sep 1955, CWH, HHH; (7) 4.4 mi E of Blakely on St Rte 62 (Hobbs and Hart, 1959:169), 1 ovig ♀, 2 Sep 1955, CWH, HHH; (8) North Fork of Kolomoki Creek on St Rte 20 at Clay Co line, 1j♀, 26 Jun 1975, DJP, JEP, HHH; (9) along creek 1.8 mi W of Jakin on US Hwy 84, 1♂II, 25 Jun 1975, DJP, JEP, HHH; (10) along creek 0.4 mi W of Cedar Springs on St Rte 273, 1♂II, 1j♂, 1j♀, 25 Jun 1975, DJP, JEP, HHH. *Effingham County:* (11) ravine on Savannah River Bluff about 0.5 mi N of St Rte 119, 1♀, 20 Apr 1974, DJP, HHH. *Jones County:* (12) 9 mi N of Macon on US Hwy 129, 1j♂, 29 Aug 1955, CWH, HHH. *Lee County:* (13) banks of Muckalee Creek at St Rte 32, 1♂I, 2♂II, 1♀, 1j♀, 26 Oct 1974, R. M. Gaddis, B. A. Caldwell; (14) trib to Muckalee Creek, 1♂II, 2♀, 13 Aug 1932, Mark Becker; (15) banks of Muckaloochee Creek at Smithville, 1♂II, 14 Apr 1968, HHH; (16) banks of Muckalee Creek 3 mi E of Leesburg on St Rte 32, 1j♂, 14 Apr 1968, HHH; (17) banks of Muckalee Creek 6 mi WSW of Sumter Co line on St Rte 118, 1♂I, 1♂II, 15 Apr 1968, HHH. *Miller County:* (18) banks of Spring Creek 0.6 mi W of Colquitt on US Hwy 27, 1♂II, 1♀, 1j♂, 16 Apr 1968, HHH; 2♂II, 2♀, 1j♂, 25 Jun 1975, DJP, JEP, HHH; (19) trib to Spring Creek 3.1 mi N of Colquitt on St Rte 45, 1j♂, 26 Jun 1975, DJP, JEP, HHH. *Pulaski County:* (20) 4.2 mi S of Hawkinsville on US Hwy 129, 1j♂, 1j♀, 21 Apr 1966, ETH, HHH. *Quitman County:* (21) along Pataula Creek at US Hwy 82, 4.2 mi W of Randolph Co line, 1♂II, 17 Apr 1975, DJP, JEP, HHH. *Randolph County:* (22) along trib to Pataula Creek 6 mi W of Cuthbert on US Hwy 82 (Hobbs III, 1970:182), 1♂II, 2♀, 4 Apr 1968, G. B. Hobbs, HHH. *Richmond County:* (23) Spirit Creek 8.8 mi S of Augusta on St Rte 56, 1j♀, 17 Apr 1977, C. E. Carter, CWH, JEP, HHH. *Schley County:* (24) banks of trib to Muckalee Creek 3.8 mi SW of Ellaville on St Rte 153, 3♀, 1j♂, 15 Apr 1968, GBH, HHH. *Stewart County:* (25) roadside ditch 2.2 mi N of Quitman Co line on St Rte 39, 1j♂, 26 Jun 1975, DJP, JEP, HHH. *Sumter County:* (26) between DeSoto and Cobbs on US Hwy 280, 1j♂, 18 Aug 1952, HHH; (27) Kinchafoonee Creek Swamp at Webster Co line on St Rte 45, 1j♀, 15 Apr 1968, HHH. *Talbot County:* (28) bank of Flint River 8.2 mi E of Woodland on St Rte 36, 1♀, 27 Sep 1970, R. Little. *Terrell County:* (29) banks of creek 8 mi S of Dawson on St Rte 55, 1♂II, 1♀, 15 Apr 1968, HHH. *Troup County:* (30) Long Cane Creek 1.3 mi E of

West Point on St Rte 18, 1j♀, 17 Sep 1967, J. R. Ramsey (fide, R. W. Bouchard: I have not examined the specimen). These localities lie within the Chattahoochee, Flint, Ocmulgee, and Savannah basins.

VARIATIONS.—The Georgia specimens assigned to *Cambarus (L.) diogenes diogenes* differ from specimens from the vicinity of the type-locality in possessing a narrower and thus apparently a more highly vaulted carapace; the chelae are more strongly depressed, particularly the fingers, and are provided with a well-defined lateral costa. In addition, the rostral margins are usually distinctly more convergent; the eyes, particularly of specimens from the Chattahoochee, Flint, and Ocmulgee basins, are proportionately larger; and the sternum immediately anterior to the annulus ventralis is more broadly U-shaped as opposed to the almost V-shaped sternum in specimens from the area of the District of Columbia. Other characters taken into consideration seem to lie within the limits of variation exhibited by specimens from the latter area.

Too few specimens are available from Georgia to determine whether or not differences noted are individual ones or characteristic of local populations. In general, however, the adult specimens from the several watersheds appear to be rather uniform.

SIZE.—The largest specimen from Georgia is a first form male having a carapace length of 48.4 (postorbital carapace length 41.4) mm. The corresponding lengths of the smallest first form male available are 36.8 (31.8) mm. Those of the only ovigerous female are 44.5 (38.2) mm.

LIFE HISTORY NOTES.—As may be observed in the tabulation of seasonal data, first form males were collected in January, April, and October, and the single ovigerous female was found in September. The latter was carrying 40 eggs, the diameters of which were approximately 3 mm.

Hobbs (1942b:166) reported that first form males from the Florida panhandle had been collected in April, May, October, November, and December, one ovigerous female in April, and one carrying young in May. In Alabama, first form males have been found in March, April, and May, and two ovigerous females were obtained in April. One female with well developed cement glands was observed in August.

Seasonal Data

Sex/stage	*J*	*F*	*M*	*A*	*M*	*J*	*J*	*A*	*S*	*O*	*N*	*D*
♂I	1			1						1		
♂II				6		5		1	2	2		
♀				9		2	2	2		1		
♂j				4		4		2	5			
♀j				3		4			3	1		
♀ ovig									1			

ECOLOGICAL NOTES.—Among the several reports on the ecology of this crayfish is that of Harris (1903a:85–96), who presented an excellent summary of our knowledge of the habitat and habits of the species at that time. Some three years later, Ortmann (1906b:416–424, 480–486) gave a most comprehensive account of the ecology and life history of the species in Pennsylvania, and many of his observations coincide with the few data available on the species in Georgia. The most recent summary is that of Williams and Leonard (1952:1007–1009). Other reports are briefer and do not add appreciably to the studies cited.

The earliest observations on this crayfish in Georgia were those of Hobbs (1942b:166) who stated that

> along the banks of a small stream in Early County, Georgia, each burrow had one opening below the water level, penetrated for about a foot into the bank, and usually continued to an above water opening by way of a single passage upward. Over some of these were small chimneys. When the crayfish were dug out it was found that they were usually below the water table.

This crayfish was among those that he classified as a primary burrowing species. According to Hobbs and Hart (1959:188–189),

> it is occasionally taken in open water. In this region it is found burrowing along the banks of both large and small streams, and occasionally in seepage areas in the headwaters of small streams. In many instances the burrows have at least two openings, one below water level and the other above it, and in such situations seldom have more than two or three passageways. In seepage areas the burrows may branch in several directions and have several chimneys. The chimneys are usually neatly constructed and often attain a height up to at least 1 foot. Burrows along the banks of the

Apalachicola River with openings 10 to 15 feet above the water level are almost certainly excavated by this species.

In many burrows the vertical passageway above the water table branches once or twice so that there may be as many as three chimneys marking the excavation. Little else can be added to the above except for remarks concerning the presence of individuals in open water. Most of the ovigerous females that I have collected outside of Georgia were taken from streams, and on several occasions during April I have found a first form male in the seine. Small juveniles also occur in open water of streams and temporary bodies of water; however, except during the season when the females are ovigerous, I have never found adult crayfishes outside of burrows.

GEORGIA CRAYFISH ASSOCIATES.—The following crayfishes have been collected with *Cambarus (L.) diogenes diogenes* in adjacent burrows or nearby streams (the number of times is noted in parentheses): *C. (D.) latimanus* (4), *C. (D.) reflexus* (1), *C. (D.) striatus* (3), *Fallicambarus (C.) hedgpethi* (1), *Faxonella clypeata* (7), *Procambarus (O.) acutissimus* (1), *P. (O.) enoplosternum* (1), *P. (O.) pubescens* (1), *P. (Pe.) gibbus* (3), *P. (Pe.) spiculifer* (14), *P. (S.) howellae* (2), *P. (S.) paeninsulanus* (8), and *P. (S.) troglodytes* (1).

REMARKS.—Why this crayfish has been encountered so infrequently outside of the Flint-Chattahoochee watershed in Georgia is not known; however, competition with other primary burrowers in the Altamaha, Ogeechee, and Savannah drainage systems could contribute to its apparent rarity in them. At the locality in Effingham County, along the Savannah River bluff, I obtained the single specimen from a burrow adjacent to those of *C. (D.) reflexus*, and my data indicate that the latter species occurs more commonly in the Savannah and Ogeechee basins than does *C. (L.) d. diogenes* (no records of its presence in the latter basin are available). By contrast, it is rather abundant in the Flint-Chattahoochee watershed in spite of the presence of *C. (D.) striatus*, which in some colonies appears to be the sole crayfish inhabitant. Where the ranges of the two overlap, the latter species is found most frequently in low-lying or seepage areas, whereas *C. (L.) d. diogenes* seems to dominate stream banks.

Subgenus *Puncticambarus*

Subgenus *Bartonius* Ortmann, 1905a:97 [in part].

Subgenus *Cambarus* Fowler, 1912:341 [in part; not Erichson, 1846:97].

Subgenus *Puncticambarus* Hobbs, 1969a:101 [type-species: *Cambarus extraneus* Hagen, 1870:73].

DIAGNOSIS.—Eyes large and pigmented. Rostrum with or without marginal spines or tubercles and margins seldom thickened. Postorbital and cervical spines usually present (latter absent in *C. (P.) hiwasseensis* and *C. (P.) parrishi*). Suborbital angle acute or obtuse. Branchiostegal spine small or large. Areola 1.9 to 4.6 times as long as broad and constituting 29.4 to 35.9 percent of total length of carapace (39.2 to 45.2 percent of post-orbital carapace length). Chela elongate, seldom strongly depressed and with mesial margin of palm long (width of palm less than 1.5 times length of mesial margin) and usually bearing at least 2 rows of tubercles (only 1 in *C. (P.) georgiae*, *C. (P.) nerterius* Hobbs (1964:189), and *C. (P.) veteranus* Faxon (1914:389)); mesialmost row consisting of 8 or more (except in *C. (P.) chaugaensis* and occasionally in *C. (P.) cumberlandensis*); mesial half of dorsal surface of palm tuberculate or punctate; lateral margin of fixed finger costate and punctate; fingers seldom widely gaping, with well-defined longitudinal ridges dorsally, proximal opposable margin of dactyl never deeply concave; opposable base of fixed finger lacking conspicuous tuft of setae (except sometimes in *C. (P.) coosae* and *C. (P.) scotti*). First form male with hook on ischium of third pereiopod always opposed by tubercle on basis; first pleopod with terminal elements consisting of (1) short bladelike central projection curved at angle greater than 100 degrees to main shaft of appendage and with distinct subapical notch; (2) somewhat inflated mesial process, usually subacute distally and directed at angle of 90 to 120 degrees to main shaft of appendage; caudal knob absent or, at best, rudimentary. Female with annulus ventralis subsymmetrical; cephalic area usually not conspicuously more membranous than caudal, slightly movable and not hinged; caudal portion with tilted S-shaped sinus (sometimes reversed); first pleopod present.

RANGE.—From Michigan, Ontario, and New York southward, west of the Appalachians, onto the Cumberland Plateau, in and flanking the southern part of the Appalachians as far south as Chilton County, Alabama (Coosa Basin), and headwaters of the Savannah River, from there throughout most of the piedmont and lower slopes of the Blue Ridge to southern Maryland.

In Georgia, the members of this subgenus are confined to the Ridge and Valley, Blue Ridge, and the northwestern part of the Piedmont provinces, where they are found in the South Chickamauga Creek basin and in the Coosa, Hiwassee, Little Tennessee, and Savannah watersheds.

SPECIES OCCURRING IN GEORGIA.—*Cambarus (Puncticambarus) chaugaensis*, *C. (P.) coosae*, *C. (P.) extraneus*, *C. (P.) georgiae*, *C. (P.) hiwasseensis*, *C. (P.) parrishi*, , and *C. (P.) scotti*.

HABITAT.—All of the members of the subgenus *Puncticambarus* are inhabitants of streams, where they occupy a rather wide variety of habitats, ranging from riffles to rather sluggish sectors. They seek cover under rocks, in various types of litter, and infrequently have been found in burrows in the stream bed. They are often abundantly represented among the assemblage of crayfishes taking cover among exposed roots of shoreline plants and are common inhabitants of undercut banks of streams. In segments of water courses in which few other crayfishes occur, they apparently utilize virtually all available habitats. In sharing a section of a stream with members of the subgenus *Hiaticambarus*, they relinquish to the latter most of the riffle areas and dominate the pools or less swiftly flowing segments of the stream. In company with members of other subgenera, they inhabit most of the stream bed but share the littoral areas with their congeners.

REMARKS.—Seven of the 15 members (for extralimital species, see Hobbs, 1974b:20–22) of the subgenus *Puncticambarus* occur in Georgia, and, of these, perhaps the most generalized is *Cambarus (P.) extraneus*, which has retained marginal spines on the rostrum, cervical spines, a broad densely punctate areola, long fingers on the cheliped, first pleopods of the male that are rather widely spaced basally and bear short terminal elements, and, like all members of the subgenus, a subsymmetrical annulus ventralis. Furthermore, the presence of a dark saddle on the caudal part of the carapace and the longitudinally striped abdomen are features (one or both) that occur in some of the more primitive members of the genus *Procambarus* and in other subgenera of *Cambarus*.

Closely allied to *C. (P.) extraneus* is *C. (P.) georgiae*, which also possesses most of the features just mentioned, but the terminal elements of the first pleopod are longer, the shape of the chela is even more *Procambarus*-like than in *C. (P.) extraneus*, the mesial margin of the palm bears only a single row of tubercles, and the stripes on the abdomen are represented by a series of oblique splotches. *Cambarus (P.) parrishi*, while retaining fewer of these features, is also closely allied to *C. (P.) extraneus* and *C. (P.) georgiae*. It has lost all traces of cervical spines; the marginal spines on the rostrum are reduced; the chela is shorter and broader; the dark saddle is lacking on the caudal part of the carapace; and the stripes on the abdomen are segmented, resembling those of *C. (P.) georgiae*. The characteristics of *C. (P.) hiwasseensis* are much like those of *C. (P.) parrishi*, but in it there are no traces of marginal spines on the rostrum, and the chelae, while variable, generally have longer fingers.

A fifth closely related species is *C. (P.) chaugaensis*, which, paralleling *C. (P.) hiwasseensis*, has lost the marginal spines on the rostrum but has retained the cervical spine; the chela is rather short, the bases of the first pleopods of the male are almost contiguous, and the terminal elements are comparatively long as they are in *C. (P.) georgiae*. Like the latter species, the color pattern is a mottled one, in which traces of the saddle on the carapace and the stripes on the abdomen occur in splotches. These five species are collectively referred to elsewhere as the *extraneus* Group.

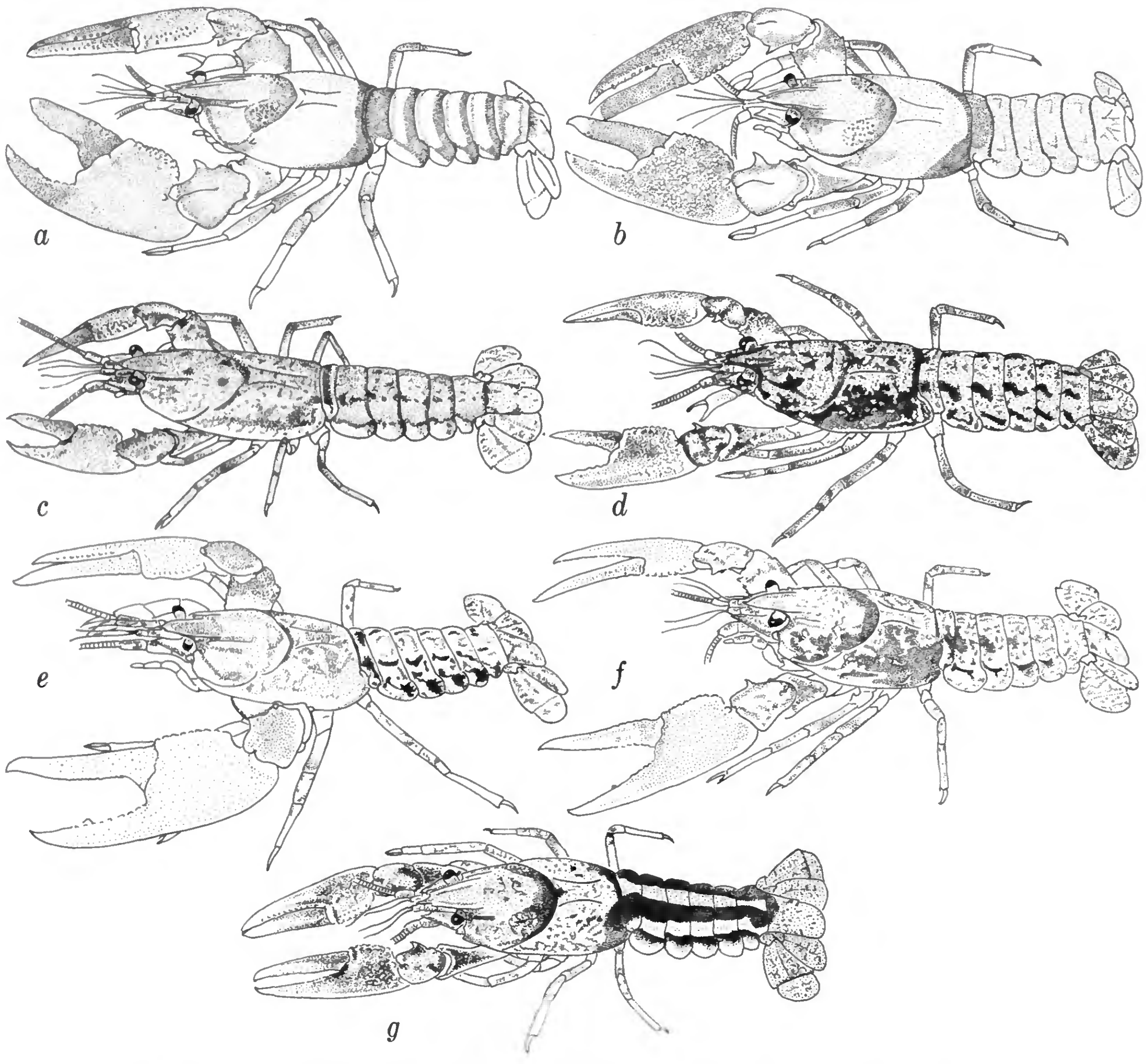


FIGURE 89.—Color patterns in members of subgenus *Puncticambarus*: *a*, *Cambarus (P.) coosae* from Little Cedar Creek at Cave Spring, Floyd Co; *b*, *C. (P.) scotti* from Chattooga River just NW of Trion, Chattooga Co; *c*, *C. (P.) chaugaensis* from Chauga River at US Hwy 76, Oconee Co, South Carolina; *d*, *C. (P.) georgiae* from Little Tennessee River at US Hwy 441, Rabun Co; *e*, *C. (P.) parrishi* from Soapstone Creek 4.4 mi above mouth, Towns Co; *f*, *C. (P.) hiwasseensis* from tributary to Nottely Lake 15.2 mi SW of Towns Co line, Union Co; *g*, *C. (P.) extraneus* from Little Tiger Creek off St Rte 2 at Catoosa-Whitfield Co line.

The two members, here designated as comprising the *coosae* Group of the subgenus, frequent streams in the Coosa Basin and differ rather conspicuously from the other five Georgia representatives in possessing deeply punctate chelae, a heavier, more tuberculate carapace, and a strikingly different color pattern. The more generalized of the two is *C. (P.) coosae*, which has many features in common with *C. (P.) extraneus*, including both rostral and strongly developed cervical spines, a broad densely punctate areola, and short terminal elements on the first pleopod of the male. The conformation of the chela, however, is strikingly different, the general shape resembling that of *C. (P.) georgiae*, but there are two well-defined rows of tubercles on the mesial surface of the densely punctate palm. The saddle on the caudal part of the carapace is clearly defined but all traces of longitudinal stripes on the abdomen are lacking; instead, the abdominal terga are provided with rather broad, dark transverse bands, and the entire animal is more colorful with yellow to vermilion occurring on ridges and tubercles on the carapace and appendages. Its close ally *C. (P.) scotti* differs from it primarily in possessing a long acute rostrum devoid of marginal spines and in the reduction in width of the transverse bands on the abdomen. The two species of the *coosae* Group seem to represent a transitional facies toward the members of the subgenus *Hiaticambarus*, which approaches rather closely the mien of *C. (H.) speciosus*, the species indicated earlier to share as many features with other members of the subgenus *Puncticambarus* as with those of *Hiaticambarus*.

Key to Georgia Members of Subgenus *Puncticambarus*

1. Rostrum with marginal spines or tubercles 2
   Rostrum without marginal spines or tubercles 5
2. Cervical spine absent .... ***parrishi***
   Cervical spine present 3
3. Chela with single well-developed row of tubercles .... ***georgiae***
   Chela with at least 2 well-developed rows of tubercles 4
4. Dactyl of chela twice as long as mesial margin of palm, latter with squamous tubercles more abundant than punctations dorsally; fingers not gaping .... ***extraneus***
   Dactyl of chela less than twice as long as mesial margin of palm, latter densely punctate dorsally; fingers gaping .... ***coosae***
5. Cervical spine absent; mesial row of tubercles on ventral surface of merus of cheliped seldom consisting of fewer than 12 tubercles .. ***hiwasseensis***
   Cervical spine present; mesial row of tubercles on ventral surface of merus of cheliped always consisting of fewer than 12 tubercles 6
6. Cervical and postorbital spines strong; width of palm of chela less than 1.3 times length of mesial margin .... ***scotti***
   Cervical and postorbital spines weak, subtuberculiform; width of palm of chela greater than 1.3 times length of mesial margin ..... ***chaugaensis***

The *coosae* Group

Cambarus (Puncticambarus) coosae, new species

FIGURES 21*c*, 89*a*, 90, 91, 223

Cambarus extraneus.—Bundy, 1877:174*.—Faxon, 1884:145* [in part]; 1885a:84-85*, (160, 167, 173, 178, 179)* [in part]; 1898:650.—Underwood, 1886:368* [in part].—Harris, 1903a:59*, 97*, 144, 151, 156*, ?159*, 161 [in part].—Ortmann, 1905b:311* [in part]; 1918:849* [in part].—Newcombe, 1929:279, 280 [in part].—Hobbs, 1956c:115-120* [in part]; 1959:896* [in part].—Anonymous, 1967a, tab. 6; 1970b:211*.

Cambarus extraneous.—Adams, 1901:849 [in part; erroneous spelling].

Cambarus (Bartonius) extraneus.—Ortmann, 1905a:116, 120, 121*, 129 [in part].

Cambarus (Cambarus) extraneus.—Ortmann, 1931:97 104* [in part].

"an undescribed species closely related to *C. extranius*" [sic].—Unestam, 1969:203*, tab. 1*.

Cambarus (Puncticambarus) species B.—Hobbs, 1969a:102, 135*, fig. 7*.
Cambarus sp. nov. A.—Anonymous, 1969a:(C-23, C-27, C-28, C-32, C-33)*; 1970b: (162–164, 169, 170, 191–193, 196, 197)*.
Cambarus species A.—Hobbs and Hall, 1974:204*.
Cambarus (Puncticambarus) sp.—Hart and Hart, 1974:58*, 73*, 79*, 87, 88*, 90*, 134*.
Cambarus nov. sp. A.—Wharton, 1978:220*.

The above bibliographic citations comprise what I believe to be a complete synonomy as well as including all published references to the species. Those listings mentioning localities or specimens from Georgia are indicated by an asterisk.

SUMMARY OF LITERATURE.—The first record of the occurrence of this crayfish in the state is that of Bundy (1877), who, in describing his *Cambarus spinosus* [= *Orconectes spinosus*], stated that the latter occurs in the "Etowah, Oostanaula and Coosa Rivers, in the vicinity of Rome, Georgia," in company with *C. extraneus* [= *C. coosae*]. Faxon (1884) also cited the locality, "Etowah River, Rome, Georgia," one that was repeated by him in 1885 and, together with Bundy's record, was the source for all subsequent citations until 1967. The first precise localities known were recorded by Anonymous (1967a) from three localities in Alabama: (1) Walnut Creek, 4 miles northwest of Clanton, Chilton County; (2) Hatchett Creek at County Road, 6 miles west of Rockford, Coosa County; and (3) Weogufka Creek, 1 mile northwest of Hillwood, Coosa County. Anonymous (1969a) reported this crayfish from five localities in the Conasauga, Coosawattee, and Oostanaula river basins east and south of Dalton, Whitfield County, Georgia. Hobbs (1969a) indicated that the *extraneus*-like crayfish in the Coosa Basin belonged to an undescribed species. Anonymous (1970b) recorded it as *Cambarus extraneus* from Town Creek, 0.6 mile east of U.S. Highway 27 on Route S2557, Walker County, Georgia, and as *Cambarus (Puncticambarus)* sp. nov. A, from some 10 localities in the Conasauga, Coosawattee, Oostanaula, and Etowah basins in Georgia. Hobbs and Hall (1974) noted that it was found in the Conasauga River where the oxygen concentration was 6 mg/l but was absent downstream where the concentration had dropped to 3.6 mg/l or less. Hart and Hart (1974) recorded the species as *Cambarus (Puncticambarus)* sp. from some 15 localities in the Coosa Basin of Alabama and Georgia, where it served as host to the following entocytherid ostracods: *Dactylocythere falcata* (Hobbs and Walton, 1961), *Dt. suteri* (Crawford, 1959), *Donnaldsoncythere hiwasseensis* (= *Dn. donnaldsonensis*), *Entocythere elliptica*, *E. internotalus*, and *Uncinocythere simondsi*. All known Georgia records are plotted on Figure 91.

DIAGNOSIS.—Body pigmented, eyes well developed. Rostrum with subparallel margins variable in thickness and bearing marginal spines or tubercles. Areola 2.6 to 4.6 times as long as wide and comprising 30.2 to 35.9 percent of entire length of carapace (39.6 to 45.2 percent of postorbital carapace length) and bearing 6 to 13 punctations across narrowest part. Cervical spines strongly developed. Suborbital angle acute to obsolete. Postorbital ridges terminating cephalically in spines or subacute tubercles. Antennal scale approximately 2.5 times as long as broad, mesial and lateral margins subparallel near and at midlength; distomesial margin subtransverse. Chela with almost entire dorsal surface bearing deep punctuations and with 2 or 3 rows of tubercles along mesial margin of palm, mesialmost row consisting of 6 to 11; lateral margin of palm mostly rounded with costa of fixed finger extending onto distal portion; both fingers with well-defined longitudinal ridges dorsally; fixed finger not conspicuously impressed at base; disregarding regenerated chelae, dactyl never more than twice as long as mesial margin of palm. Basis of third pereiopod with tubercle opposing hook on ischium. First pleopod with short terminal elements: corneous central projection not tapering distally, recurved at approximately 115 degrees to main shaft of appendage, and bearing prominent subapical notch; and mesial process inflated, tapering distally, often with acute tip, and directed caudally at angle of about 90 degrees to main shaft. Female with annulus ventralis shallowly embedded in sternum and somewhat asymmetrical; first pleopod present. Carapace with

FIGURE 90.—*Cambarus (Puncticambarus) coosae* (*a, d, h–j, l*, from holotype; *b, f, g*, from paratopotypic male, form I; *c, e*, from morphotype; *k*, from allotype): *a*, lateral view of carapace; *b, c*, mesial view of first pleopod; *d*, caudal view of first pleopods; *e, f*, lateral view of first pleopod; *g*, antennal scale; *h*, epistome; *i*, proximal podomeres of third, fourth, and fifth pereiopods; *j*, dorsal view of carapace; *k*, annulus ventralis; *l*, dorsal view of distal podomeres of cheliped.

dark saddles immediately anterior to cervical groove and abutting posterior margin. Abdomen with transverse dark bands on caudal part of second through fifth terga.

HOLOTYPIC MALE, FORM I.—Body subovate, depressed (Figure 90*a,j*). Abdomen narrower than thorax (17.7 and 20.8 mm); maximum width of carapace greater than height at caudodorsal margin of cervical groove (20.8 and 14.9 mm). Areola 4.3 times as long as broad with crowded punctations, 8 across narrowest part; length of areola 35.7 percent of total length of carapace (44.2 percent of postorbital carapace length). Rostrum with slightly thickened, elevated, subparallel margins bearing corneous tubercles at base of moderately long acumen; latter reaching midlength of distal podomere of antennular peduncle and terminating in corneous upturned tip; dorsal surface of rostrum concave with many punctations extending from base almost to apex of acumen. Subrostral ridge well developed and evident in dorsal aspect to marginal tubercles of rostrum. Postorbital ridge moderately prominent, grooved dorsolaterally, and ending cephalically in subacute corneous tubercle. Suborbital angle subacute. Branchiostegal spine strong and acute. Cervical spine well developed. Carapace densely punctate dorsally and strongly granulate laterally on branchiostegites and on all except dorsalmost part of hepatic region.

Abdomen longer than carapace (39.1 and 37.6 mm); pleura rounded to subtruncate ventrally with subangular caudoventral extremities on second through sixth segments. Cephalic section of telson with 2 spines in caudodextral corner, caudosinistral corner injured; free margin of caudal section evenly rounded. Proximal podomere of uropod with acute tip on each lobe; mesial ramus with low submedian dorsal keel ending in small premarginal spine.

Cephalomedian lobe of epistome (Figure 90*h*) broadly subtriangular with thickened, slightly elevated (ventrally) cephalolateral margins and weakly convex ventral surface; main body with prominent median fovea and epistomal zygoma broadly arched. Ventral surface of proximal segment of antennule with small spine at base of distal third. Antenna broken, in other specimens reaching telson; basis and ischium with spines. Antennal scale (Figure 90*g*) about 2.6 times as long as broad, with mesial and lateral margins parallel for some distance proximal and distal to midlength; strong distal spine almost reaching distal extremity of antennular peduncle. Mesial half of ischium of third maxilliped with rows of punctations bearing long stiff plumose setae; lateral half possessing submarginal row and few scattered punctations with or without small short setae; laterodistal extremity acute.

Right chela (Figure 90*l*) about 2.4 times as long as broad and moderately depressed; mesial margin of palm with row of 8 tubercles subtended ventrally by 4 or 5 irregularly placed, and dorsally by row of 3 widely spaced ones, and row of 10 tubercles immediately dorsolateral to latter. Mesial half of dorsal surface of palm with punctations proximally and small squamous tubercles more distally; remainder of palm mostly punctate but with 2 prominent tubercles on ventral surface opposite base of dactyl and group of 3 or 4 proximal to them. Both fingers with low, rounded dorsomedian ridge flanked by setiferous punctations. Fixed finger with row of 13 rounded corneous tubercles on right chela (11 on left) extending from base of opposable margin almost to corneous tip; prominent large tubercle at lower level of margin opposite ninth tubercle in row and smaller one opposite eleventh; also narrow band of minute denticles flanking dorsal row ventrally from level of seventh tubercle from base distally; lateral surface of finger rounded but rather distinctly costate in dorsal aspect; ventral surface punctate. Dactyl with opposable margin bearing row of 11 tubercles similar to those on fixed finger and narrow band of minute denticles extending distally from sixth tubercle from base, band interrupted by succeeding distal tubercles; ventral surface punctate, and mesial surface with subsquamous tubercles along proximal half and row of widely spaced punctations along distal half.

Carpus of cheliped longer than broad (14.2 and

10.0 mm), with deep longitudinal furrow dorsally flanked by punctations laterally and mesially, and with few inconspicuous tubercles dorsomesially; mesial surface with prominent procurved spine and 2 small tubercles near proximomesial articular boss; lateral surface punctate and ventral surface with 2 large acute tubercles on distal margin and 2 proximomesial to mesiodistal tubercle. Dorsal surface of merus with 2 subdistal spiniform tubercles distally, sparsely punctate to smooth mesially and laterally, and with subspiniform tubercle distolaterally; ventral surface with mesial row of 9 tubercles and only 2 in lateral row. Ischium with ventromesial row of 6 tubercles.

Hook on ischium of third pereiopod only, hook (Figure 90*i*) overreaching basioischial articulation and opposed by tubercle on basis. Coxa of fourth pereiopod with rather weak, vertically disposed but low caudomesial boss. Boss on coxa of fifth pereiopod vestigial, ventral membrane sparsely setiferous.

First pleopod (Figure 90*b,d,f*) reaching coxa of third pereiopod when abdomen flexed. Mesial process bulbous, tapering distally, and ending in acute tip directed caudolaterally at slightly more than 90 degrees to main axis of shaft; central projection uniformly broad, strongly arched with distal extremity directed caudoproximally and bearing distinct subapical notch. (See "Diagnosis" for description.)

Allotypic Female.—Differing from holotype, other than in secondary sexual characters, as follows: abdomen subequal in width to thorax; acumen reaching distal end of ultimate podomere of antennular peduncle; subrostral ridge poorly developed and evident dorsally only in caudal orbital region; more lateral row of tubercles along mesial surface of palm reduced to 5 situated along proximal part of palm; area lateral to row entirely punctate; tubercles on ventrodistal surface of palm reduced in size and number; opposable margin of fixed finger with rather conspicuous mat of plumose setae at base and with row of only 8 tubercles; minute denticles on both fingers arranged in single row; only 10 tubercles present in row on opposable margin of dactyl; furrow on dorsal surface of carpus of cheliped broad and shallow. (See "Measurements.")

Annulus ventralis (Figure 90*k*) subquadrangular, about 1.6 times as broad as long and situated shallowly in sternum; cephalic half not so strongly calcified as caudal half and bearing median longitudinal trough flanked by pair of ridges; sinus originating in caudodextral extremity of trough and, following tilted S-shaped curve, cutting caudal margin of annulus on median line; tongue extending dextrally with fossa occurring along its caudal margin. Postannular sclerite about 3 times as broad as long and approximately two-thirds as wide as annulus. First pleopod reaching midlength of annulus when abdomen flexed.

Morphotypic Male, Form II.—Differing from holotype in following respects: areola with 11 punctations across narrowest part; mesial surface of palm of chela with both rows consisting of 9 tubercles each; fixed finger with plumose setae in basal portion flanking row of 6 tubercles on opposable margin; corresponding margin of dactyl with row of 8 tubercles; carpus of cheliped with only 1 tubercle on proximomesial surface and ventral surface with only 2 distal ones; merus with 9 tubercles in ventromesial row and strong one ventrolaterally. Hook on ischium of third pereiopod much reduced, not overreaching basioischial articulation, opposable tubercle on basis well developed; boss on caudomesial angle of coxa of fourth pereiopod slightly reduced and that on fifth obsolete. (See "Measurements.")

First pleopod (Figure 90*c,e*) with mesial process not differing in most respects from that of holotype; central projection much broader and with only faint indication of subapical notch; shaft of appendage distal to juvenile oblique suture inclined cephalically.

Color Notes (Figure 89*a*).—Carapace basically tan to olive green with dark brown band on and flanking cephalic side of cervical groove; another transverse band on caudal part of carapace broader and fading cephalically on branchiostegites; dark brown to orange reticulate pattern marking mandibular adductor region; hepatic region bluish green ventral to postorbital ridges and cream marginal band extending across cephalic parts of antennal and mandibular regions; dark splotch present on branchiostegite enveloping cervical spine; rostrum with greenish suffusion dorsally, its margins together with postorbital ridges and cervical spines vermilion. Abdomen olive to olive tan; tergum of first segment with transverse dark purplish-brown band, and it and remaining terga with very narrow, deep burgundy transverse band on caudal margin, fading on pleura; 5 caudal terga also with paired, narrow, angular dark olive to reddish oblique markings dorsolaterally (these sometimes absent); pleuron of first abdominal segment cream with vermilion cephaloventral spot; pleura of succeeding segments with pale marginal band tapering caudoventrally from cephalic extremity. Uropods and telson bluish green with basal podomere bearing reddish orange markings. Antennae and antennules olive tan; antennal scale with orange brown lateral marginal stripe and vermilion distolateral spine, thicker lateral part olive cream and lamella olive tan fading proximomesially. Cheliped with same basic colors as carapace; dorsal surface from merus distally olive to tan with reticulate or speckled pattern on palm of chela; fingers dark proximally and fading to cream or white over distal third; spines, tubercles, and articular condyles vermilion, some tipped with cream. Remaining pereiopods paler than carapace with proximal podomeres cream and distal half of merus progressively dark distally; carpus and propodus light proximally, becoming gradually darker distally; dactyl very pale; dorsodistal margins of merus and carpus with very narrow burgundy band.

In at least one locality in Polk County, Georgia, and in another in Coosa County, Alabama, dark areas on carapace broader and almost black, also bands on caudal margin of each abdominal tergum broader and darker.

Types.—The holotypic male, form I, the allotypic female, and the morphotypic male, form II, are deposited in the National Museum of Natural History, Smithsonian Institution, numbers 145603, 145604, 145605, respectively, as are the paratypes that comprise only the following, all collected in Georgia: tributary to Conasauga River 4.6 mi N of Dalton on US Hwy 76, Whitfield Co, 2♂I, 5♂II, 4♀, 4j♂, 4j♀, 16 Apr 1962, J. F. Fitzpatrick, Jr., HHH, collectors; type-locality, 3♂I, 2♀, 1j♂, 1j♀, 4 ovig ♀, 27 Apr 1968, E. T. Hall, Jr., HHH; Conasauga River at St Rte 2, Whitfield Co, 6♂I, 1♂II, 11♀, 1j♂, 1j♀, 12 Oct 1969, ETH, HHH; tributary Conasauga River 9.3 mi S of Dalton, Whitfield Co, 5♂I, 2♂II, 6♀, 6j♂, 4j♀, 1 ovig ♀, T. L. Johnson, HHH.

Measurements (mm)

	Holotype	*Allotype*	*Morphotype*
Carapace			
Height	14.9	12.9	10.9
Width	20.8	17.3	13.9
Entire length	37.6	33.5	26.9
Postorbital length	30.1	26.3	21.0
Areola			
Width	3.3	3.2	2.4
Length	13.3	11.4	9.3
Rostrum			
Width	4.9	4.9	4.0
Length	9.2	8.8	6.9
Chela			
Length of mesial margin of palm	14.4	8.5	6.7
Width of palm	17.6	10.3	8.3
Length of lateral margin	42.6	23.5	20.0
Length of dactyl	25.0	13.4	11.9
Abdomen			
Width	17.8	17.2	12.4
Length	39.4	36.2	30.1

Type-Locality.—Spring Creek, 8 miles east-southeast of Rome, Floyd County, Georgia, on U.S. Highway 411. There, the clear, swiftly flowing stream is some seven meters wide and 0.3 meter deep. The stream bed is littered with rocks, and while macrophytes are absent, the rocks are coated with algal growths. This area of the stream is partially shaded by *Platanus occidentalis*, *Acer rubrum*, and *Salix nigra*.

Range.—The Coosa River basin from Polk and Bradley counties, Tennessee (fide R. W. Bouchard), Murray, Pickens, and Paulding counties,

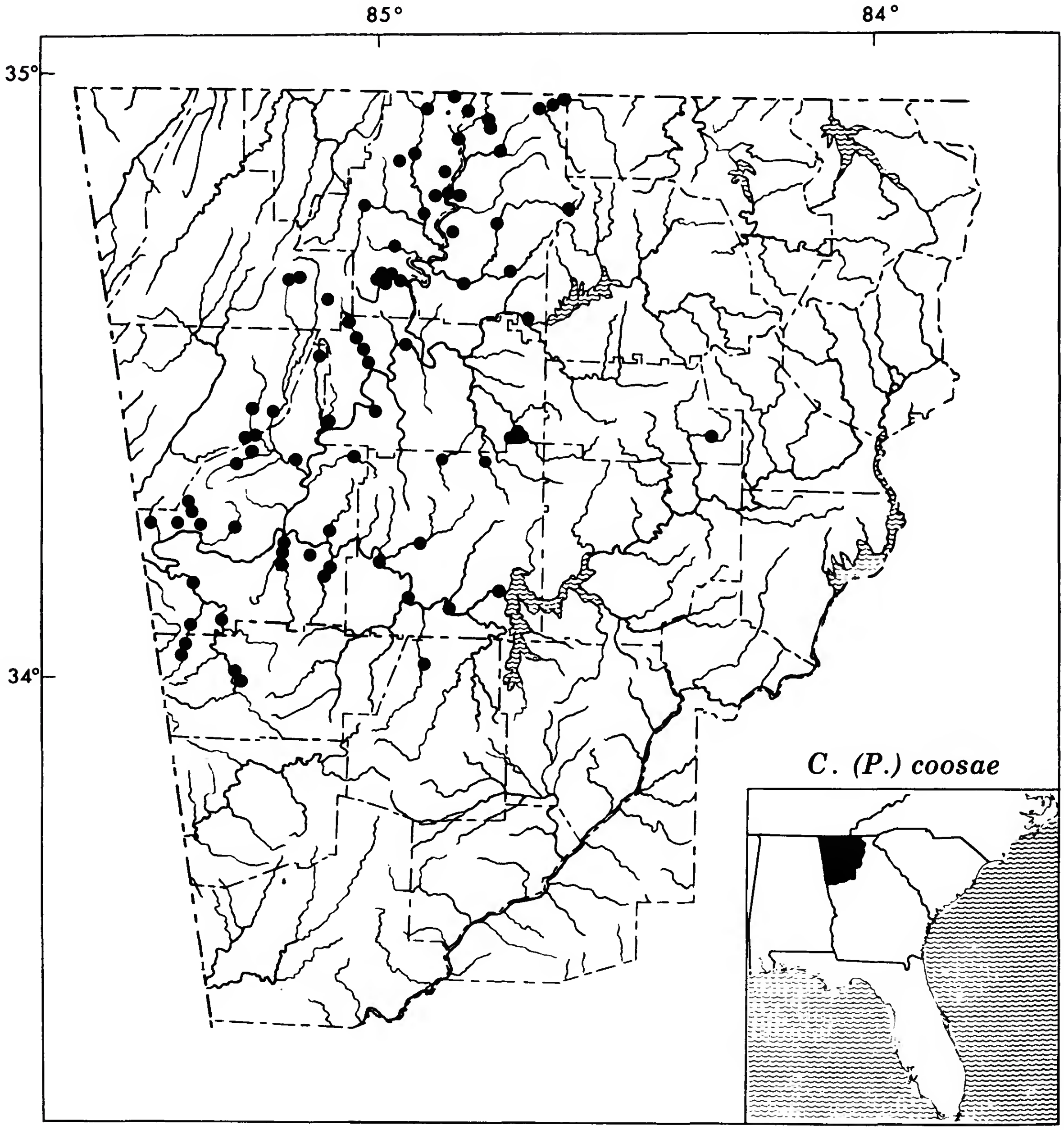


FIGURE 91.—Distribution of *Cambarus (P.) coosae* in Georgia.

Georgia, to Bibb, Calhoun, Cherokee, Chilton, Clay, Coosa, Shelby, and Talladega counties, Alabama.

SPECIMENS EXAMINED.—I have examined 690 specimens from 81 localities (Figure 91) in the following counties in Georgia: Bartow (7), Chattooga (4), Floyd (21), Gordon (10), Murray (16), Paulding (1), Pickens (1), Polk (4), Walker (3), and Whitfield (14); an additional 51 specimens from the Alabama counties listed under "Range" have also been studied.

VARIATIONS.—In several characteristics, this crayfish is one of the more variable of the Georgia species, but none of the variations noted seem to be isolated in a restricted part of the range of the species. In general, the populations in the Conasauga drainage (northernmost tributary of the Coosa) tend to have fewer (sometimes none) setae at the mesial base of the fixed finger of the chela than are usually present in specimens from elsewhere in the Coosa Basin. The following variations frequently occur among specimens from a single locality. The rostral margins may be comparatively thick and rounded or not noticeably thickened and ridge-like; in addition they vary from almost parallel to strongly convergent, and the marginal spines may be sharp and prominent or reduced to tubercles. The suborbital angle ranges from acute to vestigial and in a limited number of older specimens is obsolete. The areola, always densely punctate (six to 13 across narrowest part), comprises from 29.9 to 35.8 percent of the total length of the carapace (39.6 to 45.6 percent of the postorbital carapace length). The chela is strikingly variable in shape, often with a subrectangular palm as opposed to a more rounded one in dorsal aspect, and, as pointed out above, the fingers may or may not bear a prominent tuft of setae; the gap between the fingers generally is greater in larger individuals; the mesial margin of the palm possesses a well-defined row of six to 11 tubercles flanked dorsally by another row usually of one or two fewer, and occasionally a moderately well defined third row flanks the mesial one ventrally; more often, however, only one or a very few tubercles represent the ventral row.

SIZE.—The largest specimen available is a first form male having a carapace length of 44.4 (postorbital carapace length, 35.0) mm; the corresponding lengths of the largest female are 35.7 and 28.2 mm, of the smallest male, form I, 25.2 and 19.6 mm, and of the smallest ovigerous female, 25.2 and 19.9 mm.

LIFE HISTORY NOTES.—First form males have been collected from March to October. No collections containing adults are available from November through February when presumably the major part of the mature male population is in the first form. A number of freshly molted first form males were found in Whitfield County, Georgia, on 11 and 12 October 1969, and of the 29 adult males collected, 23 were in the first form. Collections made in July and August indicate distinctly fewer first form males present than those in the second form, suggesting that few first form males are in populations from late July to early October. Ten ovigerous females were collected in April and one in July.

Listed here are the ovigerous females and the numbers and diameters of the eggs carried by them:

Carapace and postorbital carapace lengths (mm)	*Number of eggs*	*Diameter of eggs (mm)*
25.2 (19.9)	102	shriveled
26.1 (20.5)	88	2.2–2.3
26.7 (20.7)	84	2.2–2.3
27.2 (21.2)	131	2.2–2.4
- (21.4)	100	2.2–2.3
28.1 (21.6)	88	2.2–2.3
28.6 (22.4)	145	2.2–2.3
29.9 (22.5)	137	2.3–2.4
30.2 (23.7)	74	shriveled
32.4 (25.8)	167	2.3–2.4
- (26.9)	160	2.2–2.4

Seasonal Data (Alabama and Georgia)

Sex/stage	*J*	*F*	*M*	*A*	*M*	*J*	*J*	*A*	*S*	*O*	*N*	*D*	*?*
♂I			3	29	9	9	2	1	1	42			6
♂II			6	32	9	9	13	12	17	10			9
♀			5	39	5	13	10	19	9	62	2		11
♂j			9	35	11	9	4	8	70	53	3		1
♀j			4	29	8	3	6	15	23	45			2
♀ ovig				10			1						

ECOLOGICAL NOTES.—Like other members of the subgenus *Puncticambarus*, this crayfish is a stream dweller. In all of the localities in which it has been collected, rocks constitute a component of the substrate, and the crayfish were sheltered beneath them or among debris entrapped by the rocks. The size of the stream seems not to be important, for *C. (P.) coosae* occurs abundantly both in comparatively large rivers and in shallow brooks hardly more than four or five centimeters deep. Their preferred habitat appears to be a rock-littered segment of a permanently flowing stream. In the Conasauga River, which receives heavy industrial pollution, *C. (P.) coosae* (= *Cambarus* species A) was reported (Anonymous, 1970b: 162–164) to be present upstream from the mouth of Coahulla Creek but was absent downstream. When collections were made in the area immediately above the confluence, the oxygen content of the water was 6 mg/l, and at the collection site downstream, it was only 3.6 mg/l. The absence of this crayfish in the latter locality—one in which two other species, *Cambarus (D.) striatus* and *Orconectes spinosus*, were present as they were in other upstream localities (Anonymous, 1969a:C27–C29)—suggests at least a preference on the part of *C. (P.) coosae* for waters in which the oxygen concentration is above 3.6 mg/l (Hobbs and Hall, 1974:204).

RELATIONSHIPS.—*Cambarus (P.) coosae* is allied to *Cambarus (P.) scotti, C. (P.) extraneus, C. (P.) cumberlandensis, C. (P.) georgiae*, and *C. (P.) parrishi*. It differs from the latter in that in *C. (P.) parrishi* the cervical spines are lacking; *C. (P.) georgiae* bears only one row of tubercles on the palm of the chela; the dactyl of the chela of the male of both *C. (P.) extraneus* and *C. (P.) cumberlandensis* is typically more than twice as long as the mesial margin of the palm as opposed to less than twice as long in *C. (P.) coosae*; and it differs from its closest relative *C. (P.) scotti* in possessing marginal spines on the rostrum.

CRAYFISH ASSOCIATES.—*Cambarus (P.) coosae* has been collected with the following crayfishes in Georgia (the number of times is noted in parentheses): *C. (C.) bartonii* (3), *C. (D.) latimanus* (28), *C. (D.) striatus* (18), *C. (H.) manningi* (6), *C. (L.) acanthura* (9), *Orconectes erichsonianus* (1), *O. spinosus* (25), *Procambarus (O.) lophotus* (2), and *P. (Pe.) spiculifer* (14). In Alabama, it has been associated with *Cambarus (D.) latimanus, C. (D.) striatus, C. (L.) acanthura, Orconectes erichsonianus, Procambarus (O.) acutissimus*, and *P. (O.) lophotus*.

ETYMOLOGY.—This crayfish is named for the Coosa River basin, in which it seems to be endemic.

Cambarus (Puncticambarus) scotti, new species

FIGURES 21*b*, 89*b*, 92, 93, 228

Cambarus (Cambarus) montanus acuminatus.—Ortmann, 1931: 110.
Cambarus extraneus.—Anonymous, 1970b:211.
Cambarus (Puncticambarus) sp.—Hart and Hart, 1974:58.

SUMMARY OF LITERATURE.—Ortmann (1931) reported this crayfish as *Cambarus (C.) montanus acuminatus* from the Chattooga River at Trion, Chattooga County. In order to determine what crayfish he might have had, I collected there, and among the specimens obtained, *C. (P.) scotti* was the only species found with which he might have confused Faxon's species. Anonymous (1970b) recorded the presence of this crayfish in Town Creek, at Route S2557, north of LaFayette, in Walker County, as *Cambarus extraneus*. I have examined these specimens and found them to be members of *C. (P.) scotti*. It was also cited by Hart and Hart (1974) as a host of *Dactylocythere falcata*, an entocytherid ostracod, in a stream 5.2 miles south of Summerville on U.S. Highway 27, Chattooga County.

DIAGNOSIS.—Body pigmented, eyes well developed. Rostrum tapering, acuminate, lacking marginal spines or tubercles. Areola 2.9 to 4.0 times as long as broad and constituting 30.6 to 35.5 percent of total length of carapace (40.4 to 44.9 percent of postorbital carapace length) with 7 to 10 punctations across narrowest part. Cervical and branchiostegal spines well developed; hepatic spines absent; suborbital angle strong and acute; postorbital ridges with acute spines or spiniform tubercles. Antennal scale approximately 2.8 times as long as wide, broadest almost at, or distal to, midlength. Chela with 2 well-defined rows of tubercles along mesial surface of palm (mesialmost row of 6 to 10) and with additional ones dorsolateral to rows; lateral margin of chela subcostate with moderate depression at lateral base of fixed finger; width of palm less than 1.3 times length of mesial margin; dactyl less than twice length of palm. Hook on ischium of third pereiopod of first form male overreaching basioischial articulation and opposed by tubercle on basis. First pleopod of first form male with central projection bearing subapical notch, recurved at angle of approximately 125 degrees, and constituting, if straightened, approximately 10 percent of total length of appendage; mesial process moderately inflated, directed caudally at angle only slightly less than that of central projection. Female with annulus ventralis shallowly embedded in sternum and slightly asymmetrical; first pleopod present. Carapace with dark saddle immediately anterior to cervical groove and bordering posterior margin of carapace; abdomen with paired series of L-shaped markings dorsolaterally but lacking series along bases of pleura and transverse dark bands.

Holotypic Male, Form I.—Body subovate, depressed (Figure 92*a,j*). Abdomen narrower than cephalothorax (19.1 and 21.8 mm); greatest width of carapace greater than depth at caudodorsal margin of cervical groove (21.8 and 16.4 mm). Areola 3.7 times as long as broad with 8 punctations across narrowest part, punctations small and crowded; length 35.5 percent of total length of carapace (44.9 percent of postorbital carapace length). Rostrum with strongly convergent margins lacking marginal spines or tubercles; acumen, not distinctly delimited basally, long, its slightly upturned apex almost reaching distal end of antennular peduncle; upper surface of rostrum deeply concave with thickened margins, punctations flanking mesial side of margin prominent, few in distal two-thirds, and those in proximal third coalescing horizontally, forming shallow, irregular transverse grooves. Postorbital ridge of moderate length, grooved dorsolaterally, and with acute corneous-tipped tubercle. Suborbital angle acute with distinct spine at apex. Cervical spine very strong. Carapace punctate dorsally and tuberculate laterally.

Abdomen subequal in length to carapace; pleura of moderate length, truncate ventrally, and angular caudoventrally. Cephalic section of telson with 2 spines in each caudolateral corner. Proximal podomere of uropod with distal spine on each lobe; mesial ramus of uropod with weak submedian ridge terminating in short premarginal spine. Dorsal surface of uropods and telson scabrous.

Cephalomedian lobe of epistome (Figure 92*i*) broadly rounded with margins elevated ventrally and with shallow submedian emargination cephalically; fovea well defined; epistomal zygoma broadly arched. Ventral surface of proximal podomere of antennule with prominent spine slightly distal to midlength. Antennal peduncle with spine on lateral surface of basis and on ventral surface of ischium; flagellum broken in holotype but reaching to fifth abdominal tergum in other specimens; antennal scale (Figure 92*g*) about 2.8 times as long as broad, broadest in vicinity of midlength, its mesial margin almost parallel to lateral margin at and somewhat distal to midlength; distal spine reaching level of apex of acumen. Ventral surface of ischium of third maxilliped with mesial half bearing clusters of long stiff setae and with submarginal lateral row of much smaller ones; distolateral angle subacute.

Right chela (Figure 92*l*) about 2.5 times as long as broad and mesial margin of palm occupying about one-third of its total length. Mesial margin of palm with row of 9 tubercles flanked dorsolaterally by second row of 7, with few additional ones between rows and laterally; most of palm conspicuously punctate. Both fingers with poorly defined longitudinal ridges dorsally and ventrally, flanked by setiferous punctations. Fixed finger weakly costate laterally; opposable margin with row of 13 tubercles (fifth from base largest) and single large tubercle on lower level at base of distal two-fifths; band of minute denticles between and distal to tubercles in distal half of finger. Opposable margin of dactyl with row of 12 tubercles (fifth from base largest), minute denticles dispersed as on fixed finger; mesial margin with row of 6 or 7 subsquamous tubercles along proximal half of finger (tubercles progressively smaller and more depressed distally) followed distally by setiferous punctations and flanked proximally by other tubercles.

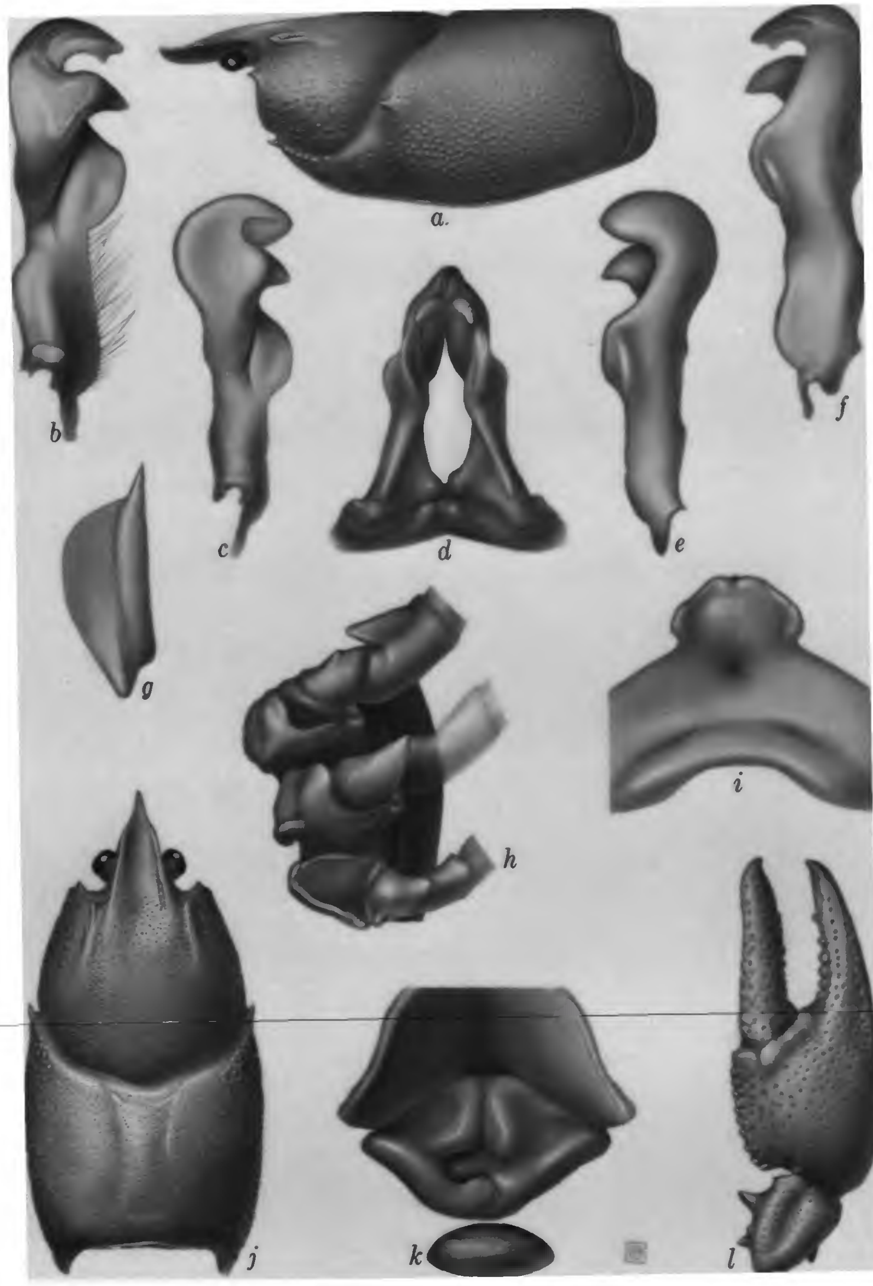


FIGURE 92.—*Cambarus* (*Puncticambarus*) *scotti* (all from holotype except *c*, *e*, from morphotype, and *k*, from allotype): *a*, lateral view of carapace; *b*, *c*, mesial view of first pleopod; *d*, caudal view of first pleopods; *e*, *f*, lateral view of first pleopod; *g*, antennal scale; *h*, basal podomeres of third, fourth, and fifth pereiopods; *i*, epistome; *j*, dorsal view of carapace; *k*, annulus ventralis; *l*, dorsal view of distal podomeres of cheliped.

Carpus of cheliped punctate with prominent furrow dorsally; mesial surface with large conical tubercle and smaller one proximal to it; ventrodistal margin with massive tubercle at lateral articular knob and another submedian one. Merus sparsely punctate; dorsal surface with 2 preapical spiniform tubercles, ventromesial row of 8 progressively more spiniform ones distally, 2 large tubercles representing ventrolateral row and small spiniform one on distolateral extremity. Ventromesial margin of ischium with row of 4 tubercles.

Ischium of third pereiopod with simple hook extending proximally over basioischial articulation (Figure 92*h*) and opposed by tubercle on basis. Coxa of fourth pereiopod with obliquely vertically disposed caudomesial boss; that of fifth lacking boss, its ventral membrane with few scattered setae.

First pleopods (Figure 92*b,d,f*) with slight gap between bases and reaching coxae of third pereiopods; both terminal elements recurved caudally at angle of about 125 degrees to main shaft of appendage. Mesial process somewhat inflated, tapering, and directed caudolaterally. Central projection short, not tapering, and bearing distinct subapical notch.

ALLOTYPIC FEMALE.—Differing from holotype, except in secondary sexual characters, in following respects: cephalomedian lobe of epistome lacking cephalomedian emargination; mesial surface of palm of chela with more lateral row of 10 tubercles; opposable margin of fixed finger with 11 or 10 (left) tubercles, tubercle on lower level absent on right chela; opposable margin of dactyl with 10 or 11 (left) tubercles; merus of cheliped with ventrolateral row of 4 tubercles and ventromesial one of 9 or 8 (left). (See "Measurements.")

Annulus ventralis (Figure 92*k*) about 1.7 times as broad as long, situated rather shallowly in sternum; cephalic area traversed by submedian furrow, sinus originating caudodextrally in furrow at about midlength of annulus, extending dextrally and slightly caudally; after making hairpin turn, returning to median line, there making arc crossing line and turning caudally; caudal extremity of sinus situated slightly sinistral to median line on caudal wall. Postannular sclerite subspindle shaped and about one-half as wide as annulus. First pleopod reaching cephalic margin of annulus when abdomen flexed.

MORPHOTYPIC MALE, FORM II.—Differing from holotype in following respects: all spines on carapace and chelipeds much more distinctly acute than in either holotype or allotype, and cervical spines procurved; mesial margin of palm of chela with more lateral row consisting of only 5 tubercles; fixed finger with row of 9 tubercles and that present on lower level in holotype absent; opposable margin of dactyl with row of 12 tubercles; mesial surface of carpus lacking small proximal tubercle but with bispinose major one, ventral surface with additional tubercle proximomesial to large submedian distal one; merus of cheliped with 3 tubercles in ventrolateral row and 12 in ventromesial one on left cheliped; ischium with row of 3. Hook on ischium of third pereiopod much reduced, not reaching basioischial articulation but tubercle on basis as in holotype. (See "Measurements.")

First pleopod (Figure 92*c,e*) with much broader central projection disposed at angle of approximately 90 degrees, lacking even trace of subapical notch.

COLOR NOTES (Figure 89*b*).—(Based on holotype which somewhat encrusted, obscuring considerable details). Carapace largely pinkish tan dorsally fading to cream ventrally; rostral margins and postorbital ridges vermilion; mandibular adductor region with reticulate dark pattern fusing with broad dark brown band covering and lying cephalic to cervical groove; caudal margin with narrow transverse band expanding onto caudal part of branchiostegites. First abdominal tergum dark brown, remaining ones much lighter tan with caudal edge dark reddish brown. Chela with olive suffusion dorsally, extending onto basal half of fingers; distal half of fingers pale orange cream. All tubercles bright orange to vermilion; carpus and distal half of merus with coloration similar to dorsum of carapace; remaining pereiopods mostly pale with orange splotches on articular areas.

Measurements (mm)

	Holotype	*Allotype*	*Morphotype*
Carapace			
Height	16.4	17.9	10.5
Width	21.8	23.8	13.9
Entire length	40.9	45.0	27.1
Postorbital length	32.3	35.3	20.7
Areola			
Width	3.9	4.5	2.5
Length	14.5	15.3	8.8
Rostrum			
Width	6.0	6.1	4.0
Length	10.2	11.2	7.3
Chela			
Length of mesial margin of palm	15.0	12.4	6.0
Width of palm	17.1	15.1	7.3
Length of lateral margin	42.3	35.3	18.7
Length of dactyl	23.6	20.5	11.1
Abdomen			
Width	19.1	23.9	12.3
Length	41.0	47.0	27.5

TYPES.—The holotypic male, form I, allotypic female, and morphotypic male, form II (numbers 146479, 146480, and 146481, respectively), are deposited in the National Museum of Natural History, Smithsonian Institution, as are the paratypes consisting of the following: 19♂I, 9♂II, 14♀, 31j♂, 24j♀, and 4 ovigerous ♀. The juvenile specimens from "Etowah River, Georgia," are excluded from the type series as are the specimens from Calhoun and Saint Clair counties, Alabama.

TYPE-LOCALITY.—Clarks Creek, 1 mile north of Holland, Chattooga County, Georgia, on State Route 100. There the creek, some 3 meters wide and as much as 0.5 meter deep, flows swiftly over a rock-littered bed. The only macroscopic vegetation in the stream was a moss growing on the rocks. Overhanging and nearby shrubs and trees included *Pinus* sp., *Cornus florida*, *Alnus rugosa*, and *Salix nigra*; a luxuriant growth of *Lonicera japonica* grew between and partially obscured some of the shrubs. Associated with this crayfish were *Orconectes erichsonianus* and *Cambarus (D.) latimanus*.

RANGE.—The typical form of this crayfish is confined to the Chattooga River basin in Chattooga and Walker counties, Georgia, and Cherokee County, Alabama. (See "Remarks.")

SPECIMENS EXAMINED.—I have examined a total of 176 specimens (127 from Georgia and 49 from Alabama) from the following localities. GEORGIA. *Chattooga County:* (1) type-locality, 2♂I, 1 May 1967, T. Unestam, HHH, collectors; 1♂I, 2♀, 3j♂, 1j♀, 1 ovig ♀, 22 Apr 1968, E. T. Hall, Jr., HHH; (2) Lyerly Creek near S city limits of Lyerly on St Rte 114, 7♂I, 3♂II, 2♀, 6j♂, 3j♀, 1 ovig ♀, 19 Apr 1954, J. E. Pugh, S. R. Telford, HHH; (3) Chattooga River at Summerville, 1♀, date and collector unknown; (4) Chappel Creek, 1 mi S of Walker Co line on US Hwy 27, 1♂I, 1♀, 1j♀, 1 ovig ♀, 22 Apr 1968, ETH, HHH; (5) Chattooga River 8 m downstream from confluence with Spring Creek, 1♂II, 1j♂, 12 Sep 1974, B. A. Caldwell; (6) Cane Creek at Welcome Hill Rd at Trion, 1♂II, 11 Sep 1974, BAC; (7) Perennial Spring Run 0.9 airmi WNW of Berrytown, 4♂II, 1♀, 25 Jul 1974, J. McCaleb; (8) Chattooga River just NW of Trion on unnumbered rd, 4♂I, 1♂II, 3♀, 21 Oct 1976, T. A. English, Jr., HHH. *Walker County:* (9) Cane Creek about 6 mi S of Lafayette, 1j♂, 12 Nov 1947, E. A. Lachner, P. S. Handwerk; 2♂I, 1♂II, 4♀, 25 Mar 1961, P. C. Holt; 2♂I, 2♂II, 2♀, 4j♂, 2j♀, 16 Apr 1962, J. F. Fitzpatrick, Jr., HHH; (10) Cane Creek at St Rte 151, 8♂I, 2♂II, 5♀, 13j♂, 3j♀, 8 Oct 1977, W. D. Kennedy, HHH; 3♂II, 2♀, 9 Oct 1977, WDK, HHH; (11) Town Creek about 3 mi N of Lafayette, 1♀, 1j♂, 6j♀, 14 Aug 1969, ETH; (12) Duck Creek 14 m above confluence with Chattooga Creek, 1♂I, 1j♂, 4 Sep 1974, BAC; (13) Town Creek at Rte S2557, 4j♂, 1j♀, 4 Sep 1974, BAC. *County Unknown:* (14) "Etowah River, Georgia," 1j♂, 2j♀, date?, D. S. Jordan. ALABAMA. *Cherokee County:* (15) creek 3.0 mi N of Gaylesville on St Rte 75, 5♂I, 2♂II, 1♀, 15j♂, 10j♀, 1 ovig ♀, 19 Apr 1954, JEP, SRT, HHH; (16) Terrapin Creek 5.9 mi N of Piedmont on St Rte 9, 1♀, 17 Sep 1969, C. R. Gilbert; (17) Terrapin Creek, "Coloma," 1♂II, date and collector unknown; (18) Chattooga River, 1 mi N of Cedar Bluff, 1j♀, date and collector unknown. (See "Remarks.")

VARIATIONS.—In most respects the available specimens from the Chattooga Basin in both Alabama and Georgia are remarkably uniform. Some differences occur in development of tubercles; particularly noticeable are the comparatively conspicuous ones on the lateral surface of the carapace in the larger specimens as opposed to the comparatively smooth branchiostegal and hepatic regions of the smaller individuals. The differences in the relative width of the areola are at least partially reflected in the number (7 to 10)

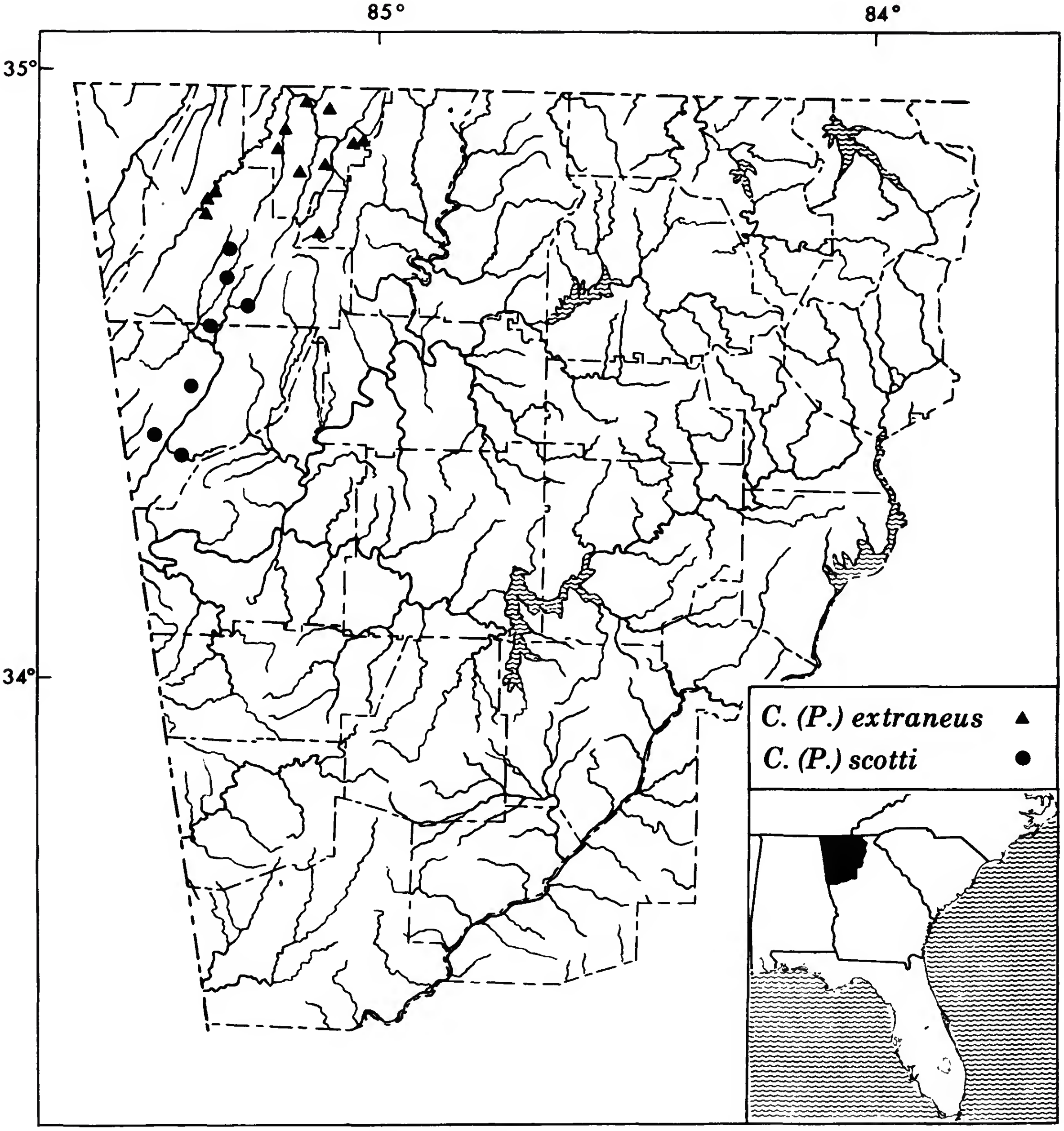


FIGURE 93.—Distribution of *Cambarus* (*P.*) *extraneus* and *C.* (*P.*) *scotti* in Georgia.

of punctations arranged across the narrowest part. On the cheliped, the number of tubercles borne by the ischium ranges from two to four; on the dorsodistal part of the merus there are one or two tubercles and ventrally the mesial row comprises seven to 12 and the lateral one, two to four. Rarely, the small proximal tubercle is lacking on the mesial surface of the carpus, and occasionally accessory small ones occur dorsomesially and ventromesially. The row of tubercles on the mesial margin of the palm consists of six to 10, and that flanking it dorsolaterally is decidedly variable, sometimes so irregular and intermingling with other tubercles that the row is difficult to delineate. In larger, presumably older specimens, the longitudinal ridges on the fingers are not nearly so clearly defined as in the young adults. (See "Diagnosis" and "Measurements.")

SIZE.—The largest specimen available is the allotypic female, having a carapace length of 45.0 (postorbital carapace length, 35.3) mm. The largest and smallest first form males have corresponding lengths of 41.8 (32.1) and 24.5 (18.6) mm. The corresponding lengths of the smallest ovigerous female are 30.9 (24.3) mm.

LIFE HISTORY NOTES.—First form males have been collected in March, April, May, September, and October, and four ovigerous females were found in April. The number of eggs carried by these females are as follows:

Carapace and postorbital carapace lengths (mm)	*Number of eggs*	*Diameter of eggs (mm)*
30.9 (24.3)	145	2.1–2.2
31.9 (24.5)	110	2.1–2.2
34.5 (27.5)	231	2.2–2.3
39.9 (31.7)	310	2.1–2.2

Seasonal Data (Alabama and Georgia)

Sex/stage	*J*	*F*	*M*	*A*	*M*	*J*	*J*	*A*	*S*	*O*	*N*	*D*	*?*
♂I			2	19	4				1	12			
♂II			1	8			4		3	6			1
♀			4	9			1	1		10			2
♂j				30	1			2	7	13	1		2
♀j				17	1			6	1	3			2
♀ ovig				4									

ECOLOGICAL NOTES.—In the Chattooga watershed, this crayfish seems to be vicariating for its stream-dwelling relative, *Cambarus (P.) coosae*, which has a much broader range in the Coosa Basin. Its habitat differs in no obvious respect from that of the latter and other allied species, for it occurs comparatively abundantly in areas of the streams where there is rather swift water flowing over a rock-littered bed. There it takes cover under the rocks, in tree litter, or among other debris found in the stream.

RELATIONSHIPS.—*Cambarus (P.) scotti* is closely allied to *C. (P.) coosae*. The densely punctate and similarly shaped chela and the markedly similar color pattern suggest a closer affinity between them than exists between either and the other members of the subgenus. It may be distinguished from *C. (P.) coosae* by the long acuminate rostrum that is devoid of marginal spines or tubercles.

CRAYFISH ASSOCIATES.—*Cambarus (P.) scotti* has been collected with the following species in Georgia (the number of times they have been found together is noted in parentheses): *Cambarus (D.) latimanus* (6), *C. (D.) striatus* (3), *C. (H.) longirostris* (1, introduced?), *Orconectes erichsonianus* (10), *O. spinosus* (1), and *Procambarus (O.) lophotus* (3). In Alabama, it has been found with *C. (L.) acanthura*.

ETYMOLOGY.—This crayfish is named in honor of my friend Donald C. Scott, who has contributed greatly to our knowledge of not only the fishes of Georgia, but also, through saving the crayfishes entrapped in his seine and donating them to me for study, has added materially to this investigation of the crayfishes of the state.

REMARKS.—Five lots of specimens in the collection of the National Museum of Natural History from the Coosa Basin in Calhoun and Saint Clair counties, Alabama, are tentatively assigned to this species. They resemble it closely but exhibit the following features that are not shared by specimens comprising the type series, which were collected from the Chattooga Basin: (1) chela with fingers distinctly gaping and bearing conspicuous setal tuft at opposable base of finger; (2) second row of tubercles on mesial surface of palm of chela rather obscure; and (3) longitudinal ridges on fingers almost obsolete. These three characteristics are ones usually associated with members of the subgenus *Hiaticambarus*. In other respects including color pattern, these specimens are indistinguishable from *C. (P.) scotti*. Nevertheless, had I examined them without having seen representatives of the species here described as *C. (P.) scotti*, I should have assigned them to the subgenus *Hiaticambarus* and suggested a close affinity with *C. (H.) girardianus*, at least some members of which are similarly colored.

These specimens were collected from the following localities in Alabama: *Calhoun County*: (1) Choccolocco Creek E of St Rte 9 on farm road just N of White Plains, 1♂I, 30 Apr 1970, P. L. Holcomb, HHH, collectors; (2) Terrapin Creek, 4.6 mi S of Piedmont on St Rte 9, 1♂I, 1♀, 2j♂, 30 Apr 1970, PLH, HHH; (3) trib to Terrapin Creek 2.5 mi NW of Piedmont on US Hwy 278, 1♀, 29 Apr 1970, PLH, HHH; (4) Choccolocco Creek, Oxford, 1♀, date and collector unknown. *Saint Clair County:* (5) stream 4.1 mi E of Blount Co line on US Hwy 231, 2♂I, 1j♂, 1j♀, 1 May 1968, HHH.

The extraneus Group

Cambarus (Puncticambarus) chaugaensis Prins and Hobbs

FIGURES 21*h*, 87, 89*c*, 94, 222

Cambarus (Puncticambarus) species E.—Hobbs, 1969a:102, 135, fig. 7.
Cambarus (Puncticambarus) chaugaensis Prins and Hobbs, 1972: 413–419, fig. 1.—Hobbs, 1974b:21, fig. 75.

SUMMARY OF LITERATURE.—The above is believed to be a complete list of the published references to this crayfish. Hobbs (1969a), in reviewing the composition of the genus *Cambarus*, pointed out its presence in the upper Savannah River Basin, and, together with Prins (1972), described the species from 18 localities in Oconee County, South Carolina. It was included by Hobbs (1974b) in his checklist of the crayfishes of North and Middle America. There are no published records of its occurrence in Georgia.

DIAGNOSIS.—

Body pigmented, eyes moderately large and well developed. Rostrum with gently convergent margins, lacking marginal spines or tubercles. Areola 2.2 to 3.2 times longer than wide and comprising 29.3 to 35.5 (only one individual more than 34.8) percent of entire length of carapace with 5 to 8 punctations across narrowest part. Cervical spines comparatively small, only slightly larger than adjacent tubercles. Suborbital angle moderately strong, frequently acute. Postorbital ridges terminating cephalically bluntly in small subspiniform tubercles. Antennal scale approximately 2.5 times longer than broad, broadest slightly distal to midlength. Chela with width of palm greater than 1.3 times length of mesial margin, with 2 rows of tubercles along mesial surface of palm, mesial row consisting of 5 to 7 tubercles; distolateral margin of palm and fixed finger costate, and both fingers with well-defined longitudinal ridges on upper surface. First pleopod of first form male with moderately long, corneous central projection recurved caudally at angle of approximately 90 degrees, slightly tapering, and with subapical notch; mesial process noncorneous, somewhat inflated, with slenderer apical portion directed caudolaterally. [Female with] annulus ventralis slightly movable, shallowly embedded in sternum, subsymmetrical, and comparatively weakly sculptured; [first pleopod present. Carapace and abdomen mottled, latter with linear series of irregular dark splotches dorsolaterally and on pleura.] (Prins and Hobbs, 1972:413).

COLOR NOTES (Figure 89*c*).—

Carapace olive green dorsally fading to light green lateroventrally, and mottled (conspicuously so dorsally) with dark olive brown to black markings; lower half of hepatic area and branchiostegites with large irregular splotches, those on caudodorsal surface of branchiostegites forming base of irregular and broken dorsolateral longitudinal stripes on abdomen; lateral surfaces of branchiostegites with splotches loosely united to form second band continuous with that extending along bases of pleura of abdomen. Dorsal surfaces of podomeres distal to ischia of chelipeds and other pereiopods bearing coloration similar to that on body proper; carpus of cheliped with prominent proximo- and distolateral splotches as well as one at base of major mesial spine and another on mesiodistal angle; tips of fingers of chelae yellowish to red; ventral surfaces of pereiopods and sternum cream colored, and antennae reddish brown (Prins and Hobbs, 1972:418).

TYPES.—Holotype, allotype, and morphotype, USNM 131926, 131927, 131928 (♂I, ♀, ♂II); paratypes, USNM.

TYPE-LOCALITY.—Chauga River at Cassidy Bridge (off County Road 290), Oconee County, South Carolina.

RANGE.—Tributaries of the Savannah River in Oconee County, South Carolina, and in Rabun County, Georgia.

GEORGIA SPECIMENS EXAMINED.—*Rabun County:* Gold Mine Creek, trib to Warwoman Creek, about 9.5 airmi E of Clayton, 3♂II, 4j♂, 3j♀, 15 May 1952, B. Martof, collector.

VARIATIONS.—Variations noted among the few specimens available from Georgia are only slight. The mesial surface of the palm of the chela bears a row of six or seven tubercles flanked by a

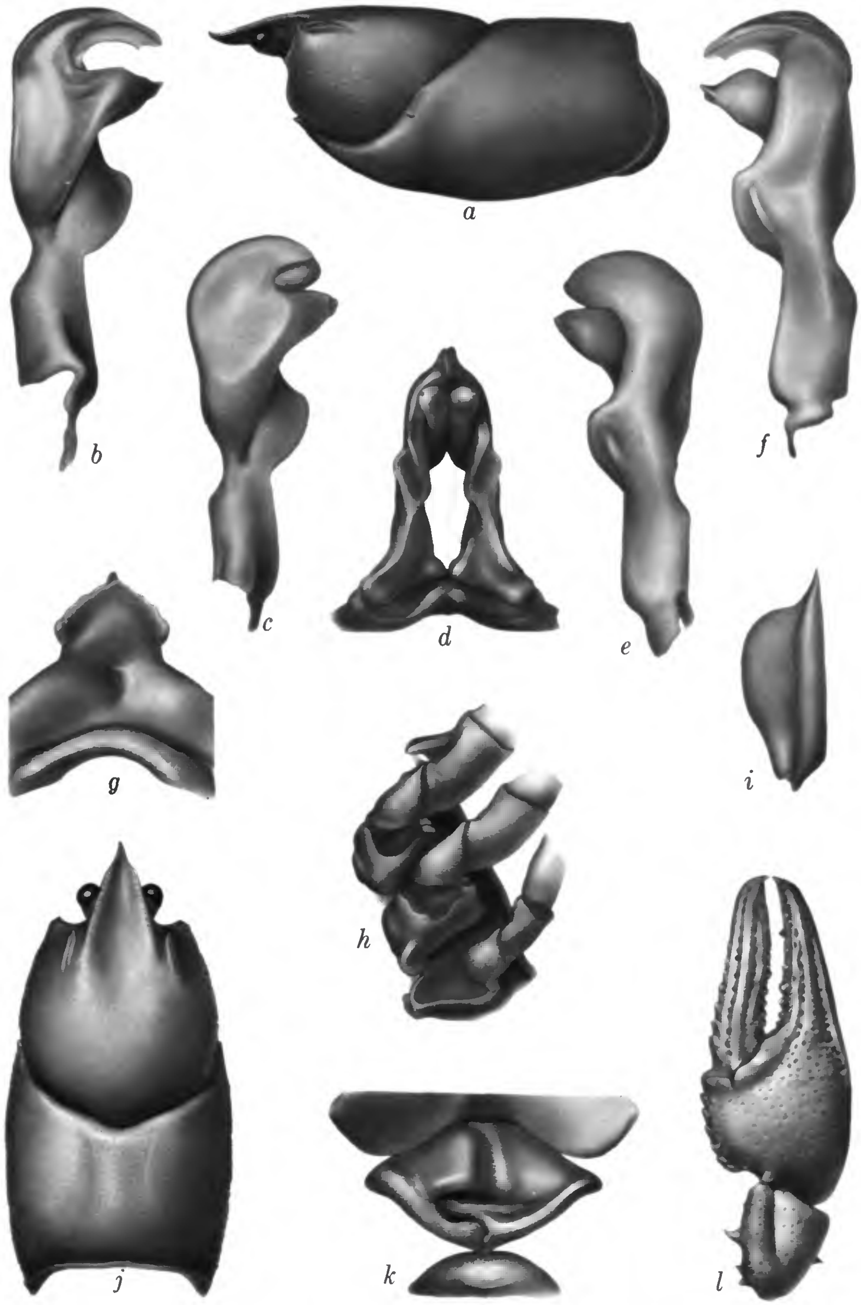


FIGURE 94.—*Cambarus (Puncticambarus) chaugaensis* (*a*, *g*, *h*, *j*, *l*, from holotype; *b*, *d*, *f*, *i*, from paratopotypic male, form I; *c*, *e*, from morphotype; and *k*, from allotype): *a*, lateral view of carapace; *b*, *c*, mesial view of first pleopod; *d*, caudal view of first pleopods; *e*, *f*, lateral view of first pleopod; *g*, epistome; *h*, proximal podomeres of third, fourth, and fifth pereiopods; *i*, antennal scale; *j*, dorsal view of carapace; *k*, annulus ventralis; *l*, dorsal view of distal podomeres of cheliped. (From Prins and Hobbs, 1972.)

dorsolateral row of two to four; the mesial surface of the carpus always bears a large spikelike tubercle, and in most of the specimens there is a single one proximal to it; the ventral surface of the merus has a lateral row of two or three tubercles and a mesial one of seven to 10. The aerola constitutes from 33.6 to 34.5 percent of the total length of the carapace (41.4 to 42.0 percent of the postorbital carapace length) and ranges from 2.8 to 3.1 times as long as broad with six punctations across the narrowest part.

SIZE.—The largest of the Georgia specimens, a second form male, has a carapace length of 38.1 (postorbital carapace length, 31.4) mm. Prins and Hobbs (1972:418) reported a first form male having a carapace length of 38.9 and that of the smallest first form male 25.1 mm. Their largest and smallest ovigerous females had comparable lengths of 34.7 and 25.2 mm.

LIFE HISTORY NOTES.—The only data available for the species in Georgia suggest that by 15 May the adult males have returned to the second form. No first form males or ovigerous females have been collected in the state. Prins and Hobbs (1972:419) indicated that first form males had been found in March, May, July, October, and November, and 11 ovigerous females were collected in April and May. They also stated: "On the basis of the size ranges in the specimens examined, it seems probable that *C. chaugaensis* has a life cycle virtually identical to that outlined by Smart (1962) for *Cambarus longulus* Girard."

ECOLOGICAL NOTES.—Insofar as is known this crayfish is confined to lotic habitats with a rocky substrate. There are no ecological data accompanying the only specimens that have been found in Georgia.

CRAYFISH ASSOCIATES.—In the single collection of *C. (P.) chaugaensis* from Georgia, specimens of *C. (J.) asperimanus* were also present.

REMARKS.—Repeated endeavors by me to collect this species in the state have resulted in failure. Some 20 collections have been made in tributaries of Warwoman Creek and other feeder streams to the Chattooga River (Savannah Basin) in Rabun County, where I found *Cambarus (C.) bartonii* and *C. (J.) asperimanus*. Because of the relative inaccessibility of Gold Mine Creek, I have not been able to return to the locality where Martof obtained the only specimens known from Georgia. There is every reason to suspect its presence in a number of lower tributaries of the Chattooga River, and I am confident that in Georgia it is not confined to Gold Mine Creek.

Cambarus (Puncticambarus) extraneus Hagen

FIGURES 21*f*, 89*g*, 93, 95, 224

Cambarus extraneus Hagen, 1870:32, 57, 58, 73–74*, 98*, 100*, 105, 107, pl. I: figs. 88, 89, pl. III: fig. 156.—Brocchi, 1875:27.—Faxon, 1884:119, 145* [in part]; 1885a:59, 79, (84–85, 160, 170, 174, 178, 179)* [in part]; 1885b:359*; 1914:422*.—Underwood, 1886:368* [in part].—Hay, 1899b:959, 966; 1902a:436.—Ortmann, 1902:277; 1918: 849* [in part].—Harris, 1903a:59*, 97*, 146, 152*, 154 (?), 156, 159, 161 [in part]; 1903b:602.—Newcombe, 1929: 279*, 280 [in part].—Fleming, 1938:299, 301, 302*.—Hobbs, 1956c:115, 119, 120* [in part]; 1959:896* [in part]; 1965:272; 1968b:K-15*, fig. 32g; 1976, fig. 1*d*.—Hobbs and Barr, 1960:14–15, 23.—Hobbs, Holt, and Walton, 1967:66.—Bouchard, 1972:17, 31, 43, 58, 71, 86, 91, 104, 106; 1976a:573; 1976b:585, 586.—Wharton, 1978:220*.

Cambarus extraneous.—Adams, 1901:849 [in part; erroneous spelling].

Cambarus extranus.—Steele, 1902:7 [erroneous spelling].

Cambarus (Bartonius) extraneus.—Ortmann, 1905a:116, 118, 120, 121*, 129, 130 [in part].—Stiles and Hassall, 1927: 219*.—Creaser, 1931a:6 [by implication].

Cambarus (Cambarus) extraneus.—Fowler, 1912:341 [by implication].—Ortmann, 1931:95, 96, 97*–101*, 129 [in part].—Bouchard, 1972:103; 1976a:572.

Cambarus extranius.—Unestam, 1969:203*, tab. 1* [erroneous spelling].

Cambarus (Puncticambarus) extraneus.—Hobbs, 1969a:101, 102, 129, 130*, 133*, 135*, 141, figs. 1b, 7*, 13b, 14b, 17m; 1972b:128*, 146*, figs. 90b, 111c; 1974a:11; 1974b:20, 21*, fig. 71.—Hobbs and Bouchard, 1973:41*, 49, 50.—Bouchard, 1972:58–59*; 1976a:572, 575; 1976b:595–596*.

The above is believed to be a complete list of all published references to this crayfish. Citations mentioning Georgia are noted by asterisks.

SUMMARY OF LITERATURE.—Although the name *Cambarus extraneus* has appeared frequently in the literature since this crayfish was described, little is known concerning the species. Confusion relating to it began with the label accompanying the syntypes, "Tennessee River, Georgia." In describing the species, Hagen (1870:74) pointed out that "no portion of the Tennessee River flows through Georgia," and cited the locality "Tennessee River, (near the borders of?) Georgia." Faxon (1884:145), by identifying the *extraneus*-like crayfish from the "Etowah River, Rome, Georgia" as Hagen's species, set the stage for repeated misidentifications for more than three-quarters of a century. The erroneous report of the occurrence of this crayfish in the Santee Basin, South Carolina (Faxon, 1885a:178, apparently an error, for no specimens were cited by him earlier or in subsequent publications) and the record noted by him (1898:650) from the "Big Cahawba River, Alabama," led to additional misunderstandings of the species. (Faxon's specimens have decayed and been discarded, but inasmuch as *C. (P.) coosae* is known to occur in the Cahaba River in Shelby County, in all probability his specimens belonged to that species.) Further ambiguity occurred when Ortmann (1905b:310–311) reported *C. extraneus* from the Rockcastle River, Kentucky, a record based on a crayfish that was recently described by Hobbs and Bouchard (1973:42) as *Cambarus (P.) cumberlandensis*. Ortmann's (1931:97–105) treatment of the species was rather generally accepted until Hobbs (1969a) suggested that four species were represented within the assemblage that Ortmann had assigned to *C. extraneus*. One of these, *C. girardianus*, was assigned to the subgenus *Hiaticambarus* and the others to the subgenus *Puncticambarus*: *C. extraneus* (in the South Chickamauga Creek basin), *C. (P.)* species A (= *C. (P.) cumberlandensis* in the Cumberland and Green river basins in Tennessee and Kentucky), and *C. (P.)* species B (= *C. (P.) coosae* in the Coosa Basin in Alabama and Georgia). All additional specific localities cited for the species in the literature subsequent to Hagen (1870), except "South Chickamauga Creek" (first cited by Hobbs and Bouchard, 1973), are based on misidentifications of one or more of the species just mentioned. The references not discussed here involve extractions from Hagen, Faxon, and/or Ortmann, contain discussions of relationships, and/or refer to remarks on its distribution.

Diagnosis.—Body pigmented, eyes well developed. Rostrum with convergent margins, not thickened, and bearing marginal spines or tubercles. Areola 2.7 to 3.8 times as long as wide and comprising 30.3 to 33.4 percent of entire length of carapace (39.2 to 43.9 percent of postorbital carapace length) and bearing 8 to 10 punctations across narrowest part. Cervical spines weak to moderately strong. Suborbital angle basically obtuse but often with short acute tip. Postorbital ridge terminating cephalically in spine or acute tubercle. Antennal scale approximately 3 times as long as broad, with mesial and lateral margins subparallel near and at midlength; distomesial margin strongly sloping. Chela with almost entire dorsal surface studded with squamous tubercles and bearing 2 or 3 rows of tubercles along mesial margin of palm, mesialmost row consisting of 6 to 9, usually 8; lateral margin of fixed finger and distal third of palm strongly costate; both fingers with well-defined longitudinal ridges dorsally; fixed finger usually distinctly impressed at base; disregarding regenerated chelae, dactyl of first form male approximately twice as long as mesial margin of palm. Basis of third pereiopod with tubercle opposing hook on ischium. First pleopod of first form male with short terminal elements: corneous central projection not tapering distally, recurved at approximately 125 degrees to main shaft of appendage, bearing prominent subapical notch; and mesial process inflated, tapering, rounded to acute distally, and directed caudolaterally at angle of about 90 degrees to main shaft. Female with annulus ventralis shallowly embedded in sternum and slightly asymmetrical; first pleopod present. Carapace with narrow dark saddles anterior to cervical groove and on posterior margin, horns poorly developed, and abdomen with paired, longitudinal dark stripes dorsolaterally and along bases of pleura.

Color Notes (Figure 89*g*).—Basic coloration occurring in two phases differing only in color; tan with brown markings and olive with black markings. A description of the latter follows.

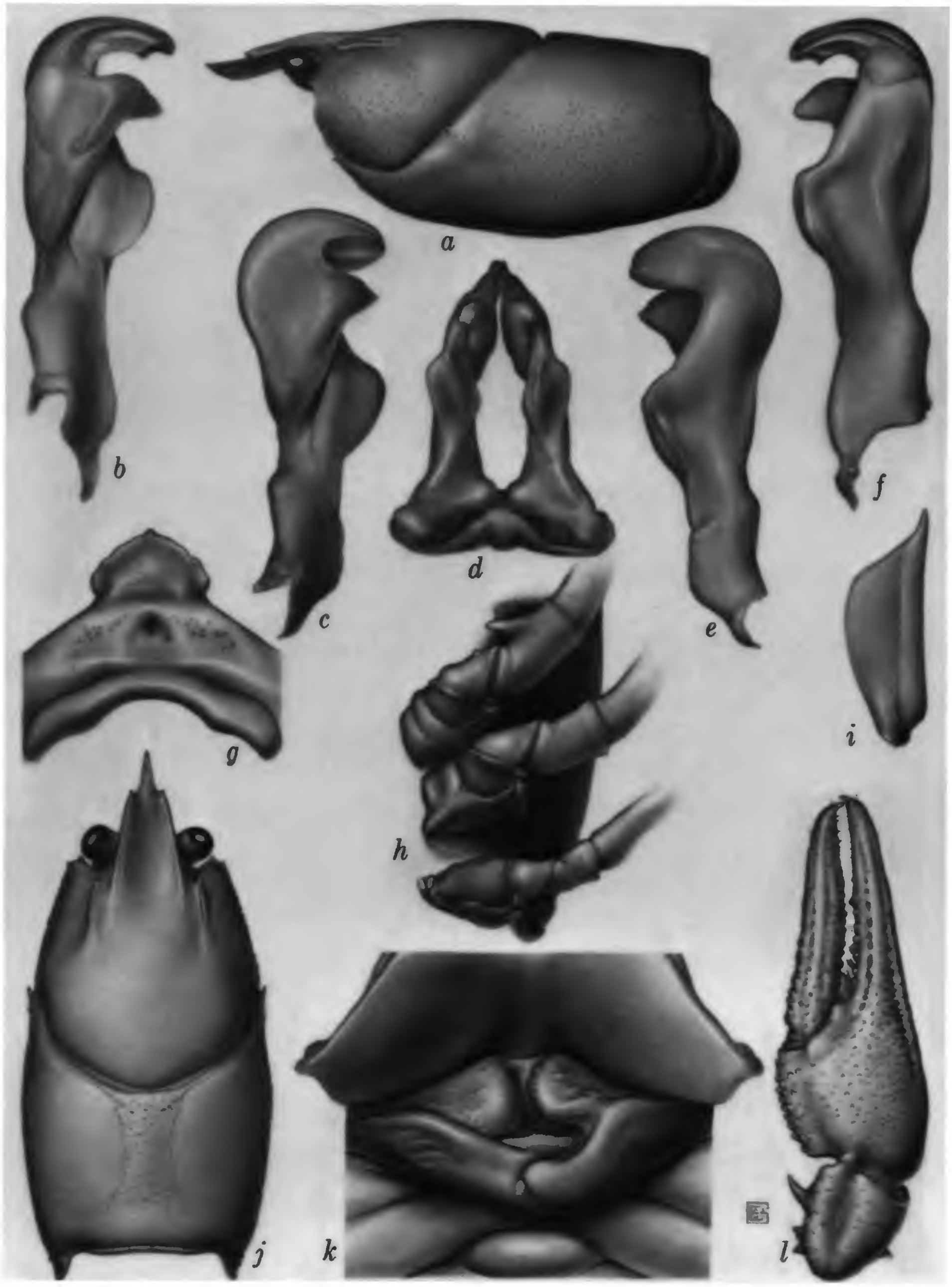


FIGURE 95.—*Cambarus (Puncticambarus) extraneus* from Little Tiger Creek 2.5 mi W of Varnell on St Rte 2, Catoosa Co (all from male, form I, except *c*, *e*, from male, form II, and *k*, from female): *a*, lateral view of carapace; *b*, *c*, mesial view of first pleopod; *d*, caudal view of first pleopods; *e*, *f*, lateral view of first pleopod; *g*, epistome; *h*, basal podomeres of third, fourth, and fifth pereiopods; *i*, antennal scale; *j*, dorsal view of carapace; *k*, annulus ventralis; *l*, dorsal view of distal podomeres of cheliped.

Ground color of carapace olive with slightly darker reticulate overlay; black saddle-like marking over gastric area immediately cephalic to cervical groove, its cephalolateral extensions becoming reticulate and dilute; saddle-like black mark also present on caudal part of carapace, median segment of saddle reduced to transverse line and ventrolateral portions broadened, somewhat paralleling horns of saddle on gastric region. Margins of rostrum and postorbital ridges dark orange basally, becoming almost black toward cephalic extremities. Abdomen with paired, longitudinal, broad, dorsolateral black stripes extending from base of dorsolateral horns of caudal saddle on carapace to base of telson, flaring on sixth tergum, and uniting on cephalic part of telson. Additional long black stripe extending along bases of second through fifth pleura; broad, very light cream stripe interposed between black stripes, and ventral parts of second through fifth pleura cream to white. Telson and uropods rather uniformly olive. Antennular and antennal peduncles olive with cream splotches; flagella of both very dark olive with black rings; lateral margin of antennal scale very dark, often black. Chela dark olive dorsally with cream to orange tubercles, swelling at dorsal articular condyle of dactyl vermilion; fingers fading to cream distally, and fixed finger and palm similarly fading laterally. Carpus and distal half of merus of cheliped dark olive dorsally, former with large black spot dorsomesially and latter almost black distally; tubercles and articular condyles olive cream. Remaining pereiopods with dorsal surface of distal part of merus, carpus, and propodus mottled with dark olive, otherwise pale olive to cream.

TYPES.—Syntypes, MCZ 175 (3♂II, ♀); USNM 4957 (♀). Hagen (1870:74) indicated that among the 6 specimens available there were "Male Form I. and II. Fem." The first form male is no longer in this lot and was missing from it when I examined the series in the early 1940s.

TYPE-LOCALITY.—"Tennessee River, (near the borders of?) Georgia" (Hagen, 1870:74). The emendation offered by Ortmann (1931:97) must be rejected because *Cambarus (P.) extraneus* does not occur in the Coosa (Etowah) Basin. Ortmann confused *C. (P.) coosae*, new species, with Hagen's species. (See "Summary of Literature".)

RANGE.—*Cambarus (P.) extraneus* is known only from the South Chickamauga Creek basin [Tennessee River drainage] in Catoosa, Walker, and Whitfield counties, Georgia, and in the same basin in Hamilton County, Tennessee (Bouchard, 1972:58).

GEORGIA SPECIMENS EXAMINED.—I have examined 156 specimens from the following localities. (1) type-locality, "Tennessee River, near border of Georgia," syntypes, 3♂II, 2♀. *Catoosa County:* (2) South Chickamauga Creek at Rte S819 at Graysville, 1j♂, 26 Aug 1969, E. T. Hall, Jr., M. W. Walker, collectors; (3) East Fork of South Chickamauga Creek at Rte S2210, 6 mi SE of Ringgold, 2j♀, 26 Aug 1969, ETH, R. F. Holbrook; (4) South Chickamauga Creek 4.1 mi W of St Rte 71 on St Rte 2, 3♂I, 3♂II, 9♀, 1j♂, 9j♀, 2 May 1967, Torgny Unestam, HHH; (5) South Chickamauga Creek 10 mi NE of Lafayette, 2♀, 30 Aug 1929, E. P. Creaser; (6) Hurricane Creek on Co Rd off St Rte 151, 4.3 mi N of Ringgold, 5♂II, 3♀, 6j♂, 10j♀, 24 Apr 1968, ETH, HHH; 1♀, 1j♂, 25 Apr 1977, J. E. Pugh, HHH; (7) Peavine Creek approximately 2 mi upstream from St Rte 2 on Co Rd, 1♂II, 1♀, 3j♂, 23 Apr 1968, ETH, HHH; 1♀, 25 Apr 1977, JEP, HHH; (8) Peavine Creek at Rte S820, 1j♀, 25 Apr 1977, JEP, HHH; (9) Little Tiger Creek 2.5 mi W of Varnell on St Rte 2, 11♂I, 13♂II, 11♀, 11j♂, 14j♀, 24 Apr 1968, ETH, HHH; 1♂I, 6♀, 4j♂, 22 Oct 1976, T. A. English, Jr., HHH. *Walker County:* (10) creek 0.5 mi N of St Rte 143 on Rt 342, 1j♂, 1j♀, 23 Apr 1968, ETC, HHH; (11) South Chickamauga Creek 0.2 mi downstream from St Rte 143, 1♂II, 27 Aug 1969, ETH, MWW; (12) stream 9.8 mi E of Dade Co line on St Rte 143, 1♀, 2 May 1967, TU, HHH. *Whitfield County:* (13) East Fork of South Chickamauga Creek 7.1 mi SW of US Hwy 76 on St Rte 201, 1♀, 1j♀, 4 Sep 1953, R. L. Gibbs; 1♂II, 2♀, 4j♂, 5j♀, 16 Apr 1962, J. F. Fitzpatrick, Jr., HHH.

VARIATIONS.—The most conspicuous variations are in the degree of development of the cervical, rostral, and postorbital spines and in the size and conformation of the chela of the males. In general, the smaller the individual, the more conspicuous and proportionately elongate the spines, but occasional large individuals have spines that are as prominent as those usually characteristic of the smaller ones.

The variation in the size and conformation of the chela is puzzling. The adult males with reduced chelae occur in a larger proportion than would seem likely were the difference due to loss and regeneration in earlier instars. In relatively few of the large males is the usual dimorphism associated with sex obvious. Fewer than half of the chelae observed in the first form males are as well developed as that illustrated (Figure 95*l*).

SIZE.—The largest specimen available is a first form male with a carapace length of 44.5 (postorbital carapace length 34.6) mm. Corresponding lengths of the smallest first form male are 31.3 and 24.4 mm, and of the largest female, 39.6 and 31.2 mm, respectively. No ovigerous females have been collected.

LIFE HISTORY NOTES.—Available specimens were obtained in April, May, August, September, and October, and first form males were found in April, May, and October. Amplexus was observed on 24 April 1968. Ovigerous females or those carrying young are unknown.

Seasonal Data

Sex/stage	*J*	*F*	*M*	*A*	*M*	*J*	*J*	*A*	*S*	*O*	*N*	*D*	*?*
♂I				11	3					1			
♂II				21	3			1					3
♀				18	10			2	1	6			2
♂j				25	1			1		4			
♀j				31	9			2	1				

ECOLOGICAL NOTES.—*Cambarus (P.) extraneus* is a stream dweller, frequenting moderately flowing, small, shallow, rock-littered streams, where they find cover under the rocks or in entrapped tree litter. Fewer of my specimens were collected from broader, deeper streams, where they were driven from exposed root mats or undercut banks. Even though most of those collected by me were in comparatively clear water, in at least two of the localities the stream bed had an abundant silt cover and the water was carrying a heavy load of reddish brown, finely divided particulate matter.

GEORGIA CRAYFISH ASSOCIATES.—The following crayfishes have been collected with *Cambarus (P.) extraneus* (the number of times they have been found together is noted in parentheses): *Cambarus (D.) striatus* (4), *C. (H.) girardianus* (12), *C. (L.) acanthura* (1), *Orconectes erichsonianus* (13), *O. forceps* (2), and *Procambarus (O.) lophotus* (3).

Cambarus (Puncticambarus) georgiae, new species

FIGURES 21*g*, 87, 89*d*, 96, 225

Cambarus (Puncticambarus) sp.—Anonymous, 1973e:2*.

The only previous record of this crayfish is based on my determination of specimens from Rabun County, Georgia, and Macon County, North Carolina. Based on information obtained from me, it was noted by Anonymous (1973e) as being rare in North Carolina.

DIAGNOSIS.—Body pigmented, eyes well developed. Rostrum with marginal spines or tubercles. Areola 2.3 to 3.2 times as long as broad and constituting 30.7 to 35.6 percent of total length of carapace (40.7 to 44.8 percent of postorbital carapace length) with 8 to 10 punctations across narrowest part. Cervical and branchiostegal spines well developed; hepatic spines absent; suborbital angle usually strong and acute; postorbital ridges with acute spines or tubercles. Antennal scale approximately 2.5 times as long as wide, broadest at about midlength. Chela with single well-defined row of 8 to 10 tubercles on mesial surface of palm, occasionally with few in second poorly defined row immediately dorsal to mesial row; lateral margin of chela costate; lacking conspicuous impression dorsally and ventrally at base of fixed finger; dactyl less than twice length of mesial margin of palm. Hook on ischium of third pereiopod of first form male overreaching basioischial articulation and usually opposed by tubercle on basis. First pleopod of first form male with central projection bearing subapical notch, recurved at angle of about 106 degrees; mesial process inflated with undulating, distal lobe, and directed caudolaterally at angle slightly greater than 90 degrees. Female with annulus ventralis shallowly embedded in sternum and somewhat asymmetrical; first pleopod present. Carapace and abdomen mottled, latter with linear series of oblique dark splotches dorsolaterally and on pleura.

HOLOTYPIC MALE, FORM I.—Body subovate, compressed (Figure 96*a,j*). Abdomen narrower than cephalothorax (11.6 and 13.2 mm); maximum width of carapace greater than depth at caudodorsal margin of cervical groove (13.2 and 10.7 mm). Areola 2.3 times as long as broad, with 9 punctations across narrowest part, punctations small and somewhat crowded; length 33.2 percent of total length of carapace (43.2 percent of postorbital carapace length). Rostrum with slightly convergent, weakly thickened margins bearing acute marginal spines; acumen moderately long, curved dorsally, and reaching midlength of ultimate podomere of antennular peduncle; upper surface of rostrum concave with numerous closely set punctations. Subrostral ridge weak and evident in dorsal aspect only along basal portion of rostrum. Postorbital ridge comparatively short, not strongly elevated, grooved dorsolaterally and bearing acute spine cephalically. Suborbital angle and branchiostegal spine strong and acute. Cervical spine moderately well developed and flanked dorsally by large tubercle. Carapace punctate dorsally and with very fine granulations laterally.

Abdomen longer than carapace (29.4 and 25.6 mm); pleura of moderate length, somewhat truncate ventrally and subangular caudoventrally. Cephalic section of telson with 2 spines in each caudolateral corner. Proximal podomere of uropod with distal spine on each lobe; mesial ramus of uropod with weak submedian ridge terminating in short premarginal spine.

Cephalomedian lobe of epistome (Figure 96*i*) subtriangular, with cephalolateral margins somewhat thickened and undulating; main body with prominent median fovea; epistomal zygoma strongly arched. Ventral surface of proximal podomere of antennule with spine at base of distal third. Antennal peduncle with spine on lateral surface of basis and ventral surface of ischium; flagellum broken in holotype but reaching sixth abdominal tergum in other specimens; antennal scale (Figure 96*g*) about 2.5 times as long as broad, broadest near midlength, its mesial margin evenly rounded, and distal spine reaching level of apex of acumen. Ventral surface of ischium of third maxilliped studded with clusters of long stiff setae on mesial half and with submarginal lateral row of much smaller ones; distolateral extremity subangular.

Right chela (Figure 96*l*) about twice as long as broad and mesial margin of palm constituting about one-third total length. Mesial margin of palm with row of 8 tubercles, excluding articular prominences, palm otherwise punctate. Both fingers with moderately prominent submedian longitudinal ridges dorsally and ventrally, flanked by setiferous punctations. Fixed finger costate laterally, with costa extending proximally onto palm, lacking tubercles except for row of 4 large, rounded ones on basal two-fifths of opposable margin and single subacute one on lower level of opposable surface at base of distal two-fifths; narrow band of minute denticles extending distally from row of tubercles to base of corneous tip of finger. Opposable margin of dactyl with row of 6 rounded tubercles along proximal half, followed distally by narrow band of minute denticles; mesial surface of finger with few low tubercles basally, giving way to row of setiferous punctations.

Carpus of cheliped with shallow oblique furrow and scattered punctations dorsally; mesial surface bearing single prominent acute spine; ventral surface provided with 2 marginal spines, 1 on articular prominence and other submedian; and lateral surface punctate. Merus with prominent spine and large tubercle on distal part of dorsal surface, mesial and lateral surfaces punctate; ventral surface with lateral row of 3 prominent spines and mesial one of 8 tubercles, most of which spiniform. Ventromesial margin of ischium with row of 3 tubercles.

Ischium of third pereiopod with simple hook extending proximally over basioischial articulation (Figure 96*h*), hook opposed by small tubercle on basis. Coxa of fourth pereiopod with obliquely, vertically disposed caudomesial boss; that of fifth pereiopod lacking boss, ventral membrane with few scattered setae.

First pleopods (Figure 96*b,d,f*) with gap between bases and reaching coxae of third pereiopods, both terminal elements recurved at angle

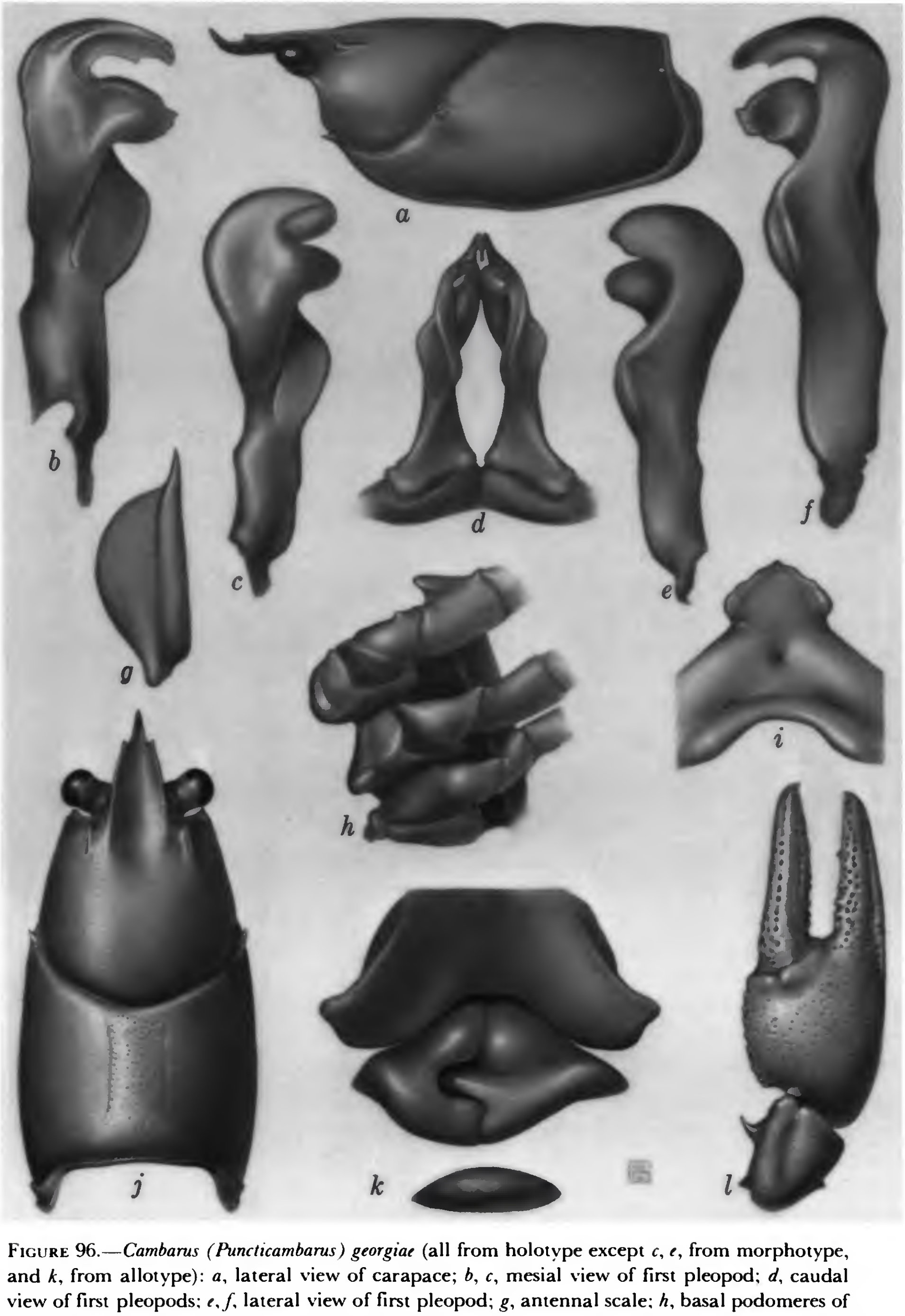


FIGURE 96.—*Cambarus (Puncticambarus) georgiae* (all from holotype except *c*, *e*, from morphotype, and *k*, from allotype): *a*, lateral view of carapace; *b*, *c*, mesial view of first pleopod; *d*, caudal view of first pleopods; *e*, *f*, lateral view of first pleopod; *g*, antennal scale; *h*, basal podomeres of third, fourth, and fifth pereiopods; *i*, epistome; *j*, dorsal view of carapace; *k*, annulus ventralis; *l*, dorsal view of distal podomeres of cheliped.

slightly greater than 90 degrees to main shaft of appendage. Mesial process somewhat inflated, although biconcave basally and terminating in caudolaterally directed, undulating lobe reaching level of apex of central projection. Latter with well-defined subapical notch.

ALLOTYPIC FEMALE.—Differing from holotype, other than in secondary sexual characters, as follows: margins of rostrum thicker and more strongly convergent; suborbital angle broadly rounded, virtually obsolete; lacking accessory tubercles immediately dorsal to cervical spine; cephalic section of telson with single spine in each caudolateral corner; mesial margin of palm of chela with row of 6 or 7 tubercles flanked by 1 or 2 squamous ones dorsally; opposable margin of fixed finger of chela with row of 5 tubercles and that of right with 2 on lower level; opposable margin of dactyl with row of 4 tubercles; dorsal surface of merus with only 1 spine, ventral surface with lateral row of 2 or 3 spines and mesial row of 7, mostly very weak, tubercles; basal opposable portions of both fingers with more conspicuously long setae than in holotype. (See "Measurements.")

Annulus ventralis (Figure 96*k*) about twice as broad as long; situated rather shallowly in sternum; elevated (ventrally) cephalic area traversed by submedian longitudinal furrow; sinus originating in caudal extremity of furrow, somewhat anterior to midlength of annulus, extending dextrally, forming hairpin curve and returning to median line, there extending caudally in low dextral arc, cutting caudal margin of annulus; prominent tongue directed dextrally and disappearing in fossa beneath dextral wall. Postannular sclerite subspindle shaped and about one-half as wide as annulus. First pleopod reaching cephalic margin of annulus when abdomen flexed.

MORPHOTYPIC MALE, FORM II.—Differing from holotype in following respects: marginal spines on rostrum stronger and more divergent; lacking accessory tubercles immediately dorsal to cervical spine; merus of right cheliped with only 2 spines ventrolaterally, and setae at base of fingers more conspicuous. Hook on ischium of third pereiopod very small but opposed by tubercle on basis; boss on coxa of fourth pereiopod much reduced. (See "Measurements.") First pleopod (Figure 96*c*, *e*) differing from that of holotype chiefly in bulbous nature of terminal elements, both shorter, and central projection much broader with only hint of subapical notch.

COLOR NOTES (Figure 89*d*).—As in many epigean crayfishes, the color pattern occurs in two phases, one in which a black pattern appears on a greenish or bluish gray background, and the other with very dark brown on a tan or orange tan background. The former phase is described here.

Ground color of carapace and abdomen greenish gray. Rostrum with black margins and white-tipped marginal spines; gastric region with pair of laterally convex markings lying between postorbital ridges, each joined by narrow, dark longitudinal line to dark gray splotch near midlength of cephalic region, and caudal gastric region with pair of black angular bars immediately cephalic to cervical groove. Paired black crescents flanking caudal parts of postorbital ridges, with cephaloventral extensions on hepatic region. Black band following cervical groove, with caudally directed triangular thickening on middorsal line, and interrupted laterally by white cervical spine just before fading and merging with light gray color of lower hepatic area. Short, oblique black bar extending from base of postorbital spine caudoventrally, bar flanked cephaloventrally and caudodorsally by narrow subparallel white bands. Areola dark gray, sometimes with black splotches. Branchiostegites with paired, irregular, broad, black longitudinal stripes dorsolaterally (stripes bearing irregular gray and white splotches), joined by narrow transverse band on caudal margin of carapace. Abdomen with terga of 5 anterior segments bearing small median gray to black spot; that on fifth joining horizontal band across caudal margin of segment, there radiating caudally on tergum of sixth segment in median longitudinal stripe and pair of caudally divergent ones. Bases of pleura with paired L-shaped black markings, apex of angle directed caudoventrally;

in addition, paired, short, oblique bars situated more ventrally, and caudoventral marginal ones also present. Telson with basal, dark gray, median patch flanked by paired, black, narrow horizontal bars near cephalic margin and with paired, black longitudinal stripes on lateral margins of cephalic section. Mesial ramus of uropod with dark gray submedian stripe and black stripe on lateral margin. Antennal scale mostly white, with black lateral margin and longitudinal stripe along lateral margin of lamellar area. Cheliped pale gray basally, becoming dark gray on distal part of merus, latter with spines on dorsal surface white; carpus mostly gray with proximolateral black spot and very dark gray splotches mesio- and laterodistally; chela with gray palm dorsally, becoming dark gray toward fingers, both of latter dark gray with preapical reddish band fading to white at tip of fingers.

Measurements (mm)

	Holotype	*Allotype*	*Morphotype*
Carapace			
Height	10.7	10.5	9.7
Width	13.2	12.8	10.5
Entire length	25.6	25.2	-
Postorbital length	19.7	19.8	18.0
Areola			
Width	3.3	3.4	3.1
Length	8.5	8.7	8.1
Rostrum			
Width	2.7	4.2	3.4
Length	6.5	6.2	broken
Chela			
Length of mesial margin of palm	6.5	4.1	4.8
Width of palm	8.3	5.3	4.8
Length of lateral margin	19.5	13.8	13.6
Length of dactyl	11.4	8.5	7.9
Abdomen:			
Width	11.6	13.2	9.5
Length	29.4	30.2	24.6

TYPES.—The holotypic male, form I, allotypic female, and morphotypic male, form II (numbers 118944, 144954, 144955, respectively), are deposited in the National Museum of Natural History, Smithsonian Institution, along with the paratypes comprising 2♂I, 14♂II, 17♀, 1j♂, 1j♀, and 1 ovigerous ♀. Specimens from the third locality listed under "Specimens Examined" are excluded from the type series.

TYPE-LOCALITY.—Little Tennessee River at U.S. Highway 441 south of Dillard, Rabun County, Georgia. At this locality the stream is some three to seven meters wide, a few centimeters to one meter deep, and flows swiftly over a sandy clay bottom of alternating riffles and quieter stretches. Stones occur abundantly at the riffles. Filamentous green algae and a moss are the only aquatic plants observed; along the shore *Alnus rugosa, Sambucus* sp., and *Rubus* sp. form dense thickets. Much more abundant than *Cambarus (P.) georgiae* at this locality is *Cambarus (C.) bartonii*. (See "Ecological Notes.")

RANGE.—Known only from the upper Little Tennessee River in Rabun County, Georgia, and Macon County, North Carolina (Blue Ridge Province).

SPECIMENS EXAMINED.—I have examined 51 specimens from the following localities. GEORGIA. *Rabun County*: (1) type-locality, 1 ovig ♀, 23 Apr 1961, D. C. Scott, collector; 1♂II, 1♀, 6 Jun 1961, Richards, Miller, Bane; 1♂I, 27 Apr 1967, T. Unestam, HHH; 2♀, 12 Apr 1968, G. B. Hobbs, HHH; 1j♂, 1j♀, 29 Nov 1970, T. A. English, Jr., E. T. Hall, Jr.; 1♂I, 9♂II, 3♀, 1 May 1971, TAE, ETH, HHH. NORTH CAROLINA. *Macon County*: (2) Little Tennessee River 7.0 mi N of Georgia St line on US Hwy 441 and 0.2 mi E on unnumbered road, 1♂I, 5♂II, 12♀, 1 May 1971, TAE, ETH, HHH; (3) Sugar Fork River 8 mi NE of Franklin on US Hwy 64, 2♂II, 3♀, 5j♂, 2j♀, 26 Jun 1957, E. A. Crawford.

VARIATIONS.—Inasmuch as this crayfish is known from only three localities in the upper Little Tennessee Basin, it is not surprising that variations are so few and of such a minor nature. Those associated with the diagnostic features are accounted for in the "Diagnosis," and others are mentioned in the brief descriptions of the allotype and morphotype. In addition, the spine on the mesial surface of the carpus of the cheliped may be simple or bispinose; the tubercles along the opposable margin of the dactyl vary from four to seven. The basis of the third pereiopod in the male may lack a tubercle opposing the hook on the ischium; and the coxa of the fifth pereiopod may possess a very small caudomesial tuberculiform boss. The mesial process of the first pleopod may exceed slightly in its caudal extension that of the central projection.

SIZE.—The largest specimen available is a first form male from the North Carolina locality, having a carapace length of 28.9 mm (postorbital length 22.7 mm). The smallest first form male is the holotype, having corresponding measurements of 25.6 and 19.7 mm, respectively. The single ovigerous female has corresponding measurements of 24.6 to 19.4 mm.

LIFE HISTORY NOTES.—First form males were collected in April and May, and one ovigerous female was found in April carrying 73 eggs with diameters of 2.3 to 2.6 mm. (See "Size" for carapace length.)

ECOLOGICAL NOTES.—Several attempts to collect this species in the type-locality have been relatively unsuccessful, and not until the collection was made farther downstream in North Carolina did it become rather obvious that *Cambarus (P.) georgiae* either did not compete successfully in the riffle areas with *Cambarus (C.) bartonii*, or it preferred the quieter areas between the riffles. In the type-locality, many man-hours of labor were expended in obtaining the relatively few specimens at hand; in contrast, the 18 specimens from the first listed North Carolina locality, where no *C. (C.) bartonii* were found, were taken in less than one-half hour, despite the lack of cover in the stream. All of the crayfish there were found in leaf debris trapped in broken limbs anchored in the sandy bottom of the river. At this locality the stream is some 17 meters wide, with a maximum depth of about one meter; the gray-tinted water flows swiftly over a sandy bottom where there are few stones, and the banks are not undercut but support dense vegetation, including plants belonging to the genera *Platanus*, *Acer*, *Ulmus*, *Sambucus*, and *Quercus*. A few of the rocks in the water were moss covered.

RELATIONSHIPS.—*Cambarus (P.) georgiae* has its closest affinities with *Cambarus (P.) chaugaensis*, *C. (P.) extraneus*, *C. (P.) reburrus* Prins (1968), and *C. (P.) spicatus* Hobbs (1956c). Although this crayfish possesses only one well-defined row of tubercles on the mesial margin of the palm of the chela (a character that occurs elsewhere in the subgenus only in *C. (P.) nerterius* and *C. (P.) veteranus*), the other features of the chela together with the broad areola bearing numerous small punctations indicate its closer relationships with the crayfishes assigned to the subgenus *Puncticambarus* than to those comprising the allied subgenus *Erebicambarus*. The presence of marginal spines on the rostrum serves to distinguish *C. (P.) georgiae* from all of its relatives except *C. (P.) spicatus*, *C. (P.) extraneus*, *C. (P.) nerterius*, and *C. (P.) cumberlandensis*. It differs from *C. (P.) nerterius* in possessing an areola comprising less than 36 percent of the total length of the carapace, from *C. (P.) spicatus* in lacking hepatic spines, from *C. (P.) extraneus* and *C. (P.) cumberlandensis* in lacking dorsal and ventral impressions at the base of the fixed finger of the chela, and from the latter three in possessing only a single well-developed row of tubercles on the mesial margin of the palm of the chela.

ETYMOLOGY.—This crayfish is named in honor of my wife, Georgia Blount Hobbs, who has not only assisted me in field work on numerous occasions but also has aided me in the preparation of virtually all of my published work.

CRAYFISH ASSOCIATES.—It has been found with *Cambarus (C.) bartonii* in two of the three known localities.

Cambarus (Puncticambarus) hiwasseensis, new species

FIGURES 21*e*, 89*f*, 97, 98, 226, FRONTISPIECE

Cambarus (Puncticambarus) species C.—Hobbs, 1969a:102, 135, fig. 7*.

Cambarus hiwasseensis.—Anonymous, 1973b:66* [nomen nudum].

Cambarus (Puncticambarus) sp.—Bouchard and Hobbs, 1976: 13 [in part].

Cambarus (Puncticambarus) species D.—Hobbs and Peters, 1977:6, 8, 12, 30, 33.—Cooper and Cooper, 1977:198*.

Cambarus hiawasseensis.—Wharton, 1978:220* [nomen nudum].

SUMMARY OF LITERATURE.—The first record of the existence of this crayfish was reported by

Hobbs (1969a), who noted its presence in the Hiwassee River basin in Georgia and North Carolina. It was next mentioned under the nomen nudum, *Cambarus hiwasseensis*, by Anonymous (1973b) as occurring in the "West Fork of Wolf Creek immediately upstream from confluence with East Fork," Union County, Georgia. Its association with *C. (J.) nodosus* was mentioned by Bouchard and Hobbs (1976). Hobbs and Peters (1977:30, 33) reported it from the Hiwassee Basin of North Carolina, where it served as a host to *Dactylocythere falcata* and *Dt. leptophylax*. Cooper and Cooper (1977) referred to its occurrence in Cherokee County, North Carolina, as well as in the Hiwassee Basin of Georgia and Tennessee.

DIAGNOSIS.—Body pigmented, eyes well developed. Rostrum with margins only slightly thickened and devoid of marginal spines or tubercles. Areola 1.9 to 3.7 times as long as wide and comprising 29.4 to 34.8 percent of entire length of carapace (39.3 to 42.6 percent of postorbital carapace length) and bearing 8 to 11 punctations across narrowest part. Small cervical tubercle present, cervical spine lacking. Suborbital angle acute. Postorbital ridge terminating cephalically in very small corneous tubercle. Antennal scale approximately 2.5 times as long as wide, broadest distal to midlength. Chela not strongly depressed, with 2 rows of tubercles along mesial margin of palm, mesialmost row consisting of 6 to 10; lateral margin of palm costate and both fingers with well-defined longitudinal ridges dorsally. Male with basis of third pereiopod bearing tubercle opposing hook on ischium. First pleopod of first form male with rather short terminal elements: central projection not tapering distally, recurved at approximately 110 degrees to main shaft of appendage, and bearing conspicuous subapical notch; and mesial process somewhat inflated, acute, and extending caudolaterally slightly beyond tip of central projection at angle of about 90 degrees to main shaft. Female with annulus ventralis shallowly embedded in sternum and subsymmetrical; first pleopod present. Carapace and abdomen mottled, latter with longitudinal series of very irregular dorsolateral splotches and smaller more distinct ones along bases of pleura.

HOLOTYPIC MALE, FORM I.—Body subovate, depressed (Frontispiece and Figure 97*a*). Abdomen narrower than thorax (16.4 and 19.3 mm); maximum width of carapace greater than depth at caudodorsal margin of cervical groove (19.3 and 13.6 mm). Areola 2.4 times as long as wide, with dense punctations, 9 across narrowest part. Cephalic section of carapace twice as long as areola, length of latter 33.8 percent of entire length of carapace (39.5 percent of postorbital carapace length). Rostrum with slightly thickened convergent margins, devoid of marginal spines or tubercles, tapering gradually from base to level of distal end of basal segment of antennular peduncle, from there converging more rapidly and forming acute tip slightly overreaching penultimate podomere of latter; dorsal surface of rostrum concave, densely punctate especially basally. Postorbital ridge short, not strongly elevated, grooved dorsolaterally, and terminating in very small corneous tubercle. Subrostral ridge weak, and evident in dorsal aspect only along basal part of rostrum. Suborbital angle acute. Branchiostegal spine only moderately well developed. Cervical spine lacking, replaced by 2 or 3 tubercles slightly larger than others nearby. Carapace punctate dorsally, with almost no polished area in gastric region, and granulate laterally; granules largest on hepatic region and in anteroventral branchiostegal region.

Abdomen longer than carapace (38.2 and 36.2 mm); pleura of moderate length, truncate ventrally and with caudoventral extremity rounded. Cephalic section of telson with 2 spines in each caudolateral corner. Proximal podomere of uropod with distal spine on each lobe; mesial ramus of uropod with weak submedian ridge terminating in short premarginal spine.

Cephalomedian lobe of epistome (Figure 97*i*) subtriangular, with cephalolateral margins thickened and somewhat undulating; main body with conspicuous median fovea; epistomal zygoma broadly arched. Ventral surface of proximal podomere of antennule with spine at base of distal third. Antennal peduncle with spine on lateral

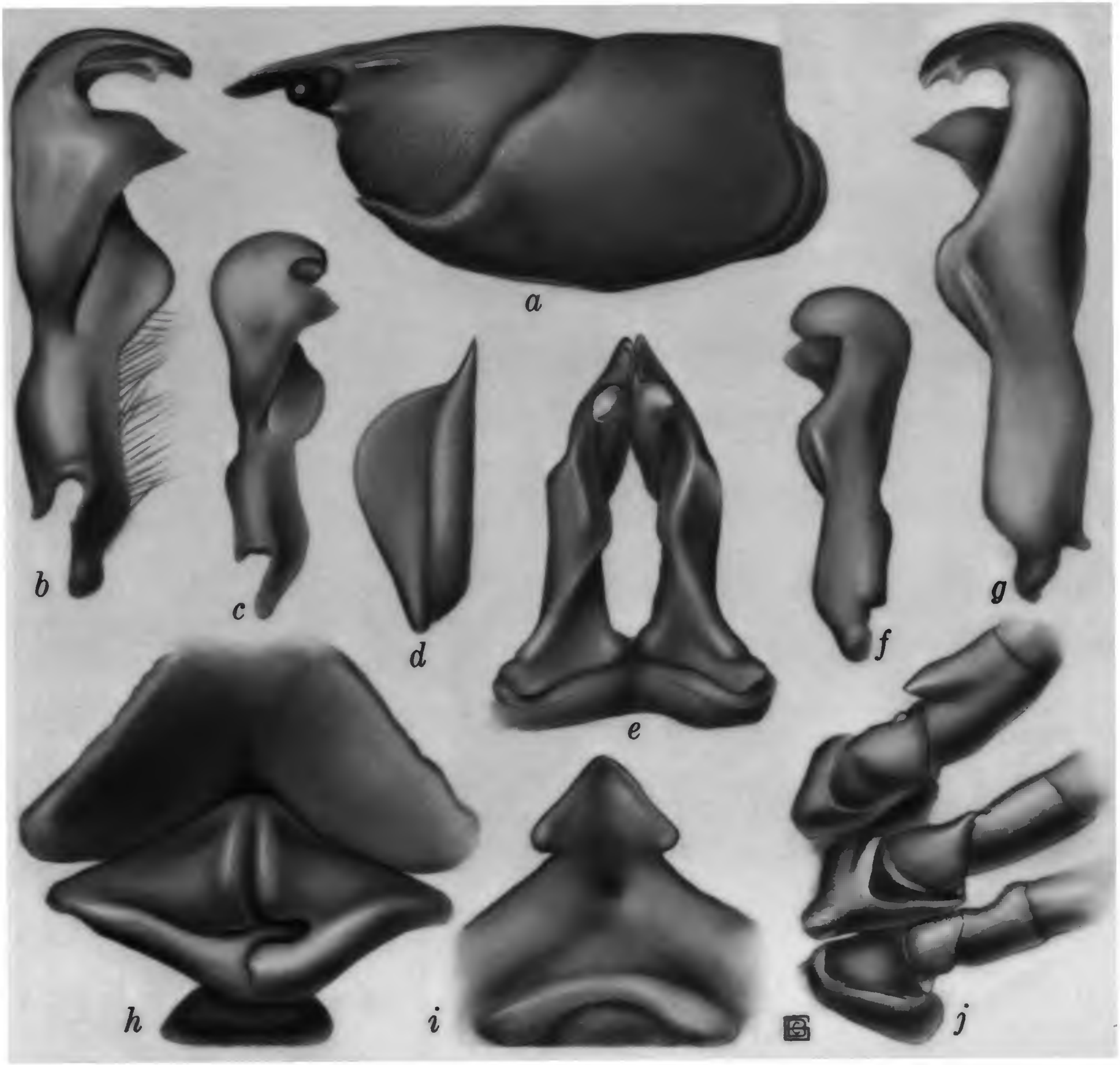


FIGURE 97.—*Cambarus (Puncticambarus) hiwasseensis* (all from paratypic male, form I, except *c*, *f*, from paratopotypic male, form II, and *h*, from allotype): *a*, lateral view of carapace; *b*, *c*, mesial view of first pleopod; *d*, antennal scale; *e*, caudal view of first pleopods; *f*, *g*, lateral view of first pleopod; *h*, annulus ventralis; *i*, epistome; *j*, proximal podomeres of third, fourth, and fifth pereiopods.

surface of basis and weak subacute tubercle on ventral surface of ischium; flagellum reaching fifth abdominal tergum; antennal scale (Figure 97*d*) about 2.4 times as long as wide, broadest distal to midlength, its mesial margin rounded, lacking angles, and its distal spine reaching end of ultimate podomere of antennular peduncle. Ventral surface of ischium of third maxilliped with mesial half bearing clusters of long stiff setae and with submarginal lateral row of much smaller ones; distolateral extremity angular.

Right chela (Frontispiece) about 2.4 times as long as broad, mesial margin of palm constituting about one-third total length, and with row of 7 tubercles subtended dorsally by another of 6; except for few very small tubercles on dorsal surface of mesial fourth, palm otherwise punctate. Both fingers with prominent submedian longitudinal ridges, flanked by setiferous punctations, dorsally and ventrally. Fixed finger strongly costate laterally with costa extending proximally for almost half length of palm; opposable margin of finger with dorsal row of 11 tubercles along basal two-thirds, ventral one of 4 tubercles along middle third, and narrow band of minute denticles between rows extending distally from level of sixth tubercle of dorsal row to corneous tip of finger. Opposable margin of dactyl with row of 14 tubercles and single row of minute denticles extending distally from tenth tubercle from base; in general, tubercles on both fingers decreasing in size distally; mesial margin of dactyl tuberculate along proximal three-fifths and bearing row of setiferous punctations along distal two-fifths.

Carpus of cheliped with broad, moderately deep, slightly oblique longitudinal furrow flanked by punctations; mesial surface with prominent spine near midlength and small tubercle proximally, spine with additional small tubercle at proximoventral base; ventral surface with 2 large tubercles on distal margin, 1 on articular knob, and smaller one proximomesially. Merus with 4 subdistal tubercles dorsally, punctate mesially and laterally, and with ventromesial row of 13 tubercles and ventrolateral one of 6. Mesial margin of ischium with row of 4 tubercles.

Ischium of third pereiopod with simple hook, overreaching basioischial articulation, opposed by prominent tubercle on basis (Figure 97*j*). Coxa of fourth pereiopod with vertically disposed caudomesial boss; that of fifth with scarcely trace of boss, its ventral membrane with few setae.

First pleopods (Figure 97*b,e,g*) with gap between bases and reaching coxae of third pereiopods; both terminal elements recurved at angle slightly greater than 90 degrees to main shaft of appendage. Mesial process inflated but tapering distally to acute tip directed caudolaterally; central projection, with uniform width, more strongly recurved than mesial process and with distinct subapical notch.

Allotypic Female.—Differing from holotype, other than in secondary sexual characters, as follows: areola with approximately 12 punctations across narrowest part; mesial margin of palm of left chela with 8 tubercles in mesialmost row subtended dorsolaterally by row of 8 smaller ones; tubercles on dorsal surface of palm of chela limited to mesial rows just mentioned; opposable margin of fixed finger of right chela (left broken) with 8 tubercles in dorsal row and 2 in ventral; opposable margin of dactyl with row of 10 and 9 tubercles on right and left chelae, respectively; mesial surface of carpus of right cheliped with 2 spines near midlength; merus of left and right chelae with 2 and 3, respectively, subdistal tubercles dorsally; ventral surface of merus of right cheliped with mesial row of 12 tubercles and lateral one of 2, that of left cheliped with 10 and 3, respectively. (See "Measurements.")

Annulus ventralis (Figure 97*h*) rather shallowly situated in sternum, somewhat diamond shaped, its angles in transverse and longitudinal planes, and almost twice as broad as long; cephalic half with median longitudinal furrow flanked by paired narrow ridges, and prominent subangular ridge forming caudal wall; sinus originating in caudal portion of median furrow, and, extending caudally for short distance, turning sinistrally at right angle before making hairpin turn and crossing to dextral side of median line; from there sinus curving caudally in gentle arc across caudal ridge and terminating on caudal face of latter almost on median line. Postannular sclerite less than half width of annulus and about half as long as wide; surface without ornamentation. First pleopod extending cephalically at least to midlength of annulus when abdomen flexed.

Morphotypic Male, Form II.—Differing from holotype in following respects: areola with 9 or

10 punctations across narrowest part; cephalomedian lobe of epistome almost truncate cephalically; mesial margin of palm of left chela with row of 9 tubercles flanked dorsolaterally by row of 9 much smaller ones (corresponding numbers on right chela, 7 and 7); except for few adjacent to rows, palm otherwise punctate dorsally; longitudinal ridges on fingers of chela less prominent; opposable margin of fixed finger of both left and right chelae with dorsal row of 6 tubercles, fourth from base largest, and only 1 tubercle replacing ventral row present in holotype; opposable margin of dactyl of left chela with row of 8 tubercles (right with 12); carpus of left cheliped lacking tubercle at proximoventral base of spine on mesial surface, and tubercle proximomesial to large marginal mesial tubercle on ventral surface rudimentary; dorsal surface of merus with only 2 conspicuous subdistal tubercles; ventral surface of merus of left cheliped with mesial row of 12 tubercles and lateral one of 4 (13 and 2, respectively, on right); hook on ischium of third pereiopod not overreaching basioischial articulation, but opposed by strong tubercle on basis. (See "Measurements.")

First pleopod with terminal elements directed caudally at right angle to main shaft of appendage; central projection broadly rounded apically and extending about as far caudally as distally directed subacute apex of mesial process (elements usually contiguous for more than half length of central projection (Figure 97*c,f*) but not so in morphotype).

COLOR NOTES (Figure 89*f*).—Ground color of body tan to greenish tan with darker reticulations dorsally; dark band present immediately cephalic to cervical groove, bearing cephalic excision middorsally. Mandibular adductor and hepatic regions dark, mottled with cream tan. Cream spot present between base of suborbital angle and cervical tubercles. Branchiostegites with grayish brown mottlings converging caudally almost to level of branchiocardiac grooves, fading ventrally to grayish cream. Abdomen with linear series of dark grayish brown spots dorsolaterally, each spot extending from cephalic margin of tergum caudolaterally, covering cephalic half to two-thirds length of tergum; that on sixth tergum, however, ending on cephalic third. Pleuron of first abdominal segment mostly cream; base of remaining pleura with grayish brown oblique splotch extending from base caudoventrally; cream spot below splotch and with dark marking on or near ventral margin. Telson and uropods with reticulate pattern. Cheliped greenish brown dorsally from midlength of merus distally, otherwise pinkish cream; all tubercles pale, and articular bosses dark brown. Remaining pereiopods mottled dorsally distal to midlength of merus, and pinkish cream ventrally and proximally. Antennules and antennae greenish brown basally, changing to reddish tan distally.

Measurements (mm)

	Holotype	*Allotype*	*Morphotype*
Carapace			
Height	13.6	13.5	12.5
Width	19.3	16.1	15.2
Entire length	36.2	31.2	28.3
Postorbital length	30.9	24.9	23.2
Areola			
Width	5.1	4.3	3.4
Length	12.2	10.2	9.9
Rostrum			
Width	5.4	5.0	4.5
Length	8.4	7.6	7.1
Chela			
Length of mesial margin of palm	10.3	6.5	7.2
Width of palm	14.8	8.7	9.4
Length of lateral margin	35.7	20.8	22.6
Length of dactyl	23.6	13.2	14.4
Abdomen			
Width	16.5	15.4	14.2
Length	38.8	32.3	35.7

TYPES.—The holotypic male, form I, the allotypic female, and morphotypic male, form II, are deposited in the National Museum of Natural History, Smithsonian Institution, numbers 129366, 129365, and 129364, respectively, as are the paratypes consisting of 19♂I, 16♂II, 26♀, 40j♂, and 36j♀.

TYPE-LOCALITY.—Tributary to Peachtree

Creek, 0.8 miles north of Peachtree School on U.S. Alternate Highway 64, Cherokee County, North Carolina.

RANGE.—The upper Hiwassee River basin (Blue Ridge Province) in Georgia and North Carolina.

SPECIMENS EXAMINED.—I have examined 395 specimens (141 from Georgia and 254 from North Carolina) from 18 localities in Georgia and 21 in North Carolina as follows. GEORGIA. *Towns County:* (1) Corn Creek at N city limits of Young Harris on US Hwy 76, 1♀, 1j♂, 1j♀, 6 Nov 1958, K. W. Simonds, collector; 2♂I, 2♂II, 6♀, 8j♂, 8j♀, 27 Apr 1967, Torgny Unestam, HHH; (2) junction of Byers and Brasstown creeks 0.6 mi NW of Young Harris on St Rte 66, 1♂II, 2♀, 1j♀, 20 Aug 1952, HHH; 3♀, 1j♂, 10 Oct 1969, K. R. Martin, HHH; (3) Hiwassee River about 0.25 mi upstream from junction with Hightower Creek, 1♀, 9 Oct 1969, KRM, HHH; (4) Hightower Creek 0.25 mi upstream from junction with Hiwassee River, 6♂I, 3♀, 2j♀, 9 Oct 1969, KRM, HHH; (5) Hightower Creek 7.3 mi E of Hiwassee on US Hwy 76 and 0.3 mi S on graded road, 3♂I, 4♀, 1j♀, 9 Oct 1969, KRM, HHH; (6) Hightower Creek near Titus on US Hwy 76, 4j♂, 4j♀, 27 Apr 1967, TU, HHH. *Union County:* (7) East Fork of Wolf Creek 0.5 mi N of Vogel State Park on US Hwy 19, 3♂I, 1♀, 2j♂, 2j♀, 5 Nov 1958, KWS; (8) Reece Creek 4.8 mi NW of Blairsville on US Hwy 19, 1♂I, 2♀, 2j♂, 1j♀, 5 Nov 1958, KWS; (9) trib to Town Creek 1.8 mi SW of St Rte 66 on Rte 180, 1♂II, 6 Nov 1958, KWS; (10) trib to Youngcane Creek 2.6 mi E of Fannin Co line on US Hwy 76, 2♂I, 1♂II, 5 Nov 1958, KWS; (11) trib to Nottely Lake 15.2 mi SW of Towns Co line on US Hwy 76, 2♂I, 4♀, 1j♂, 10 Oct 1969, KRM, HHH; (12) West Fork of Wolf Creek at confluence with East Fork, about 2 mi N of Vogel State Park, 1♀, 9 Aug 1972, E. T. Hall, Jr., W. D. Kennedy; (13) East Fork of Wolf Creek 150 m upstream from confluence with West Fork, 2♂I, 1♀, 24 Oct 1976, T. A. English, Jr., HHH; (14) Stephens Creek near Blairsville, 3♂I, 1♂II, 10♀, 7j♂, 4j♀, 13 Mar 1951, D. Ameel; (15) Seabolt Creek 7.4 mi W of Blairsville on US Hwy 76, 3♂II, 4♀, 1j♂, 8 Sep 1945, G. B. Hobbs, HHH; (16) Brasstown Creek at Towns Co line on US Hwy 76, 1♂I, 3♀, 3j♂, 3j♀, 27 Apr 1967, TU, HHH; (17) Butternut Creek 1.7 mi NE of Blairsville on US Hwy 76, 2♂I, 27 Apr 1967, TU, HHH; (18) Nottely River 1 mi N of St Rte 186 on US Hwy 19, 1♂I, 1♀, 27 Apr 1967, TU, HHH. NORTH CAROLINA. *Cherokee County:* (19) type-locality, 6♂I, 4♀, 1j♂, 2j♀, 8 Nov 1958, KWS; (20) creek 2.1 mi S of US Hwy 64 on Hwy 19, 2♂I, 8♂II, 9♀, 23j♂, 25j♀, 14 May 1960, KWS; (21) creek 1.1 mi S of US Hwy 64 on St Rte 60, 4♂I, 3♀, 5j♂, 3j♀, 5 Apr 1962, KWS, J. F. Fitzpatrick, Jr., HHH; (22) Shoal Creek at jct of St Rte 294 and road to Hiwassee Dam, 1♂II, 4j♂, 1 ovig ♀, 8 Jun 1959, KWS; (23) creek 1 mi from Shady Grove Church on Culberson Rd, 1♂I, 1♂II, 2j♂, 1j♀, 8 Jun 1959, KWS; (24) creek 8.5 mi W of Ranger on US Hwy 64, 1♂II, 5♀, 1j♀, 21 Aug 1952, HHH; (25) Martin Creek at Murphy, 1♂I, 17 Oct 1954, R. Warner; (26) creek 2.0 mi E of Murphy on US Hwy 64, 3♂II, 1♀, 27 Jun 1957, E. A. Crawford, Jr.; (27) creek 1.1 mi E of Hopewell Church on US Hwy 64, 2♂I, 1♂II, 1♀, 3j♂, 4j♀, 8 Jun 1959, KWS; (28) creek 1.6 mi W of US Hwy 64 on St Rte 60, 2♂I, 5♂II, 3j♂, 8 Jun 1959, KWS; 1♂I, 4♂II, 2♀, 14j♂, 8j♀, 12 Jun 1960, KWS; (29) Grape Creek 1.4 mi off Joe Brown Rd, 1♀, 6 Jun 1959, KWS; (30) Cane Creek 17 mi E of Tennessee line off US Hwy 64, 2♂II, 1♀, 1j♂, 15 Apr 1962, KWS, JFF, HHH; (31) Rose Creek 1.8 mi off Beaver Dam Rd, 1♀, 1j♂, 2j♀, 6 Jun 1959, KWS; (32) Camp Creek 4.5 mi E of Turtletown, 4j♂, 3j♀, 6 Aug 1959, KWS; (33) creek 6.9 mi E of Tennessee line on US Hwy 64, 2♂I, 1♂II, 1♀, 1j♂, 3j♀, 15 Apr 1962, JFF, HHH; (34) Owl Creek 1.2 mi off Beaver Dam Rd, 1♂II, 2♀, 1j♂, 2j♀, 5 Jun 1959, KWS; (35) creek at jct of US Hwy 64 and St Rte 60, 3♀, 1959, KWS; (36) Valley River 0.9 mi S of Cooper Valley, 1♂I, 2♂II, 4♀, 5j♂, 8j♀, 21 Aug 1952, HHH. *Clay County:* (37) Hiwassee River 4.0 mi E of Peachtree Rd on US Alt Hwy 64, 1♂II, 4j♂, 3j♀, 5 Jun 1959, KWS; (38) creek 8.9 mi SE of Murphy on US Hwy 64, 1♂II, 3j♂, 4j♀, 21 Aug 1952, HHH; (39) Crawford Creek at Warne, 6♂II, 9♀, 2j♀, 21 Aug 1952, HHH.

VARIATIONS.—The most conspicuous variations in this crayfish occur in the rostrum and chela; however, none of them seem to be regionally restricted, and the extremes occasionally occur in different individuals from the same locality. The rostrum is sometimes slenderer and even more strongly tapering than that illustrated for the holotype; in contrast, it is often broader and occasionally less tapering; in none of the available specimens, however, is there a trace of a marginal spine or tubercle. The number of tubercles along the mesial surface of the palm is highly variable: six to 10 occurring in the mesialmost row, and three to eight in the more lateral one; in most individuals, the former consists of seven or eight tubercles and the other of five or six. The length of the fingers in the males is also variable, and there is evidence that males in the second or third breeding season have longer fingers than do those in the first; that is, the larger first form males have longer chelae than do the smaller ones. The holotype is a comparatively large individual and has correspondingly long fingers. The costate lateral margin of the propodus and the dorsal impression at the base of the fixed finger are also

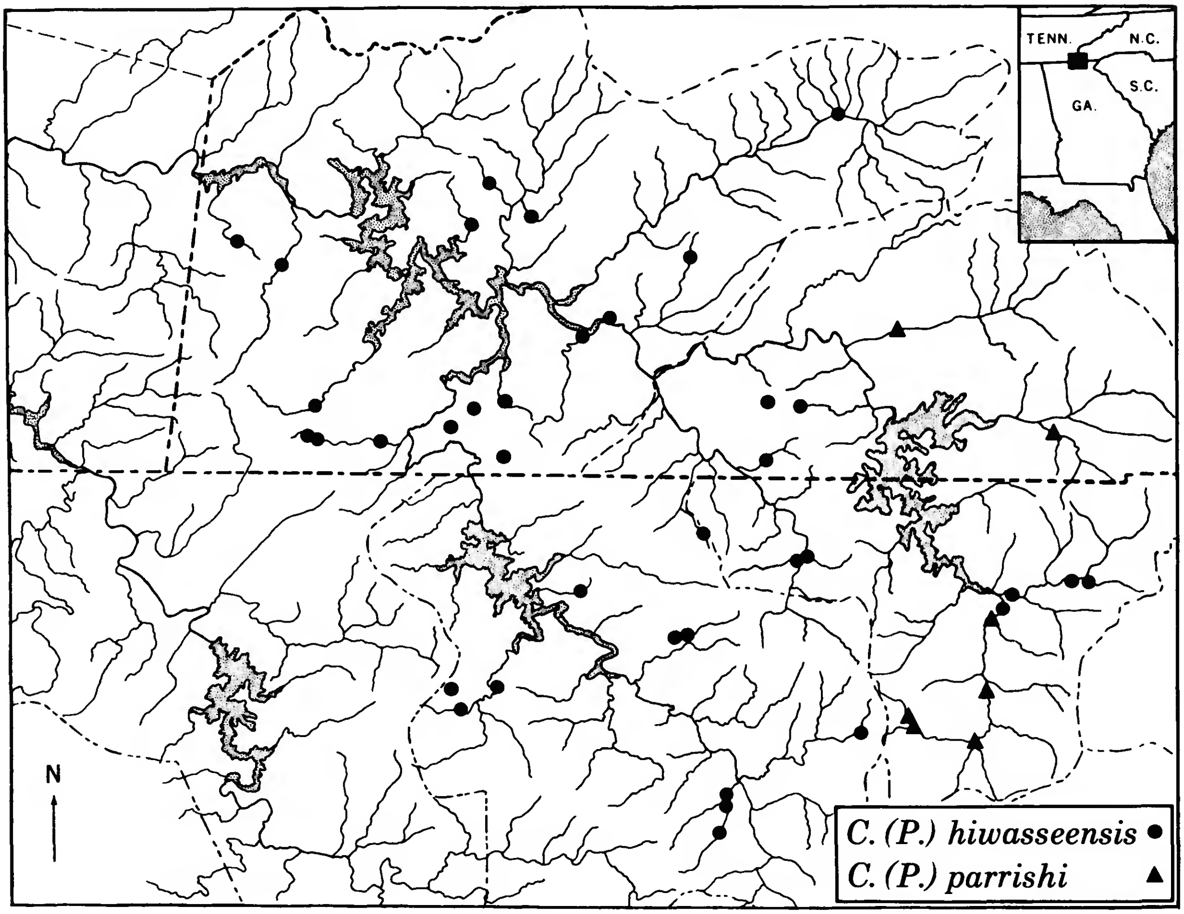


FIGURE 98.—Distribution of *Cambarus (P.) hiwasseensis* and *C. (P.) parrishi.*

more conspicuous in larger individuals. The cervical tubercles may be moderately well developed or may be virtually obsolete. For ranges in proportions of the width and length of the areola and its relation to carapace length, see "Diagnosis."

SIZE.—The largest specimen available is a male, form I, with a carapace length of 40.0 (postorbital carapace length, 32.1) mm; the corresponding lengths of the largest female are 39.5 (31.9) mm, the smallest male, form I, 24.6 (19.5) mm, and of the single ovigerous female, 30.1 (23.9) mm.

LIFE HISTORY NOTES.—First form males have been collected in every month of the year except January, February, July, September, and December, months during which no collections have been made. In August, of the 13 adult males represented, only one was in the first form; in contrast, all of the adult males (14) collected in October were in the latter form. It seems likely that the majority of the male population is in second form from July to September. The single ovigerous female (see "Size"), collected on 8 June 1959, carried 13 eggs and 51 newly hatched young.

Seasonal Data (Georgia and North Carolina)

Sex/stage	J	F	M	A	M	J	J	A	S	O	N	D	?
♂I			3	12	2	6		1		14	12		
♂II			1	5	8	17		12	3		2		
♀			10	14	9	10		21	4	15	8		3
♂j			7	22	23	35		9	1	2	6		
♀j			4	21	25	22		15		4	6		
♀ ovig						1							

Ecological Notes.—This crayfish is apparently restricted to swiftly flowing streams that, for the most part, remain clear except following heavy rains. It occurs most abundantly in areas where the streambed is littered with rocks or in debris entrapped among the rocks. *Cambarus (P.) hiwasseensis* and *C. (P.) parrishi* have never been found together and seem to vicariate for one another in different areas of the upper Hiwassee Basin. In Hightower Creek and in the lower two miles of the Hiwassee River above its confluence with the former, *C. (P.) hiwasseensis* was found in a number of localities, but, farther upstream in the River, *C. (P.) parrishi* and *C. (C.) bartonii* were the only crayfishes found. The fact that *C. (P.) hiwasseensis* and its closest relative, *C. (P.) parrishi*, occur in localities separated by no more than two miles along the same water course and occupy essentially identical habitats attests to the marked similarity in their ecological adaptations.

Relationships.—This crayfish almost certainly has its closest affinities with *Cambarus (P.) parrishi*, the two being readily distinguishable only on the basis of the occurrence of marginal spines or tubercles on the rostrum of the latter. As indicated above, both occur above Lake Chatuge in localities separated by only a short distance along the river. Nowhere in the basin have they been found together as one might suspect were the two interbreeding. *Cambarus (P.) acuminatus* Faxon (1884:113) of the Saluda River basin in South Carolina and *C. (P.) chaugaensis* are also close allies of these two crayfishes, but the former may be distinguished from them by possessing strong cervical spines and lacking a postorbital angle. The latter possesses a small cervical spine, and the rostrum is almost always distinctly shorter than that of *C. (P.) hiwasseensis*.

Crayfish Associates.—In Georgia, this crayfish has been collected with only three other species (the number of times they have been found together is noted in parentheses): *Cambarus (C.) bartonii* (16), *C. (H.) longirostris* (4), and *C. (J.) nodosus* (1). In North Carolina, it was also found with *C. (D.) latimanus* and *Orconectes erichsonianus*.

Etymology.—This crayfish bears the name of the Hiwassee River basin, in which it is endemic.

Cambarus (Puncticambarus) parrishi, new species

Figures 21*d*, 89*e*, 98, 99, 227

Cambarus (Puncticambarus) sp.—Bouchard and Hobbs, 1976: 13 [in part].

Diagnosis.—Body pigmented, eyes well developed. Rostrum with margins little thickened and bearing minute to moderately large marginal tubercles. Areola 2.8 to 4.2 times as long as wide and comprising 32.1 to 34.8 percent of entire length of carapace (38.9 to 43.3 percent of postorbital carapace length). One to 5 small cervical tubercles present, cervical spines lacking. Suborbital angle acute. Postorbital ridges terminating cephalically in acute to subacute tubercles. Antennal scale approximately 2.4 times as long as broad, broadest near midlength. Chela with 1 or 2 rows of tubercles on mesial margin of palm, mesialmost row consisting of 7 to 10; lateral margin of palm costate and both fingers with well-defined longitudinal ridges dorsally. Basis of third pereiopod with tubercle opposing hook on ischium. First pleopod of first form male with rather short terminal elements: corneous central projection not tapering distally, recurved at approximately 130 degrees to main shaft of appendage, and bearing distinct subapical notch; mesial process somewhat inflated, acute, and extending caudolaterally slightly beyond tip of central projection at angle of 90 to 115 degrees to main shaft. Female with annulus ventralis shallowly embedded in sternum and only slightly asymmetrical in outline; first pleopod present. Carapace and abdomen mottled, latter with longitudinal series of dark dorsolateral splotches and more prominent series on pleura.

HOLOTYPIC MALE, FORM I.—Body subovate, depressed (Figure 99*a,j*). Abdomen narrower than thorax (14.6 and 17.7 mm); maximum width of carapace greater than depth at caudodorsal margin of cervical groove (17.7 and 13.3 mm). Areola 3.2 times as long as wide, densely punctate, with 8 punctations across narrowest part. Cephalic section of carapace 2 times as long as areola, length of areola 33.3 percent of entire length of carapace (39.7 percent of postorbital carapace length). Rostrum with slightly thickened convergent margins, interrupted by small corneous marginal tubercles at base of acumen; acumen with corneous upturned tip reaching almost to distal margin of penultimate segment of antennule; dorsal surface of rostrum concave, with setiferous punctations submarginally and in basal half; subrostral ridges moderately well developed and evident in dorsal aspect almost to marginal tubercles. Postorbital ridge short but well defined with dorsolateral groove bearing setiferous punctations and terminating cephalically in subacute corneous tubercle. Suborbital angle acute. Branchiostegal spine small with acute corneous tip. Upper surface of carapace punctate, sparsely so in gastric region; lateral surfaces weakly granulate, tubercles somewhat larger in hepatic region and cephaloventrally, with well-defined row ventral to cephalic portion of cervical groove. Cervical spine represented by group of small tubercles, none larger than those ventral to cephalic portion of cervical groove. Abdomen longer than carapace (35.0 and 33.0 mm); pleura subtruncate ventrally, angular caudoventrally. Cephalic section of telson with 2 spines in each caudolateral corner. Proximal podomere of uropod with moderately strong spine on mesial and lateral lobes; mesial ramus with moderately well developed keel on dorsal surface produced in short premarginal spine, spine on distolateral margin no larger than that on keel.

Cephalomedian lobe of epistome (Figure 99*i*) subtriangular, about 1.6 times as broad as long, with very small cephalomedian projection, its margins slightly elevated and thickened, central portion subplane and studded with setiferous punctations; fovea moderately well defined with depressions radiating cephalically to base of cephalomedian lobe. Antennule with strong spine on distal half of ventral surface of basal segment. Antenna, reaching cephalic margin of telson, with spine on distolateral margin of basis and acute tubercle on ischium. Antennal scale (Figure 99*g*) 2.4 times as long as broad, broadest at midlength, evenly rounded mesially; lamellar area about 1.2 times width of thickened lateral portion, latter terminating in strong spine. Third maxilliped moderately setose, with lateral half of ventral surface of ischium bearing submarginal row of short setae and few scattered ones but devoid of stiff setae.

Left chela (Figure 99*l*, mirror image) somewhat depressed although with palm inflated; lateral margin of palm costate, more strongly so distally. Mesial surface of palm with 2 rows of low tubercles, mesialmost row of 8, other of 7; 4 tubercles irregularly arranged between rows; remainder of palm punctate. Both fingers with well-defined longitudinal ridges dorsally, flanked by shallow setiferous punctations. Opposable margin of fixed finger with row of 6 tubercles, third from base largest; proximal 5 somewhat evenly spaced along proximal half of finger, sixth at base of distal fourth; prominent subacute tubercle situated at lower level midway between 2 distal tubercles of above-mentioned row; crowded minute denticles extending from level of third tubercle to base of corneous tip of finger; lateral margin of finger costate; lower surface punctate, with cluster at proximomesial base bearing short plumose setae. Opposable margin of dactyl with row of 10 rounded tubercles along proximal three-fifths, fourth from base largest, and crowded minute denticles from fifth tubercle to base of corneous tip of finger; mesial surface with row of 4 squamous tubercles basally; finger otherwise punctate.

Carpus of left cheliped longer than broad and with prominent oblique furrow dorsally; mesial

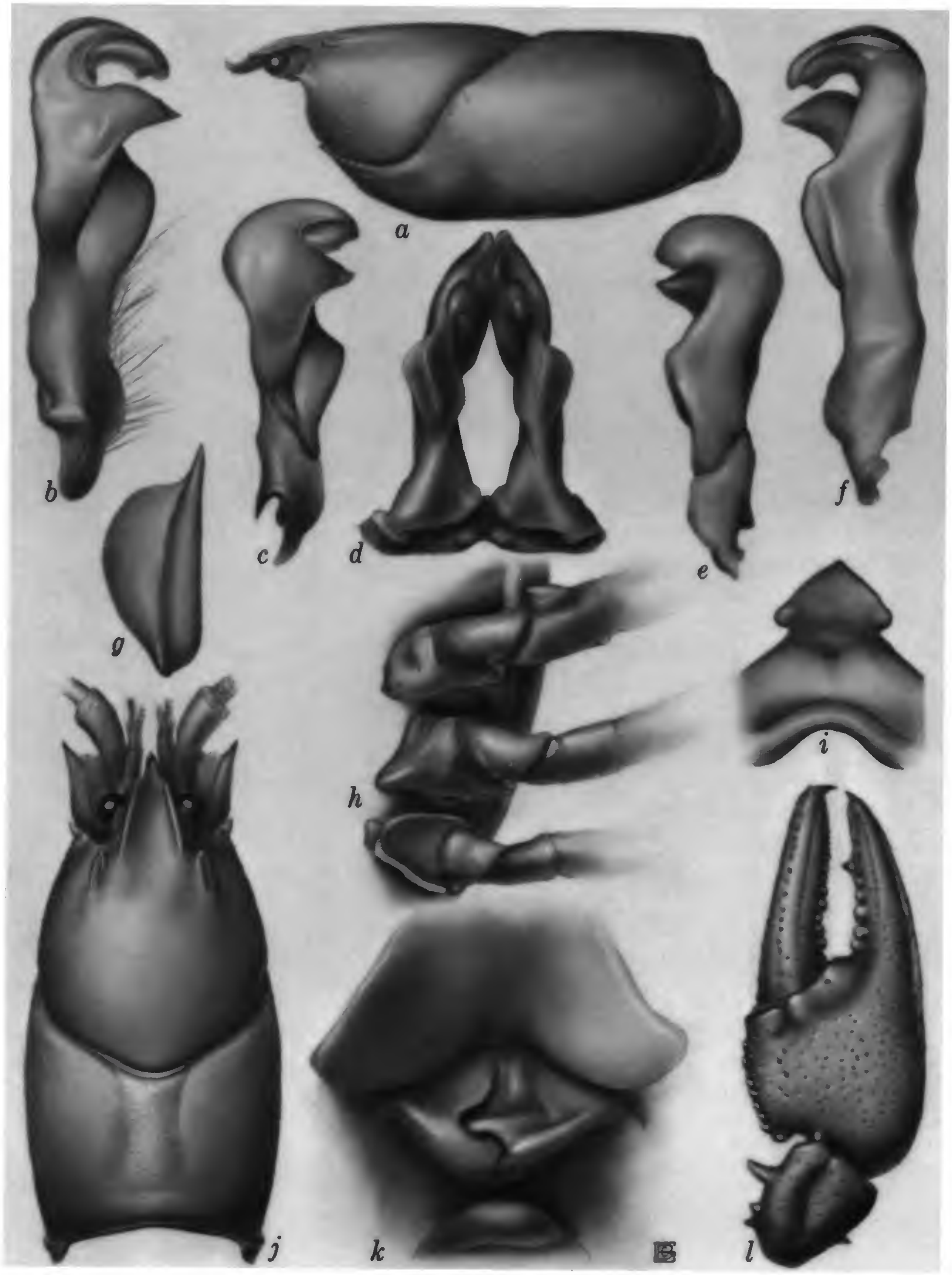


FIGURE 99.—*Cambarus (Puncticambarus) parrishi* (*a, d, g–j, l*, from holotype; *b, f*, from paratopotypic male, form I; *c, e*, from morphotype; *k*, from allotype): *a*, lateral view of carapace; *b, c*, mesial view of first pleopod; *d*, caudal view of first pleopods; *e, f*, lateral view of first pleopod; *g*, antennal scale; *h*, basal podomeres of third, fourth, and fifth pereiopods; *i*, epistome; *j*, dorsal view of carapace; *k*, annulus ventralis; *l*, dorsal view of distal podomeres of cheliped.

surface with conspicuous spikelike tubercle slightly distal to midlength and small one proximal to it; lower distal margin with 2 prominent corneous-tipped tubercles and small one proximomesial to mesial tubercle; podomere otherwise punctate. Merus with 2 acute tubercles dorsally near distal end; laterodistal condyle with small corneous-tipped tubercle; ventral surface with row of 3 acute tubercles and mesial row of 11; lateral and mesial surfaces punctate. Mesial surface of ischium with row of 4 small tubercles and more massive proximal knoblike one.

Hook on ischium of third pereiopod only (Figure 99*h*); hook simple, opposed by tubercle on basis, and extending proximally to distal end of latter; coxa of fourth pereiopod with oblique, vertically disposed caudomesial boss; coxa of fifth pereiopod with rudimentary elevated prominence ventrolateral to penis papilla.

Sternum between third, fourth, and fifth pereiopods moderately shallow and with comparatively short tufts of plumose setae extending ventromesially from margins of sternum; coxae of third and fourth pereiopods without plumose setae.

First pleopods (Figure 99*b,d,f*) symmetrical and reaching coxae of third pereiopods when abdomen flexed. (See "Diagnosis" for description.)

Allotypic Female.—Other than in secondary sexual characters, differing from holotype in following respects: acumen reaching midlength of ultimate podomere of antennule; subrostral ridges evident in dorsal aspect for only slight distance beyond caudal margin of orbit; 1 member of group of cervical tubercles slightly larger than others; mesial surface of palm of chela with 10 tubercles in mesialmost row and 8 in adjacent one, none between; opposable margin of fixed finger of chela with row of 8 tubercles; mesial surface of ischium with row of only 3. (See "Measurements.")

Annulus ventralis (Figure 99*k*) subsymmetrical in outline, shallowly embedded in sternum and, although fused to latter, slightly movable; cephalic region less strongly calcified than caudal; cephalic half with narrow median longitudinal trough flanked by subparallel rounded ridges; caudal portion of trough curving dextrally to near midlength of annulus; caudal wall somewhat elevated; sinus originating at caudal end of trough, forming dextrally tilted sigmoid curve, its caudal extremity reaching midcaudal margin of annulus; dextrally directed tongue disappearing into fossa under elevated dextral wall. Postannular sclerite between fifth pereiopods planoconvex in outline, with transverse elevation. First pleopod almost reaching midlength of annulus when abdomen flexed.

Morphotypic Male, Form II.—Differing from holotype in following respects: areola with 7 punctations across narrowest part; acumen as in allotype; cheliped with ventromesial row of 10 tubercles on merus, ischium as in allotype; hook on ischium of third pereiopod reduced, not reaching distal end of corresponding basis; boss on caudomesial angle of coxa of fourth pereiopod much reduced; sternum between third, fourth, and fifth pereiopods without plumose setae. (See "Measurements.")

First pleopod (Figure 99*c,e*) with central projection inflated, not so strongly recurved as in holotype and with distinct subterminal notch; mesial process bulbiform, directed caudolaterally at approximately 90 degrees to main shaft of appendage; juvenile suture on shaft prominent.

Color Notes (Figure 89*e*).—Ground color of carapace olive brown with light greenish tan spots and reticulations dorsally, and few scattered spots laterally. Terga of abdominal segments olive green suffused with brown and bearing pale greenish cream spots, some symmetrically arranged; each of first 5 terga with paired cephalolateral black spots, those on first and second segments somewhat broader than more caudal ones. Pleuron of first segment conspicuous because of its pale pinkish cream color. Pleura of second through sixth segments with dark, almost black, ventrally convex arc across base, and with pale greenish to pinkish cream band along cephalic and ventral margin, otherwise coloration as on tergum. Telson mostly dark brown; uropods with distinct greenish suffusion. Cheliped cream tan from base to end of proximal third of merus, there becoming gradually darker, except ventrally, and distal third and remaining podomeres very dark brown in first form males and olive brown in adult females; lateral margin, ventral surface, and prominent tubercles on chela (especially those on opposable margin of fingers) pinkish to orange cream. Remaining pereiopods pale basally, becoming dark on merus (dark olive brown on carpus and distal part of merus), and fading distally to olive or bluish olive on propodus and dactyl.

Measurements (mm)

	Holotype	*Allotype*	*Morphotype*
Carapace			
Height	13.3	14.2	9.8
Width	17.7	18.1	12.4
Entire length	33.0	35.2	24.5
Postorbital length	27.7	28.8	19.4
Areola			
Width	3.4	3.4	2.8
Length	11.0	12.2	7.9
Rostrum			
Width	4.9	5.5	3.7
Length	7.6	8.3	6.0
Chela			
Length of mesial margin of palm	10.1	9.2	6.0
Width of palm	13.5	11.9	7.1
Length of lateral margin	30.0	27.5	17.1
Length of dactyl	19.2	17.0	10.1
Abdomen			
Width	15.0	18.4	12.0
Length	36.5	39.2	29.0

TYPES.—The holotypic male, form I, the allotypic female, and morphotypic male, form II, are deposited in the National Museum of Natural History, Smithsonian Institution, numbers 144957, 144958, and 144959, respectively, as are the following paratypes: 27♂I, 21♂II, 39♀, 3j♂, 9j♀, and 2 ovigerous ♀. Specimens from Clay County, North Carolina, are excluded from the type series.

TYPE-LOCALITY.—Hiwassee River, 2 miles north of the junction of Georgia Routes 17 and 66 on Route 17, approximately 7 miles southeast of Hiwassee. There, the very swift, clear water flows over a bed, some 10 meters wide and one-half to a meter deep, consisting of sand and rocks. Trees in the area include *Platanus occidentalis*, *Juglans nigra*, *Cornus florida*, *Quercus* sp., and *Carya* sp.

RANGE.—Restricted to the headwaters of the Hiwassee River in Towns County, Georgia, and Clay County, North Carolina.

SPECIMENS EXAMINED.—I have examined a total of 143 specimens (122 from Georgia and 21 from North Carolina) from the following localities. GEORGIA. *Towns County*: (1) type-locality, 1♂I, 1♂II, 1♀, 2 ovig ♀, 27 Apr 1967, T. Unestam, HHH, collectors; 7♂I, 11♂II, 13♀, 9 Oct 1969, K. R. Martin, HHH; (2) Soapstone Creek 1.2 mi E of jct of St Rtes 180 and 66 on latter, 1♀, 6 Nov 1958, K. W. Simonds; 4♂I, 2♂II, 5♀, 9 Oct 1969, KRM, HHH; (3) Soapstone Creek close to YMCA Camp Pioneer on St Rte 66, 4 mi upstream from jct with Hiwassee River, 2♂I, 1♂II, 3♀, 22 Nov 1968, F. K. Parrish; 1♂I, 1♂II, 3 May 1969, FKP; 5♂I, 2♂II, 6♀, Aug 1969, FKP, 5♂I, 2♂II, 5♀, 9 Oct 1969, KRM, HHH; (4) Hiwassee River and mouth of Soapstone Creek at jct of St Rtes 75 and 66, 1♂I, 1♂II, 2♀, 20 Aug 1952, G. B. Hobbs, HHH; 1♀, 24 Apr 1954, D. C. Scott; 1♂I, 1j♂, 1j♀, 6 Nov 1958, KWS; 4♂I, 1♀, 27 Apr 1967, TU, HHH; 2♂I, 3♂II, 4♀, 2j♂, 8j♀, 9 Oct 1969, KRM, HHH; 2♂II, 3♀, 1j♂, 24 Oct 1976, T. A. English, Jr., HHH; (5) Center Creek (? = Cynth Creek), 3♀, 13 Aug 1943, DCS. NORTH CAROLINA. *Clay County*: (6) Shooting Creek on US Hwy 64, 1♂I, 10 Jan 1960, KWS; (7) creek 4.3 mi N of Hayesville on unnumbered rd to Andrews, 8♂II, 7♀, 2j♂, 2j♀, 1 ovig ♀, 5 Jun 1959, KWS.

VARIATIONS.—The most conspicuous variations occur in the shape of the rostrum and in the size and position of the marginal tubercles. The margins may converge gently almost from base to tip, interrupted only by very small marginal tubercles. The latter are sometimes so small that they are completely obscured by the submarginal setae of the rostrum. In contrast, the rostral margins may converge gradually to the base of the acumen, where strong spiniform tubercles conspicuously define the caudal limit of the latter. The length of the acumen is highly variable because of the distance the tubercles at its base are removed from the apex; in a few specimens, the apices of the marginal tubercles are exceeded by that of the acumen by hardly more than the length of one of the tubercles. In general the smaller individuals have more conspicuous marginal tubercles than do the larger ones. The areola, although not so variable in width, may have six to nine punctations across the narrowest part. The palm of the chela usually bears a row of eight or nine tubercles with only a few situated dorsolateral to it; in an occasional individual in which the chela is believed to have been regenerated, there are as few as six in this row, and infrequently there occur only seven tubercles in an otherwise typical chela. In a small proportion of the specimens, one or both chelae have a second well-defined row on the palm, consisting of as many as nine tubercles. The large mesial spine on the carpus of the cheliped is frequently bifid. Other variations are far less conspicuous than those mentioned and consist largely in slight differences in number and relative degree of development of tubercles on the various podomeres of the cheliped.

SIZE.—The largest specimen available is a female having a carapace length of 37.0 (postorbital carapace length, 30.4) mm. The largest and smallest first form males have corresponding lengths of 36.3 (29.6) mm and 25.0 (20.1) mm, respectively, and those of the smallest ovigerous female 26.7 (21.3) mm.

LIFE HISTORY NOTES.—First form males have been collected in January, April, May, August, October, and November. Several first form individuals taken in mid-August of 1969 had recently molted. One of the ovigerous females was collected on 5 June 1959 and two on 27 April 1969.

A tabulation of the number of eggs carried by these females follows. Fifteen eggs had become detached in the jar containing the first two females.

Carapace and postorbital carapace lengths (mm)	*Number of eggs*	*Diameter of eggs (mm)*
30.2 (24.3)	112	2.2–2.3
28.4 (22.4)	80	2.3–2.4
26.7 (21.3)	38	2.5–2.6

ECOLOGICAL NOTES.—*Cambarus (P.) parrishi* is known only from rocky stretches and riffle areas in the clear headwaters of the Hiwassee River, where it shares the stream with *C. (C.) bartonii.* Although both species are found beneath rocks in the stream, the latter is far less abundant in the localities cited and is largely limited to the swiftest water or to shallow excavations under rocks near the shore. *Cambarus (P.) parrishi* is found in greater numbers in rocky areas between riffles, where it not only finds cover under rocks but also in accumulated debris trapped among the rocks. (See corresponding notes for *C. (P.) hiwasseensis.)*

Seasonal Data (Georgia and North Carolina)

Sex/stage	*J*	*F*	*M*	*A*	*M*	*J*	*J*	*A*	*S*	*O*	*N*	*D*
♂I	1			5	1			6		18	3	
♂II				1	1	8		3		20	1	
♀				3		7		11		30	4	
♂j						2				3	1	
♀j						2				8	1	
♀ ovig				2		1						

RELATIONSHIPS.—This crayfish has its closest affinities with *Cambarus (P.) hiwasseensis, C. (P.) georgiae,* and *C. (P.) extraneus,* differing from the former most conspicuously in possessing marginal tubercles or spines on the rostrum, usually having 10 to 12 (instead of fewer than nine) punctations across the narrowest part of the areola, and in lacking or in having very weak tubercles on the proximomesial surface of the dactyl of the chela. It may be distinguished from the latter two species very readily by the absence of cervical spines.

GEORGIA CRAYFISH ASSOCIATES.—*Cambarus (P.) parrishi* has been collected with the following crayfishes (the number of times they have been found together is noted in parentheses): *Cambarus (C.) bartonii* (7) and *C. (J.) nodosus* (2).

ETYMOLOGY.—This crayfish is named in honor of my friend Fred K. Parrish, who has added materially to our knowledge of the Georgia crayfishes not only through his personal collecting efforts but also in arranging for his students to assist me in field work in several parts of the state.

Genus *Fallicambarus*

Astacus.—Cottle, 1863:217 [not Fabricius, 1775:413].

Cambarus.—Faxon, 1884:115 [in part].

Subgenus *Bartonius* Ortmann, 1905a:120 [in part].

Fallicambarus Hobbs, 1969a:111. [Type-species, by original designation, *Cambarus strawni* Reimer, 1966:111. Gender: masculine.]

Subgenus *Creaserinus* Hobbs, 1973b:463. [Type-species, by original designation, *Astacus fodiens* Cottle, 1863:217. Gender: masculine.]

DIAGNOSIS.—Antenna never with conspicuous fringe on mesial border. Third maxilliped with teeth on mesial margin of ischium. Rostrum without marginal spines in adults. Areola linear or obliterated along part of its length. Mesial margin of palm of depressed chela with row of fewer than 12 tubercles; opposable margin of dactyl with prominent excision. First pleopods of first form male symmetrical, contiguous basally, and terminating in 2 elements bent caudally at least 90 degrees to shaft of appendage: arched central projection corneous, bladelike, or tapering (but flattened laterally), and usually lacking subapical notch; noncorneous mesial process never bulbiform and often appearing twisted and usually with eminence on cephalic (morphological) border slightly distal to base; cephalic process, absent in Georgia members, but when present small, at least partly corneous, situated mesially at base of mesial process, and directed caudally or caudodistally. Branchial count 17 + epipodite.

RANGE.—From Texas to Ontario and southward in the coastal plain to the panhandle of Florida.

SPECIES.—Of the 14 members of the genus, only *Fallicambarus (Creaserinus) hedgpethi* has been found in Georgia. A second undescribed species perhaps will be found in the Savannah River basin of the state, inasmuch as it occurs in a swamp bordering the river in Barnwell County, South Carolina.

Subsequent to the publication of Hobbs' (1974b) checklist of the North and Middle American crayfishes, only two species belonging to the genus *Fallicambarus* have been described: *Fallicambarus (Creaserinus) caesius* Hobbs (1975a:24), and *F. (C.) danielae* Hobbs (1975a:28).

Subgenus *Creaserinus*

Subgenus *Bartonius* Ortmann, 1905a:120 [in part].
Subgenus *Cambarus*.—Fowler, 1912:34 [in part; not Erichson, 1846:97].
Subgenus *Creaserinus* Hobbs, 1973b:463 [type-species, *Astacus fodiens* Cottle, 1863:217].

DIAGNOSIS.—First pleopod of male lacking proximomesial spur. Cheliped with sufflamen; chela with tubercles on dorsal surface largely limited to mesial 2 rows, and lateral margin of palm and basal portion of immovable finger costate. Second pereiopod with mesial surface of chela and part of that of carpus bearing dense mats of plumose setae except in *F. byersi*. Ischium of only third pereiopod with hook. Coxa of fourth pereiopod with boss not conspicuously large. Antennal scale comparatively wide and abdomen broadly joined to thorax except in *F. byersi, F. caesius, F. danielae,* and *F. oryktes*. (Modified from Hobbs, 1973b.)

RANGE.—Same as that of genus.

SPECIES OCCURRING IN GEORGIA.—*Fallicambarus (Creaserinus) hedgpethi.*

HABITAT.—See "Ecological Notes" for *F. (C.) hedgpethi.*

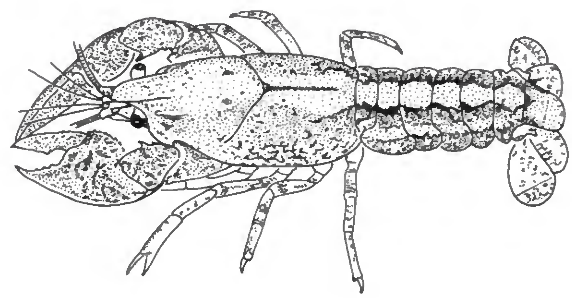


FIGURE 100.—Color pattern of *Fallicambarus (Creaserinus) hedgpethi* from 0.4 mi W of Cedar Springs on St Rte 273, Early Co.

Fallicambarus (Creaserinus) hedgpethi (Hobbs)

FIGURES 20*j*, 100–102, 229

Cambarus argillicola Faxon, 1884:115, 116, 144 [in part].
Cambarus fodiens.—Creaser, 1931b:269 [in part].—Hobbs and Hart, 1959:149*, 151, 159-161, 164, 169*, 171, 185, 187-188*, fig. 11.—Hart, 1959:204*.—Hobbs, 1968b:K-16* [in part]; 1972b:147 [in part].—Crocker and Barr, 1968: 132* [in part], fig. 86 [in part].
Cambarus hedgpethi Hobbs, 1948:224-230, fig. 17a-f,h,i,l.—Penn and Hobbs, 1958:454, 462, 465, 467, 471, 473, 476-478, figs. 11, 28, 42, 55.—Penn, 1959:8, 14-17, figs. 9, 27, 46, 64.—Reimer, 1969:50, 51, figs. 2, 39.
Cambarus uhleri.—Hoffman, 1963:330*.

Cambarus hedgepethi.—Walls and Black, 1967:60 [erroneous spelling].
Fallicambarus hedgpethi.—Hobbs, 1969a:111, 112, fig. 20f; 1972b:102, 147, figs. 82c, 83d; 1974b:23, fig. 83.—Reimer and Clark, 1974:175, figs. 27–30.
Fallicambarus (Creaserinus) hedgpethi.—Hobbs, 1973b:463, 480 [in part], fig. 4.
Fallicambarus (Creaserinus) fodiens.—Hobbs, 1973b:480 [in part].
Fallicambarus uhleri.—Hart and Hart, 1974:129*.
Fallicambarus hedgepethi.—Huner, 1977:11 [color photograph; erroneous spelling].

The above list of references is a selected one, including synonyms, illustrations, summary articles, and/or those pertaining to the occurrence of the species in Georgia. The latter are marked with an asterisk. A complete list of references prior to 1948 is included in Hobbs (1948:224).

Summary of Literature.—In his revision of the genus *Cambarus*, Hobbs (1969a) placed this crayfish in the newly erected genus *Fallicambarus*, and, in reviewing the members of the genus (1973a), he assigned it to the subgenus *Creaserinus*. Most of the literature dealing with this species is based on records of its occurrence in Louisiana, Oklahoma, Tennessee, and Texas. The few data available on its life history, habits, and habitat may be found in Hobbs (1948:228), Penn and Hobbs (1958:477–478), Penn (1959:16), Hobbs and Hart (1959:187–188), and Reimer and Clark (1974:175).

All of the references to its presence in Georgia are based on six specimens from Seminole County that were misidentified by Hobbs and Hart (1959) as *Cambarus fodiens* and by Hoffman (1963) as *C. uhleri*. Hart (1959) noted that they served as hosts to the ostracod *Entocythere equicurva* (= *Uncinocythere equicurva*). Although he did not cite a specific locality, the specimens from Seminole County were the only members of the species available to him. Uncertainty exists as to the source of the error in the identification of the same six crayfish as *Fallicambarus uhleri* (Hart and Hart, 1974); perhaps it was based on a tentative identification supplied to them by me. Hoffman (1963) recorded two of the same six specimens as the host of his new branchiobdellid worm, *Cambarincola osceola*.

An inexplicable error was made by me (Hobbs, 1973b:480) in the "Explanation of Figure 4 and Key to Species." Couplet "k" should have read as follows:

k Hump on mesial process of first pleopod never obscuring part of central projection in lateral aspect; central projection without or with rudimentary subapical notch; opposable margin of fixed finger of chela with 2 major tubercles (infrequently in Georgia) .... ***F. (C.) hedgpethi***

k′ Hump on mesial process of first pleopod obscuring part of central projection in lateral aspect; central projection with subapical notch (often abraded in middle to late intermolt stages); opposite margin of fixed finger with only 1 tubercle larger than others .... ***F. (C.) fodiens***

Diagnosis.—Body pigmented, eyes well developed. Rostrum without marginal spines or tubercles. Areola obliterated along part of length and consisting 38.4 to 40.4 percent of total length of carapace (45.6 to 48.0 percent of postorbital carapace length). Cervical spine small; branchiostegal spine represented at most by small tubercle; hepatic spines absent; suborbital angle obsolete; postorbital ridge without spine or tubercle. Antennal scale approximately 2.5 times as long as wide, broadest distal to midlength. Ischium of third maxilliped with heavy beard of plumose setae mesially, and lateral row of similar setae obscuring much of lateral half of podomere. Chela depressed, with palm bearing 2 well-defined rows of 6 to 8 tubercles mesially; opposable margin of fixed finger with 1 or 2 (latter rarely in Georgia) tubercles larger than others; corresponding margin of dactyl with prominent excision on basal third. Second pereiopod of male with mesial surface of carpus and palm of chela studded with dense mat of plumose setae. First pleopod of first

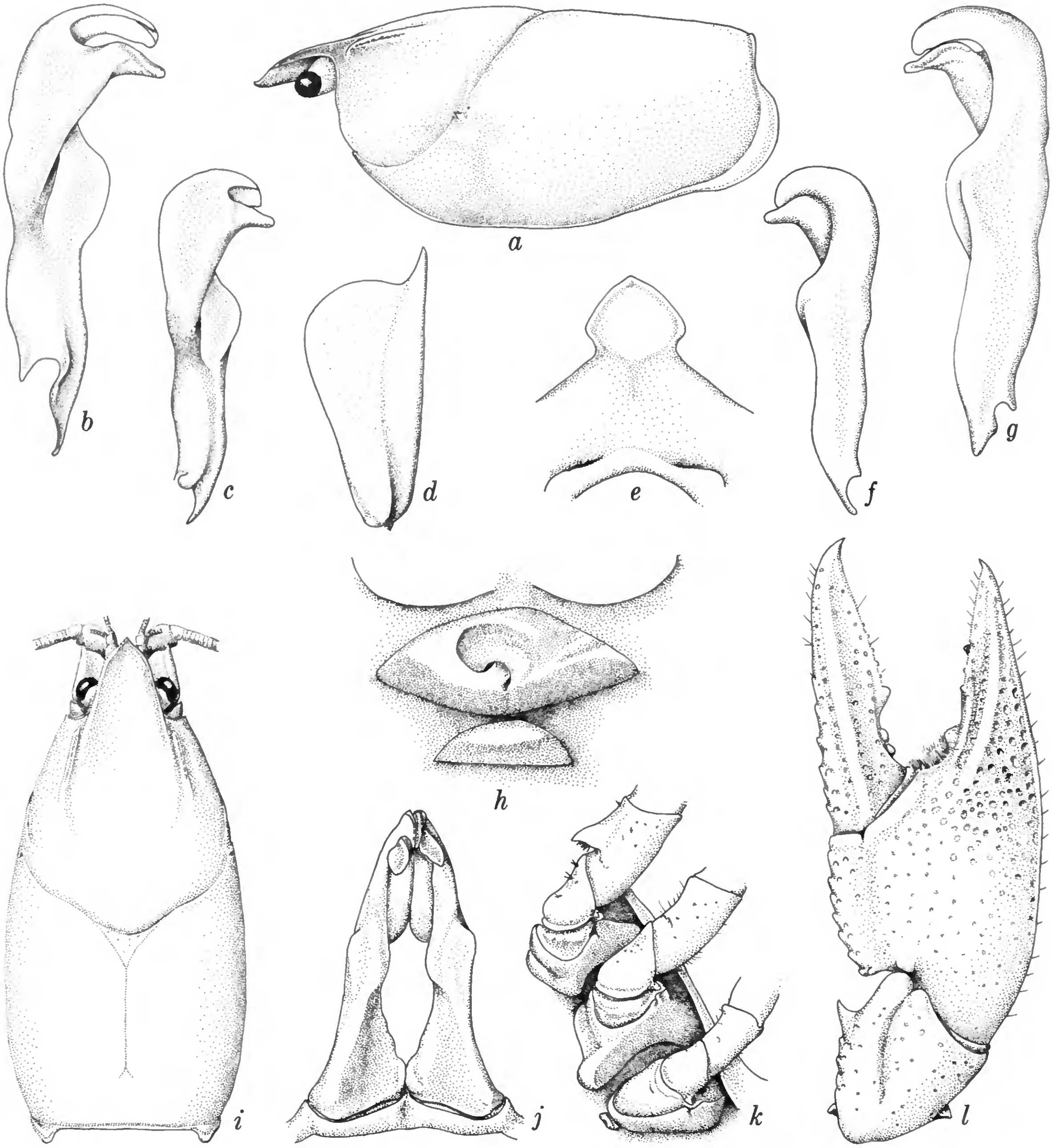


FIGURE 101.—*Fallicambarus* (*C.*) *hedgpethi* (*c, f, l*, from male, form II, collected 0.4 mi W of Cedar Springs, Early Co; *h*, from female, and others from male, form I, obtained 3.1 mi N of Iron City, Seminole Co): *a*, lateral view of carapace; *b, c*, mesial view of first pleopod; *d*, antennal scale; *e*, epistome; *f, g*, lateral view of first pleopod; *h*, annulus ventralis; *i*, dorsal view of carapace; *j*, caudal view of first pleopods; *k*, proximal podomeres of third, fourth, and fifth pereiopods; *l*, dorsal view of distal podomeres of cheliped.

form male with rather long bladelike central projection bearing rudimentary subapical notch, rounded apically, curved gently at about 120 degrees to shaft of appendage, and not reaching tip of mesial process; latter disposed subparallel to central projection, with eminence ("hump") at midlength not obscuring part of central projection, tapering to rounded apex, somewhat flattened and appearing twisted. Female with annulus ventralis subspindle shaped and firmly fused to sternum; first pleopod reduced to tuberculiform rudiment.

Color Notes (Figure 100).—Based on first form males from Choctaw County, Alabama.) Ground color of body and appendages olive tan overlain with black to greenish tan markings. Cephalic region with irregular small spots except for pale area along anterior part of mandibular and anteroventral branchiostegal region. Anterior triangular area and dorsomedian line of fusion of branchiostegites dark brown to black; dorsal part of latter with scattered dark spots becoming reticulate ventrolaterally over paler olive background; dark spots on caudodorsal part of branchiostegites arranged in paired linear series in line with those on abdomen. Linear series on latter, flanking pale olive median stripe, converging gently posteriorly and uniting at cephalic part of telson in dark spot. Bases of pleura with longitudinal series of dark splotches separated from more dorsal series by pale longitudinal stripe; otherwise pleura pale with small, dark, irregular splotches. Telson and uropods likewise pale olive with irregular pattern of small spots, some forming reticulate pattern. All cephalic and thoracic appendages olive with olive tan to brown splotches.

Types.—Holotype, morphotype, USNM 85146 (♂I, ♂II), and allotype, USNM 85147 (♀); paratypes, USNM.

Type-Locality.—Lower middle part of the Aransas National Wildlife Refuge, Aransas County, Texas.

Range.—Oklahoma and Texas eastward to Tennessee and southwestern Georgia. In the latter, it has been found in the southwestern part of the Dougherty Plain and Fall Line Hills districts. The limits of its range and that of the closely allied *F. (C.) fodiens* (Cottle, 1863:217) have not been accurately determined.

Georgia Specimens Examined.—I have examined only nine specimens from the following localities. *Early County:* (1) along Sawhatchee Creek on St Rte 273, 0.4 mi W of Cedar Springs, 2♂II, 25 Jun 1975, D. J. Peters, J. E. Pugh, HHH, collectors; (2) ditch 0.7 mi E of Blakely on St Rte 62, 1j♀, 2 Sep 1955, C. W. Hart, Jr., HHH. *Seminole County:* (3) Dry Creek 3.1 mi N of Iron City on secondary road, 3♂II, 1♀, 1 Sep 1955, CWH, HHH; 1♂I, 1♀, 9 Sep 1955, CWH, HHH.

Variations.—There are few variations of significance among the nine specimens from Georgia: the cephalic section of the telson bears two or three spines in the caudolateral angle; the mesial surface of the carpus of the cheliped has, in addition to the large spikelike tubercle, one to four tubercles proximal to it; the mesial surface of the palm of the chela bears six to eight tubercles in the mesialmost row and five or six in the other, frequently irregular, row. The opposable margin of the fixed finger usually supports one tubercle that is conspicuously the largest, but occasionally there are two larger tubercles that are subequal in size.

Size.—The largest specimen from Georgia is the first form male, which has a carapace length of 26.7 (postorbital carapace length 22.5) mm. The largest female has corresponding lengths of 20.1 (16.6) mm. No ovigerous female or one carrying young is available.

Life History Notes.—The only first form male collected in Georgia was found in June. Elsewhere they have been taken in January, February, April, June, July, September, November, and December. Ovigerous females were obtained in Texas in February and September, and one carrying young was collected in Texas in September. These data were compiled from Hobbs (1948: 228–229), Penn and Hobbs (1958:477), and from specimens in the Smithsonian Institution. In their notes on the life history of the species in Texas, Penn and Hobbs stated that "the overwhelming majority of the individuals examined are juveniles collected in February and March, indicating that egg laying occurs in January and February." The occurrence of ovigerous females and one carrying

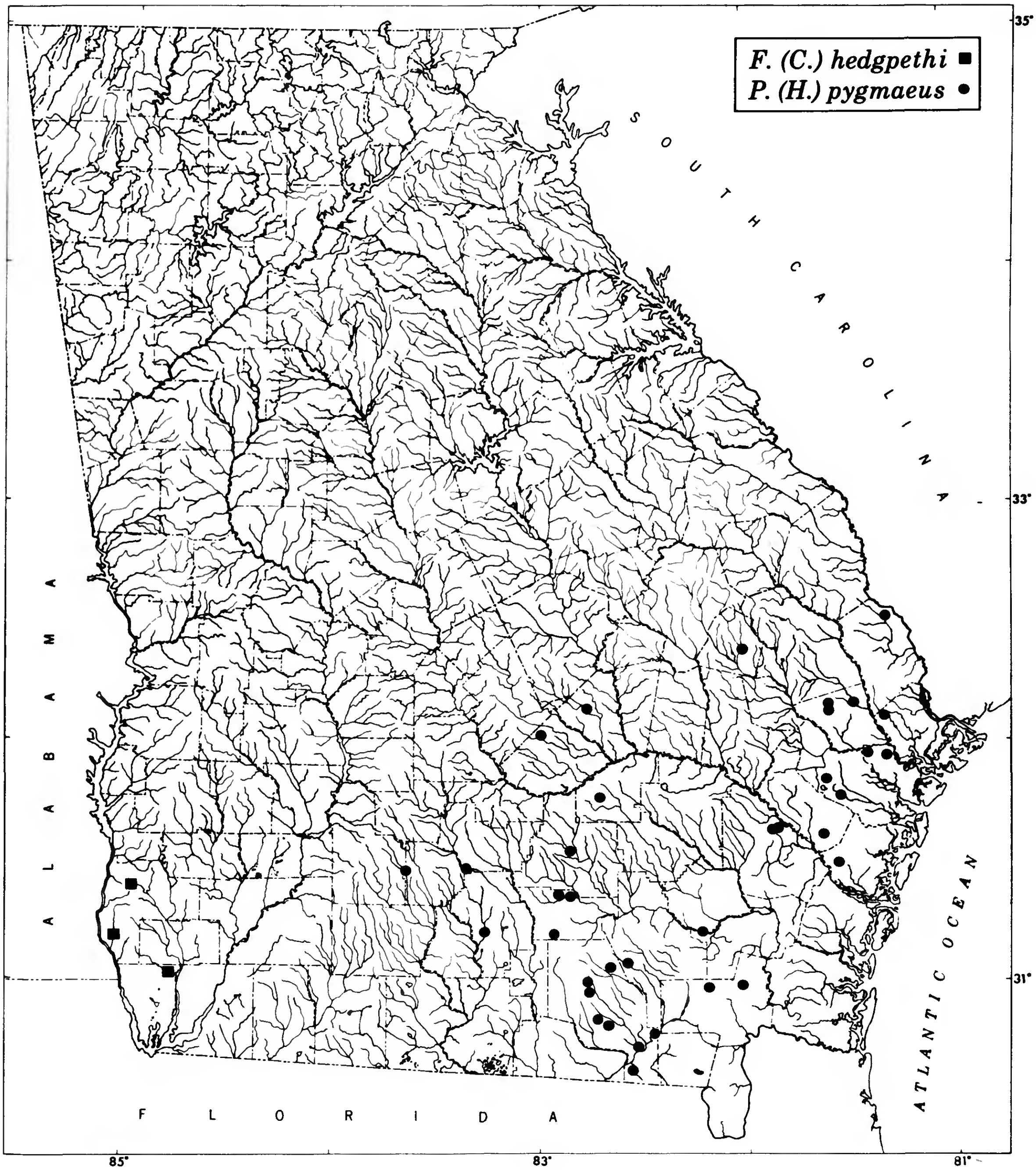


FIGURE 102.—Distribution of *Fallicambarus (C.) hedgpethi* and *Procambarus (H.) pygmaeus* in Georgia.

young in September, however, suggests at least two seasons of egg laying, if indeed it does not occur through the year.

Ecological Notes.—In Georgia, this crayfish was collected from a sluggish swamp stream and from complex burrows "in mucky soil in the creek bed ..." in Seminole County (Hobbs and Hart, 1959:187) and from burrows adjacent to a moderately flowing stream in Early County. In Louisiana, Penn (1959:16) indicated that approximately "one fourth of the specimens seen have been taken from burrows; the remainder were from a wide variety of shallow bodies of water, including roadside ditches, overflow puddles, sloughs, swamps, swamp pools and ponds." In Texas, Hobbs (1948:228), quoting from a letter from Joel W. Hedgpeth, noted that the area in which the burrows were located "is often quite damp with runoff ponds, etc., and is separated from a salt marsh by a low artificial dyke in the form of a road. At times in the spring the mud pillars are a conspicuous feature of the landscape." According to Reimer and Clark (1974: 175) this crayfish "has caused much damage to earthen dams by its burrowing activity."

Georgia Crayfish Associates.—In Early County, *C. (L.) diogenes diogenes* was found in burrows adjacent to those of *F. (C.) hedgpethi*, and *P. (Pe.) spiculifer* and *P. (S.) paeninsulanus* were found in the nearby stream. In Seminole County, its associates in the creek were *Faxonella clypeata* and *P. (S.) paeninsulanus.*

Remarks.—The chief character (the presence of two major tubercles on the opposable margin of the fixed finger of the chela) chosen by Hobbs to distinguish this crayfish from its closest kin, *F. (C.) fodiens,* has not proven to be a reliable one, and it was on the basis of this character that the Georgia specimens were identified as *Cambarus fodiens* by Hobbs and Hart (1959). The features that seem most consistently to serve as distinguishing ones between the two are the comparatively longer, less strongly arched central projection of the first pleopod of the first form males of *F. (C.) hedgpethi*, and, in the females of the same species, an annulus ventralis that is subspindle shaped in outline.

Genus *Faxonella*

Faxonella Creaser, 1933b:21. [Type-species, by monotypy, *Cambarus clypeatus* Hay, 1899a:122. Gender: feminine. Proposed as a subgenus of *Faxonius*; elevated to generic rank by Fitzpatrick, 1963:61, and questionably by Creaser, 1962:3.]

Diagnosis.—

Antenna never with conspicuous fringe on mesial border. Third maxilliped with teeth on mesial margin of ischium. Mesial margin of palm of chela with or without much reduced tubercles; lateral margin of fixed finger never with row of spines or tubercles; opposable margin of dactyl never with prominent excision. Areola moderately broad at midlength. Ischium of third pereiopod of male with hook. Coxa of fourth pereiopod of male without caudomesial boss. First pleopods of first form male symmetrical, contiguous basally, and terminating in one long (central projection) and one short (mesial process) element, latter [sometimes obsolete] no more than half length of former; central projection of paired appendages always overlapping. Female with annulus ventralis freely movable; first pleopod rudimentary to ... absent. Branchial ... [count] 17 + ep. (Hobbs, 1974a:13).

Range.—Le Flore and McCurtain counties, Oklahoma, and Cass and Marion counties, Texas, eastward to Gadsden County, Florida, and Richland County, South Carolina.

Habitat.—The members of the genus *Faxonella* are primarily inhabitants of fluctuating or temporary lentic or sluggish lotic habitats. They are found abundantly in pools or ponds in swamps and roadside ditches, in borrow pits, in backwaters and littoral areas of streams, and in simple burrows in or adjacent to such bodies of water.

Species.—Four species have been assigned to the genus: *Faxonella beyeri* (Penn, 1950a:166), *F. clypeata, F. creaseri* Walls (1968:413), and *F. blairi* Hayes and Reimer (1977:1). Of these, only *F. clypeata* occurs in Georgia.

Remarks.—Both the strong similarity in morphology and habits of the crayfishes assigned to this species group furnish evidence of their close affinities. Among them, *F. beyeri* is probably the most generalized in that the male possesses a pleopod with a relatively short central projection and proportionately long mesial process, and the annulus ventralis is less sculptured than in the other three. In respect to the pleopod, *F. creaseri*, with a long central projection and a compara-

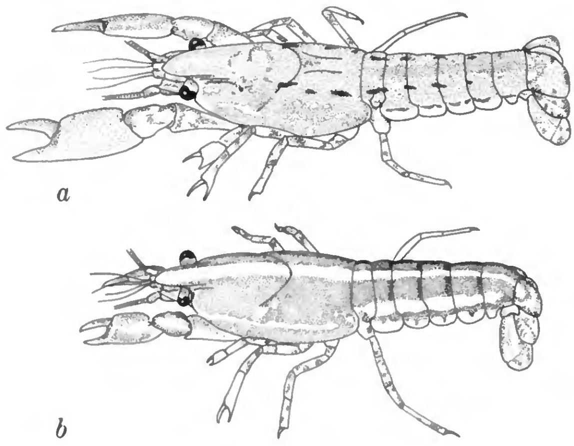


FIGURE 103.—Color patterns in *Faxonella clypeata*: *a*, first form male from 6.7 mi N of Chauncey on St Rte 165, Dodge Co; *b*, female from pools along Ogeechee River at St Rte 24, Bulloch-Screven Co line.

tively strongly developed mesial process, is somewhat transitional toward *F. clypeata* and *F. beyeri*. The latter two are distinctly more closely related than is either to their other congeners. Perhaps *F. clypeata*, which has by far the largest range of the four, is the most advanced species of the genus. Attesting to its divergence is the frequent vestigial state of the mesial process of the first pleopod.

Faxonella clypeata (Hay)

FIGURES 19*f*, 103–106, 230

Cambarus clypeatus Hay, 1899a:122–123, fig. 2.—Creaser and Ortenburger, 1933:17, 36, 40, figs. 13, 28.—Smith, 1953: 79.

Faxonius (Faxonella) clypeatus.—Creaser, 1933b:19–21, pl. I: figs. 7, 8, pl. II: figs. 1, 2.

Orconectes clypeatus.—Hobbs, 1942a:352 [by implication].—Smith, 1953:79–95, figs. 1–3.—Penn and Hobbs, 1958: 462, 481, figs. 17, 34, 47, 62.—Black, 1958:190–202, figs. 1–24.—Penn, 1959:8, 15–17, figs. 8, 30, 49, 80.

Orconectes (Faxonella) clypeata.—Hobbs, 1942b:14, 15, 20, 21, 28, 106, 148, 154–156*, figs. 181–185.

Orconectes (Faxonella) clypeatus.—Penn, 1952:746.—Hobbs and Hart, 1959:149, 151, 156, 159–161, 164, 168, 171, 172*, 175, 178, 184*, 185*, 188, fig. 25.—Fitzpatrick, 1962:246–247.

Faxonella clypeata.—Creaser, 1962:3 [by implication].—Fitzpatrick, 1963:57–62*, 64–78, figs. 1–22*.—Mobberly, 1965:45–51, figs. 1, 2.—Mobberly and Pfrimmer, 1967: 82–88.—Reimer, 1969:50, 51, 55, 56*, figs. 21, 34; 1972: 264.—Hobbs, 1972b:29, fig. 19c; 1974b:24, fig. 89.—Hart and Hart, 1974:(22, 28, 30, 32, 33, 129, 131)*.—Hobbs III, Thorp, and Anderson, 1976:3, 5, 25–26, figs. 10, 22.

Faxonella clypeta.—Unestam, 1969:203 [erroneous spelling].

Faxonella clyptea.—Spitzy, 1976:445 [erroneous spelling].

Faxonella cylpeata.—Hobbs III, Thorp, and Anderson, 1976: 13 [erroneous spelling].

The list of references cited here is a selected one, including all synonyms, summary articles, citations to most illustrations, and observations on distribution, ecology, and life history. Chief among the omissions are experimental work and additions of new locality records. Specific references to the occurrence of the species in Georgia are indicated by asterisks.

SUMMARY OF LITERATURE.—By far the most comprehensive studies of the species are those of Smith (1953) and Fitzpatrick (1963), the former devoting her attention to its life history and the latter primarily to geographic variation, although he also included additional data on its life history. Black (1958) presented an account of the ontogeny of the first and second pleopods of the male, including data on growth. Mobberly and Pfrimmer (1967) found that individuals of the species do not have a home range and that dispersal appears to be influenced by depth of water and is unrelated to population density. The first record of the occurrence of this crayfish in Georgia is that of Hobbs (1942b:155), who reported its presence in Dougherty, Emanuel, and Jenkins counties. The first specific localities cited were those of Hobbs and Hart (1959:185) in Baker, Early, and Dougherty counties. Fitzpatrick (1963: 62) reported it from Baker, Bulloch, Burke, Dooly, Dougherty, Early, Emanuel, Jenkins, Johnson, and Seminole counties. Hart and Hart (1974) noted its occurrence in localities in Bleckley, Crisp, Laurens, Montgomery, Telfair, Twiggs, Wheeler, and Wilkinson counties, where it harbored one or more of seven species of entocytherid ostracods. The only observations on its habitat in Georgia were presented by Hobbs and Hart (1959:184–185), who noted that it occurs in "roadside ditches, borrow pits, cypress ponds, sluggish silty streams, and [in] submerged vegetation in clear, sand bottomed streams. It also constructs simple burrows with well formed chimneys that range from a few inches to a foot in height." They and Fitzpatrick (1963) reported that first form males had been collected in the state from February to June and in August and September.

DIAGNOSIS.—Rostrum usually lacking marginal spines or tubercles. Postorbital ridges terminating cephalically with or without spines or tubercles. Cervical spine usually lacking but sometimes represented by small spine or tubercle. Areola 1.9 to 4.5 (average 3.3) times as long as broad and constituting 26.7 to 34.9 (average 30.7) percent of entire length of carapace (35.5 to 43.6, average 38.8, percent of postorbital carapace length). Mesial margin of palm of chela longer than dactyl in males, subequal in females; entire dorsal surface of palm studded with tubercles in large individuals; opposable margins of fingers contiguous throughout length, sometimes provided with 2 tubercles on basal half of both fingers (more often none evident in males), and always with densely crowded denticles, only single row in females and young second form males. Ischium of third pereiopod of first form male with curved hook overreaching basioischial articulation and not opposed by tubercle on basis. Caudomesial angle of fourth pereiopod of male without prominent boss. First pleopod of male with central projection reaching coxa of second pereiopod, occasionally caudal part of first, and more than twice as long as mesial process, latter ranging from spiniform to vestigial; first form male with central projection of 1 pleopod overlapping that of other member of pair, parallel in second form male. Female with annulus ventralis movable, not firmly fused to sternum anteriorly, subcircular in outline, conspicuously sculptured; first pleopod absent.

COLOR NOTES (Figure 103).—Like many of the crayfishes in Georgia, this species occurs in two rather distinctive color patterns, differing chiefly in the presence or absence of a median dorsal light stripe extending from the rostrum to the sixth abdominal tergum. The striped pattern is described in detail, and the differences in the nonstriped form are indicated.

Carapace olive tan to reddish brown, with broad, pale cream tan stripe extending from rostrum to caudal margin of carapace; orbital and most of hepatic areas pinkish cream; oblique dark olive line extending posteroventrally from antennal region; mandibular area olive; paired olive charcoal bands, narrowing posteriorly, flanking median stripe from level of cephalic ends of postorbital ridges to cervical groove. Areola bounded by paired, broad olive charcoal bands; lateral surface of branchiostegites pinkish tan with pinkish cream spots, some linearly arranged. Abdomen with median pinkish tan stripe flanked by pair of broad olive chocolate ones, converging posteriorly and uniting on telson, or sometimes to form median stripe on sixth abdominal tergum, continuing onto cephalic section of telson; olive chocolate stripe subtended laterally by pale pinkish cream one, and it, in turn, by undulating chocolate one along bases of pleura, latter with cream marginal part encompassing tan to reddish area. Cephalic section of telson with paired dark olive spots antero- and posterolaterally; otherwise it and uropods with olive to tan reticulate pattern on pale olive. Antennule and antenna olive tan with charcoal markings and olive flagella. Cheliped mostly olive tan with olive brown tubercles (occasionally in larger males pink to reddish, especially along mesial surface of merus and ventral surface of chela). Remaining pereiopods pinkish basally, giving way to pale olive with olive tan markings, sometimes appearing banded. Ventral surface of body cream.

Individuals lacking stripe, with almost concolorous pinkish brown dorsal surface of carapace marked by charcoal spot at anterior extremity of areola and paired dorsolateral spots on branchiostegites abutting cervical groove; lateral surface paler brown mottled in pinkish cream; caudal ridge suffused with charcoal. Abdomen olive tan, with transverse brown bands along caudal margin of first through fifth terga, and darker median area bounded anterolaterally by black spots on all 6 terga; spots progressively smaller in succeed-

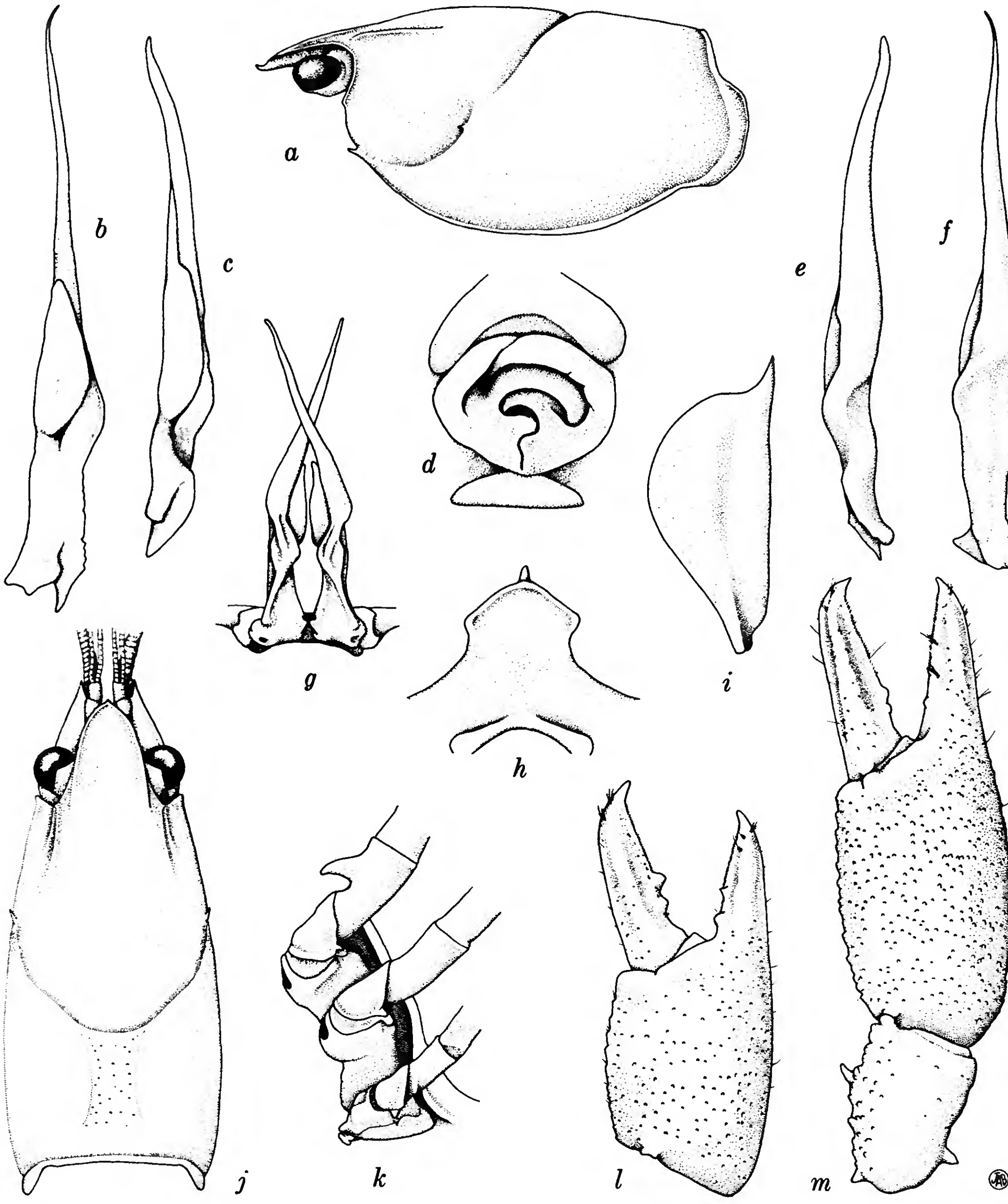


FIGURE 104.—*Faxonella clypeata* (*c*, *e*, from male, form II, from pools along Ogeechee River at St Rte 24, Bulloch-Screven Co line; *d*, *l*, from female, all others from male, form I, from 6.7 mi N of Chauncey, Dodge Co): *a*, lateral view of carapace; *b*, *c*, mesial view of first pleopod; *d*, annulus ventralis; *e*, *f*, lateral view of first pleopod; *g*, caudal view of first pleopods; *h*, epistome; *i*, antennal scale; *j*, dorsal view of carapace; *k*, proximal podomeres of third, fourth, and fifth pereiopods; *l*, *m*, dorsal view of distal podomeres of cheliped.

ing posterior terga; area between spots and undulating charcoal band at bases of pleura pinkish cream. Otherwise coloration similar to that of individuals with longitudinal dorsal stripes.

TYPES.—Holotype, USNM 17277 (♀).

TYPE-LOCALITY.—Bay Saint Louis, Hancock County, Mississippi.

RANGE.—Arkansas and Louisiana eastward, almost exclusively in the coastal plain, to Gadsden County, Florida, and Richland County, South Carolina. In Georgia, except along the Ogeechee River where it has invaded the Barrier Island Sequence District and in the single locality in the Piedmont Province (Harris County), it has been found only in the Fall Line Hills, Dougherty Plain, Tifton Upland, and Vidalia Upland districts.

The northwestern part of the range formerly cited as LeFlore and McCurtain counties, Oklahoma, and Cass and Marion counties, Texas, must be investigated in view of the recent description of *F. blairi*, which according to Hayes and Reimer (1977:1) occurs in "the Little River drainage of southeastern Oklahoma and the Red River drainage below the confluence of these two streams in southeastern [?—probably "southwestern" was intended] Arkansas. The southern boundary of this species in the Red River drainage has not yet been determined."

GEORGIA SPECIMENS EXAMINED.—I have examined 1208 specimens from 66 localities (Figure 105) in the following counties (the numbers of localities are noted in parentheses): Baker (3), Bleckley (1), Bulloch-Effingham (1), Burke (1), Calhoun (1), Crisp (2), Dodge (2), Dooly (2), Dougherty (4), Early (3), Emanuel (1), Harris (1), Jeff Davis (1), Jenkins (3), Johnson (2), Laurens (2), Lee (3), Macon (1), Miller (2), Montgomery (2), Pulaski (1), Screven (1), Seminole (4), Sumter (1), Telfair (4), Terrell (2), Tift-Worth (1), Turner (3), Twiggs (1), Washington (1), Wheeler (2), and Wilkinson (7).

VARIATIONS.—In Georgia, this crayfish demonstrates a wide degree of variation, and, whereas a few characteristics do not seem to appear throughout the range in the state, in general, as pointed out by Fitzpatrick (1963:75), for the species throughout its range, intrapopulational variations appear to be as great as interpopulational ones. Most conspicuous perhaps is the disparity in the size of individuals in different localities. The fact that males attain the first form at carapace lengths of 10.1 to 21.1 (average 14.8) mm (presumably adult females slightly increase these limits) is perhaps not noteworthy. That all of the members of the species collected in some localities have carapace lengths of no more than 13 mm, whereas those taken from others a few days before or after have corresponding lengths of no less than 18 mm, presents a striking, if not significant, feature of the populations. The rostrum (Figure 106*b*) of members in several localities in the Flint Basin possesses marginal spines or tubercles, a feature that has not been observed in representatives of the species in other parts of the state, but within the basin other populations exhibit rostra, the margins of which are entire, and in at least one locality both types of rostra were present in the specimens collected. When present, the spines are usually best developed in the smaller specimens. The areola is also highly variable in length and width: it is longest in specimens from the Altamaha Basin (Twiggs and Wilkinson counties) and shortest in some from the Suwannee Basin (Worth County), and the broadest areola (less than three times as long as wide) is found in the Chattahoochee-Flint (Baker, Early, Harris, and Lee counties), Altamaha (Wheeler County), and Ogeechee (Jenkins County) basins. The postorbital ridges may or may not terminate cephalically in spines or tubercles; in general, spines are more often present in individuals that possess rostral spines or tubercles, but they may occur in other specimens. Cervical spines are always small if present, and frequently there is hardly a trace of them. The basis and ischium of the antennule may each bear strong spines, or the latter may be represented as barely perceptible rudiments. The palm of the chela, particularly in small individuals, may appear to be virtually devoid of tubercles except along the mesial margin; in larger ones the entire dorsal surface may be studded with them; the opposable margins of the fingers always possess denticles (broad band in adult males and single row in females), but there may or may not be two teeth on the proximal half of

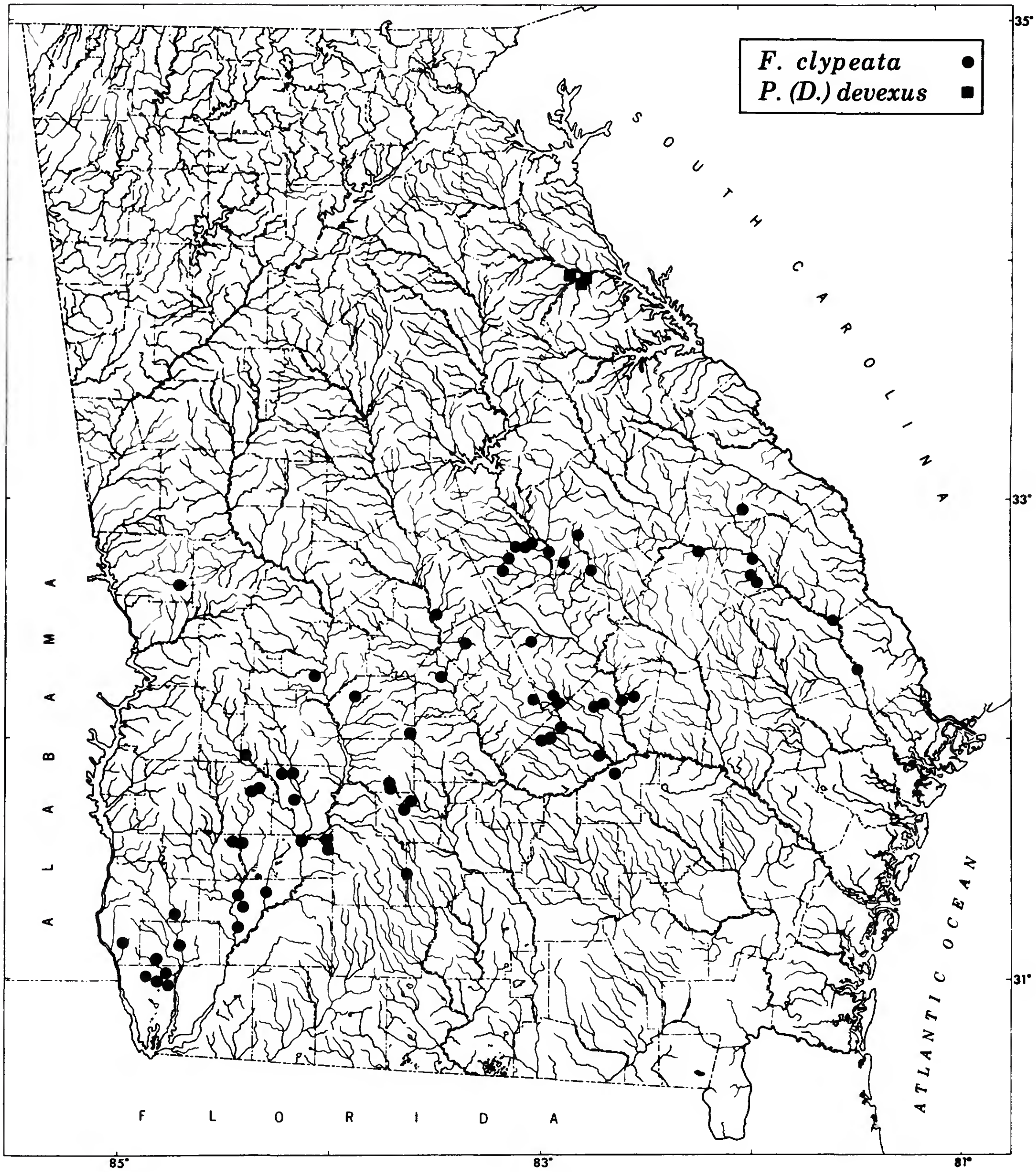


FIGURE 105.—Distribution of *Faxonella clypeata* and *Procambarus (D.) devexus* in Georgia.

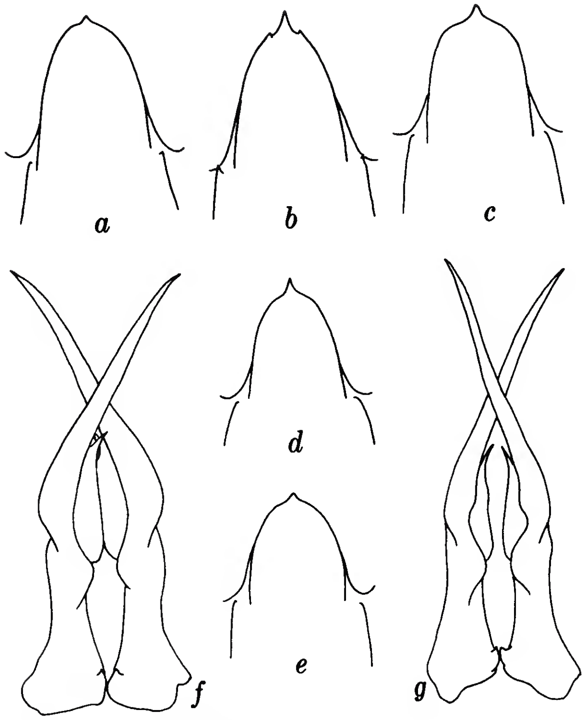


FIGURE 106.—*Faxonella clypeata*, variations (*a–e*, dorsal view of rostrum; *f*, *g*, caudal view of first pleopods of male, form I): *a*, Seminole Co; *b*, *g*, Lee Co; *c*, Dodge Co; *d*, Jenkins Co; *e*, Bleckley Co; *f*, Montgomery Co.

both fingers. The first pleopods (Figures 106*f*,*g*) of the first form male vary chiefly in their disposition and in the relative development of the mesial process, which may be spiniform or reduced to a very small tuberculiform prominence. The most conspicuous differences noted in the annulus ventralis are in the degree of development of the cephalolateral walls, which may be strongly or very weakly inflated, and also the caudal margin may be gently rounded or slightly produced submedianly. The two color patterns described above occur in both sexes from a single locality. In a population of *F. clypeata* frequenting a small borrow pit in Turner County (one mile northeast of Interstate Highway 75 on State Route 149), the color patterns of 170 specimens were recorded. Of the first form males, seven were spotted and three bore longitudinal stripes; among the 71 second form males, the respective numbers were 51 and 20; and among the 89 females, 63 and 26. Thus in the sample, 121 individuals were spotted and 49 were striped. For further data dealing with variation in the species in Georgia, see Fitzpatrick (1963).

SIZE.—The largest specimen available is a female from Seminole County, which has a carapace length of 22.9 (postorbital carapace length 18.2) mm. The corresponding lengths of the smallest and largest first form males are 10.1 (8.1) mm from Wilkinson County and 21.1 (16.7) mm from Baker County. Although no ovigerous females were found in Georgia, Fitzpatrick (1963: 76) reported that two such females examined by him had carapace lengths of 12.9 and 13.0 mm.

LIFE HISTORY NOTES.—Little is known of the life history of this species in Georgia except that first form males have been collected from February to September (Fitzpatrick, 1963:71, and table of "Seasonal Data" herein). In several localities pairs were found in burrows in April and June, but neither ovigerous females nor ones carrying young have been reported from the state. The absence of such females among the more than 1200 specimens collected in Georgia is not surprising, for, in Louisiana, Smith (1953:82) found ovigerous females only from September to December, a period during which virtually no specimens of the species were collected in Georgia. According to Smith (pp. 94, 95), females with eggs are found only in burrows, and young appear within the population from October to the first of the year, increase in size to early June, and remain "nearly static in size" until mid-July. Between then and September they again exhibit significant growth, most "presumably undergoing a maturity molt," with ovulation occurring; this is followed by a period of molting during December and January "marking the termination of the active reproductive period for the majority of the mature females." The life span of most females appears to be about one and one-half years. Some were believed to attain an age of about two years. The growth pattern of males follows that of females, and the molt to first form in most occurs between May and September. Following the breeding season, they return to the second form during December and January. Those few males that have not reached maturity by September enter into "an erratic post-seasonal spawning group" and are believed to live about two years.

Black (1958:193) noted that the average growth increment of the carapace with each molt was 0.41 mm "regardless of sex or size," and indicated that this crayfish "requires approximately twenty-two molts before reaching the minimum size (carapace length of 10.8 mm as reported by Smith) for sexual maturity."

The sex ratio of females to males in Louisiana as computed by Smith (1953:92) was 1.07; in the specimens collected in Georgia it is 1.17.

Seasonal Data

Sex/stage	*J*	*F*	*M*	*A*	*M*	*J*	*J*	*A*	*S*	*O*	*N*	*D*
♂I			4	126		21	1	1	1			
♂II	1		1	365		21						
♀	3	2	6	557		60						1
♂j			9	2								
♀j			9	17								

Ecological Notes.—Hobbs (1942b:155–156) reported that in Florida *F. clypeata* had been collected in at least four types of situations:

[1] roadside ditch in a small area of flatwoods, where they were common among the vegetation covering the bottom of the ditch and in burrows near the water. The burrows, marked by small, neatly constructed chimneys, were simple and ranged in depth from six inches to a foot... [2] from submerged vegetation in a clear sand bottomed stream... [3] in a small sluggish silty stream... [and 4] in a small [leaf littered] cypress pond [where individuals were] seen scurrying about in the water as I waded into it.

Penn (1952:742), in analyzing the habitats of this crayfish in Louisiana, noted that it occurs "most frequently in shallow water, i.e. less than 15 inches deep (84.6%), which is clear (64.5%), temporary (58.1%), static (77.0%), and exposed to full sunlight (70.6%). Most of the collections were from habitats with mud bottoms (67.7%) and with aquatic plants present (72.5%)."

According to Hobbs and Hart (1959:184–185), in the Apalachicola Basin it occurs in the same kinds of habitats as indicated above. Elsewhere in Georgia, it seems to occur most frequently in temporary or fluctuating bodies of water and in burrows. In a flooded, cleared area along the Ogeechee River, I found specimens in numbers among the terrestrial vegetation along with *Procambarus (O.) enoplosternum*, *P. (Pe.) petersi*, and *P. (S.) troglodytes*. On slightly higher ground but in a deeply shaded swamp nearby, this crayfish was present in leaf-littered pools left when the water had receded, and there specimens were also dug from simple burrows.

The burrows consist of a single subvertical passageway topped by a usually neatly constructed chimney that occasionally stands some 15 cm above the surrounding ground level. The soil in which they are constructed ranges from clay through sandy clay, or sand with rich humus, to coarse sand. In the latter, while the act of excavating the tunnel is easy, the walls often collapse so that frequently the crayfish is unobtainable. The burrows reach a depth of a few to 50 centimeters, and I have taken a number of specimens in tunnels, the bottoms of which, while moist, do not reach the water table. As pointed out above, pairs, consisting of a first form male and a female, frequently have been dug from single burrows.

Georgia Crayfish Associates.—This crayfish was found in adjacent burrows or in pools or streams in company with the following (number of times collected in same locality noted in parentheses): *Cambarus (D.) latimanus* (4), *C. (D.) striatus* (5), *C. (D.) truncatus* (1), *C. (L.) diogenes diogenes* (7), *Fallicambarus (C.) hedgpethi* (1), *Procambarus (H.) advena* (2), *P. (H.) pygmaeus* (1), *P. (H.) caritus* (3), *P. (H.) talpoides* (3), *P. (H.) truculentus* (2), *P. (O.) acutus acutus* (4), *P. (O.) enoplosternum* (6), *P. (O.) litosternum* (2), *P. (O.) seminolae* (6), *P. (Pe.) gibbus* (2), *P. (Pe.) petersi* (1), *P. (Pe.) spiculifer* (7), *P. (S.) howellae* (16), *P. (S.) paeninsulanus* (17), and *P. (S.) troglodytes* (2).

Genus *Orconectes*

Astacus.—Rafinesque, 1817:42 [not Fabricius, 1775:413].
Cambarus Erichson, 1846:95 [in part].

Orconectes Cope, 1872:419. [Type-species by subsequent designation (Fowler, 1912:339), *Orconectes inermis* Cope, 1872: 419. Gender: masculine.]
Camtarus.—Packard, 1888:156 [erroneous spelling].
Oreonectes.—Lönnberg, 1894:126 [erroneous spelling].
Camborus.—Williamson, 1899:47 [erroneous spelling].
Cambrus.—Price, 1900:155 [erroneous spelling].
Orconectis.—Harris, 1903a:113 [erroneous spelling].
Faxonius Ortmann, 1905a:97. [Type-species by original designation, *Astacus limosus* Rafinesque, 1817:42. Gender: masculine. Proposed as subgenus of *Cambarus*, elevated to generic rank by Creaser, 1933b:1.].
C[ambarus].—Ortmann, 1905a:112 [erroneous spelling].
Orconetes.—Wolf, 1934:104 [erroneous spelling].
Faxonicus.—Fleming, 1938:302 [erroneous spelling].
Cambarrus.—Fleming, 1939:305 [erroneous spelling].
Cityphlobius.—Joleaud, 1939:14 [error for *C. typhlobius*].
Fexonius.—Rioja, 1941:193 [erroneous spelling].
Orconecctes.—Williams, 1952:330 [erroneous spelling].
Orconectas.—Villalobos, 1953:351 [erroneous spelling].
Gambarus.—Croizat, 1958:908 [erroneous spelling].
Orconnectes.—Threinen, 1958:1 [erroneous spelling].
Oronectes.—Bacescu, 1967:218 [erroneous spelling].
Camburus.—Bacescu, 1967:218 [erroneous spelling].
Orchonectes.—Dimond et al., 1968:760 [erroneous spelling].
Orconectus.—Ray and Stevens, 1970:58 [erroneous spelling].
Orconcectes.—Fielder, 1972:133 [erroneous spelling].
Orconeotes.—Unestam, 1973:4 [erroneous spelling].
Orcenectes.—Hart and Hart, 1974:45 [erroneous spelling].
Oroconectes.—Hobbs III, 1975:273 [erroneous spelling].
Orcnoectes.—O'Brien, 1976:84 [erroneous spelling].
Onconectes.—Price and Payne, 1977:79 [erroneous spelling].
Oreconectes.—Yassini, 1977:201 [erroneous spelling].

DIAGNOSIS.—

Antenna never with conspicuous fringe on mesial border. Third maxilliped with teeth on mesial margin of ischium. Mesial margin of palm of chela usually with row of less than 12 tubercles; lateral margin of fixed finger never bearing row of spiniform tubercles; opposable margin of dactyl seldom with prominent excision. Areola broad to obliterated at midlength. Ischium of third, rarely third and fourth, pereiopod with hook. Coxa of fourth pereiopod of male lacking caudomesial boss except in troglobitic members. First pleopod[s] of first form male almost always symmetrical, never deeply withdrawn between bases of pereiopods nor concealed by dense setal mat extending from ventrolateral margins of sternum, and contiguous basally; terminal elements (usually 2, occasionally 3 in troglobitic members [latter not present in Georgia]) highly variable in length and disposition—divergent, straight, or curved caudodistally or caudally; central projection never abruptly curved caudally at base nor forming arc of more than 90 degrees. Female with annulus ventralis immovable or slightly movable in troglobitic species; first pleopod usually present. Branchial . . . [count] 17 + ep. (Hobbs, 1974a:14-15).

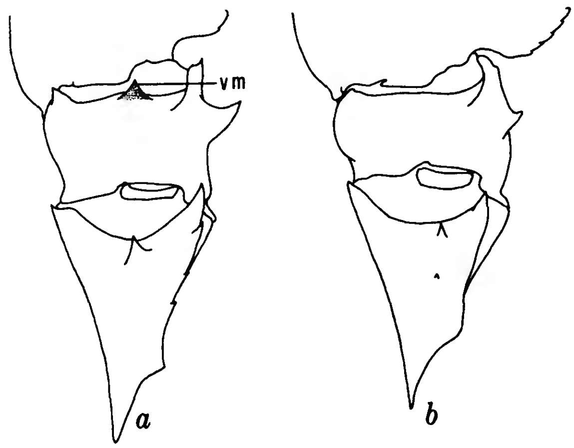


FIGURE 107.—Ventral view of merus, carpus, and proximal part of propodus of cheliped: *a*, *Orconectes spinosus*; *b*, *Orconectes forceps* (vm = ventromesial spine).

RANGE.—"North America: Arizona and Alberta eastward to the Atlantic Ocean except eastern seaboard from South Carolina to Florida . . ." (Hobbs, 1974a:15). Introduced into California, Oregon, and western Europe.

SPECIES.—Sixty-five species and 10 subspecies are currently recognized as belonging to the genus *Orconectes*. Three species have been described since the appearance of the most recent checklist (Hobbs, 1974b): *Orconectes deanae* Reimer and Jester (1975:17), *O. etnieri* Bouchard and Bouchard (1976b:459), and *O. saxatilis* Bouchard and Bouchard (1976a:439). *Orconectes juvenilis* (Hagen, 1870:66) and *O. transfuga* Fitzpatrick (1966:178) were declared synonyms of *O. rusticus* (Girard, 1852:88) and *O. neglectus* (Faxon, 1885a:142), respectively, by Bouchard (1976a:580; 1977:38).

Of the 75 species and subspecies, only three have been found in Georgia, where they are limited to lotic habitats in the Coosa and Tennessee river systems in the northwestern part of the state.

HABITAT.—The members of the genus *Orconectes* are, for the most part, stream dwellers, although a number of species have found congenital habitats in both natural and impounded lakes and

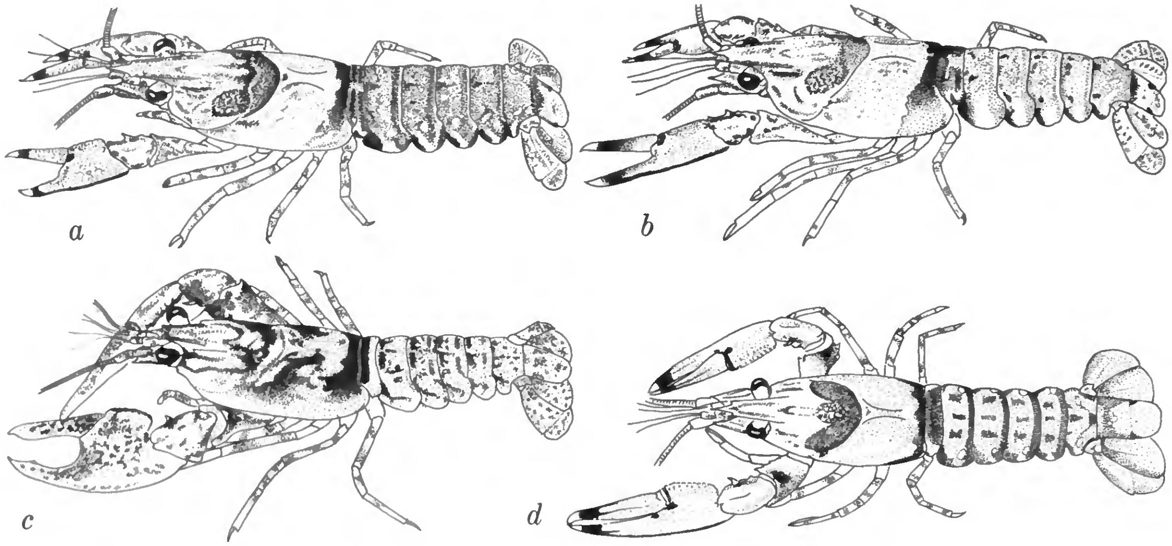


FIGURE 108.—Color patterns in members of genus *Orconectes*: *a*, *O. erichsonianus* from tributary to South Chickamauga Creek, Walker Co; *b*, *O. erichsonianus* from Hurricane Creek, Catoosa Co; *c*, *O. forceps* from South Chickamauga Creek, Catoosa Co; *d*, *O. spinosus* from Cedar Creek, Floyd Co.

ponds. A few species have become adapted to a troglobitic existence (Hobbs, Hobbs, and Daniel, 1977:3–113), and several species that occur more commonly in epigean habitats have invaded subterranean waters (Hobbs, Hobbs, and Daniel, 1977:148–149). There are no known primary burrowers, but representatives of several species have been collected from simple tunnel systems. All specimens of the Georgia members of the genus were collected in streams. To my knowledge, none have been found in impounded waters.

Key to Georgia Members of Genus *Orconectes*

1. Central projection of first pleopod of first form male constituting no more than one-third of mesial length of appendage, that of second form male no more than one-sixth; annulus ventralis lacking deep transverse fossa .... ***erichsonianus***

   Central projection of first pleopod of first form male constituting more than one-third of mesial length of appendage, that of second form male distinctly more than one-sixth; annulus ventralis with deep transverse fossa 2

2. Cephalic surface of first pleopod of first form male with distinct shoulder at base of central projection; latter constituting about one-half of mesial length of appendage, that of second form male constituting about one-third; chela with conspicuous setiferous punctations, latter not large or deep, fingers never strongly gaping; ventral surface of carpus of cheliped with distomedian spine or spiniform tubercle (Figure 107*a*) ... ***spinosus***

   Cephalic surface of first pleopod of first form male lacking shoulder at base of central projection; latter constituting distinctly less than one-half of mesial length of appendage, that of second form male constituting about one-fifth; chela with large deep punctations, bearing inconspicuous setae, fingers strongly gaping; ventral surface of carpus of cheliped lacking distomedian spine or tubercle (Figure 107*b*) .... ***forceps***

Orconectes erichsonianus (Faxon)

FIGURES 19*d*, 108*a*,*b*, 109–111, 231

Cambarus erichsonianus Faxon, 1898:659, pl. 64: figs. 7–12.
Cambarus spinosus.—Hay, 1902a:439* [not Bundy, 1877].
Cambarus erichsoni.—Ortmann, 1905a:109 [erroneous spelling].
Cambarus (Faxonius) erichsonianus.—Ortmann, 1905a:112; 1931:65, 67–71*, 72, 87, 88, 90.
Cambarus spinosus gulielmi Faxon, 1914:375–377*. [Syntypes, USNM 26379 (6♂II, 6♀, 4j♂), MCZ 7448 (♂II, ♀). Type-locality, stream from John Ross Spring, near Rossville, Walker County, Georgia.]
Cambarus gulielmi.—Ortmann, 1931:68.
Faxonius erichsonianus.—Creaser, 1933a:3 [by implication]; 1933b:7*.
Faxonius (Faxonius) erichsonianus.—Creaser, 1933b:7 [by implication].
Cambarus erichsonionus.—Fleming, 1938:299 [erroneous spelling].
Orconectes erichsonianus.—Hobbs, 1942a:350–352 [by implication]; 1968b:K-12*, K-30, K-31; 1972b:83*, 148*, 154*, figs. 62e, 65g, 66a; 1974b:29*, fig. 123.—Fitzpatrick, 1967: 134, 143, 145, 147–149, 165–168, figs. 2–18, 20.—Unestam, 1969:203*, 204.—Anonymous, 1970b:211*, 217; 1970c:(35, 36, 38, 42–45, 50, 51)*.—Hart and Hart, 1974: 58*, 63*, 134*.—Bouchard, 1976a:563, 574, 576, 579.—Wharton, 1978:220*.

The above citations do not constitute a complete bibliography for the species but include all synonyms, comprehensive treatments, most illustrations, and all known references to its occurrence in Georgia, the latter indicated by asterisks.

SUMMARY OF LITERATURE.—The best accounts of this crayfish are those of Faxon (1898, 1914), Ortmann (1931), and Fitzpatrick (1967), although few data are presented relative to its habitat or life history. The earliest record of the occurrence of the species in Georgia is that of Hay (1902a:439), who reported its occurrence (as *C. spinosus*) in the vicinity of Rossville, Walker County. Later, Faxon (1914:375) described *Cambarus spinosus gulielmi*, designating as types the same specimens that had been misidentified by Hay. The fact that Faxon's subspecies is a synonym of *Orconectes erichsonianus* was pointed out by Ortmann (1931:67), who (p. 68) also reported it from South Chickamauga Creek at Ringgold, Catoosa County. Even though Creaser (1933a), Hobbs (1968b), and Unestam (1969) mentioned the occurrence of this crayfish in the state, not until 1970 was a third precise locality in Georgia recorded: 0.6 mile east of Route S2557 off U. S. Highway 27, north of Lafayette, Walker County (Anonymous, 1970b:211). Later in the same year four additional localities were cited in Walker County, two in Dade, and three in Catoosa (Anonymous, 1970c). The only other recorded localities are those of Hart and Hart (1974:58, 63, 134), the only new one being in Walker County.

DIAGNOSIS.—Rostrum with subparallel margins bearing well-defined marginal spines or tubercles. Postorbital ridges terminating cephalically in spines. Cervical spine strong. Areola 3.9 to 7.5 (average 5.5) times as long as broad and constituting 27.4 to 32.3 (average 30.2) percent of entire length of carapace (38.7 to 44.1, average 41.7, percent of postorbital carapace length). Mesial surface of palm of chela shorter than dactyl and bearing at least 2 rows of tubercles, mesialmost consisting of 8 to 12; opposable margins of fingers contiguous in smaller individuals, often gaping in larger ones, and each bearing row of rounded tubercles along proximal two-thirds and band (males) or single row (females) of minute denticles along distal half. Ventral surface of carpus of cheliped with distomedian spine or tubercle. Ischium of third pereiopod of male with massive hook overreaching basioischial articulation; hook not opposed by tubercle on basis. First pleopods of male reaching coxae of second pereio-

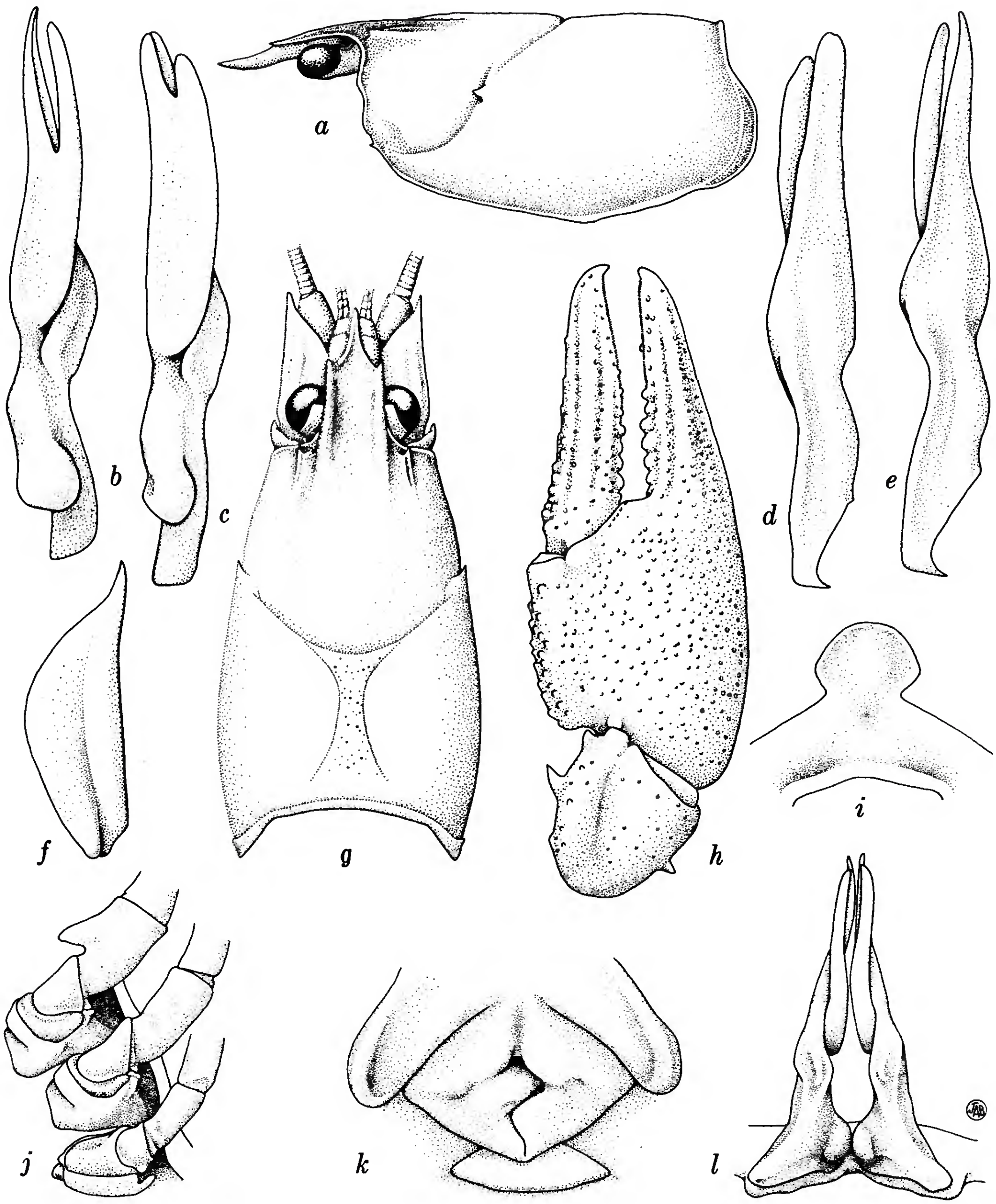


FIGURE 109.—*Orconectes erichsonianus* (from tributary to Chickamauga Creek 0.5 mi N of St Rte 143 on Rte 341, Walker Co; all from first form male except *c*, *d*, from second form male, and *k*, from female): *a*, lateral view of carapace; *b*, *c*, mesial view of first pleopod; *d*, *e*, lateral view of first pleopod; *f*, antennal scale; *g*, dorsal view of carapace; *h*, dorsal view of distal podomeres of cheliped; *i*, epistome; *j*, proximal podomeres of third, fourth, and fifth pereiopods; *k*, annulus ventralis; *l*, caudal view of first pleopods.

pods; mesial process almost or quite as long as central projection, both straight; central projection constituting no more than one-third mesial length of appendage and tapering to acute apex; mesial process truncate or acute, sometimes concealing tip of central projection in caudal aspect. Female with annulus ventralis weakly sculptured, not elevated cephalolaterally; well-developed first pleopod present.

COLOR NOTES (Figure 108*a,b*).—Predominant dorsal color of carapace pale to dark tan, mostly with overlying reticulate pattern of charcoal. Rostrum with paired dark bands flanking mesial margin of rostral ridges and acute, anteriorly directed median dark arc, marking anterior end of median light stripe, extending anteriorly from midgastric region; mandibular adductor region and midgastric region covered by trilobed cluster of charcoal reticulations; lateral surface of cephalic section pale pinkish tan with few maculations. Thoracic section of carapace with posterior dark charcoal band broadening anteroventrally on branchiostegites and with rather diffuse paired charcoal spots dorsolaterally on level about midlength of branchiocardiac grooves; caudal ridge charcoal to black, flange white. First abdominal tergum mostly dark charcoal, with small anteromedian pale tan spot; second through sixth terga with brown band across posterior part (band becoming narrower in succeeding terga), brown dorsomedian spot, and paired, oblique, similarly colored splotches lateral to median spot; lateral parts of terga with cream spot; pleuron of first segment largely cream, succeeding pleura dark anteriorly and posteriorly, with pinkish cream to cream area between, latter area often with brown flecks. Telson with narrow dark basal band, dark lateral margins of anterior section becoming almost black at posterolateral angles; remainder of telson and uropods with reticulate pattern of densely speckled brown on cream, keels dark brown; proximomesial parts of both rami very pale. Podomeres of antennular and antennal peduncles tan proximally, becoming dark charcoal distally, flagella charcoal proximally, fading rapidly to orange tan. Chelipeds basically olive tan from proximal part of merus distally; distal part of merus charcoal; carpus with charcoal markings mesially and laterally; chela with lateral margin, ridge at base of dactyl, and much of distal half of fingers black; distal fifth or sixth of fingers with vermilion area abutting black region, fading distally rapidly to yellow or cream; major tubercles on merus and carpus charcoal basally with cream to white tips. Remaining pereiopods pale tan banded with olive brown from distal part of ischium to dactyl. Ventral surface of body pinkish cream.

TYPES.—Syntypes, USNM 20787 (3♂I, 4♀), MCZ 4347 (♂I, ♀, ♂II).

TYPE-LOCALITY.—Rip Roaring Fork, 5 miles northeast of Greenville, Greene County, Tennessee.

RANGE.—Tennessee, Elk, and Coosa river systems in eastern Tennessee, southwestern Virginia, northern Alabama, and northwestern Georgia. In the latter it is confined to the Appalachian Plateau, the Ridge and Valley, and a small segment of the Piedmont provinces, where it occurs in the Lookout and South Chickamauga watersheds in the Tennessee Basin; in the Coosa Basin, it is a common inhabitant of the Chattooga drainage system but has been found in only six other localities: four in the headwaters of Pine Log Creek in Bartow County, and in Armuchee Creek and in a tributary to the Coosa River in Floyd County.

GEORGIA SPECIMENS EXAMINED.—I have examined a total of 257 specimens from 45 localities (Figure 110) in the following counties: Bartow (4), Catoosa (8), Chattooga (8), Dade (6), Floyd (2), Walker (16), and Whitfield (1).

VARIATIONS.—Most of the variations noted are indicated in "Diagnosis." The areola is highly variable in proportional length and width. In the Coosa Basin, the ratio of the length of the areola to the total length of the carapace ranges from 27.4 to 31.3 percent and in the Tennessee Basin from 28.1 to 32.3; corresponding percentages of the ratio of the areolar length to the postorbital carapace length are 39.6 to 41.8 and 40.0 to 44.1; and the range of variation in the ratio of the

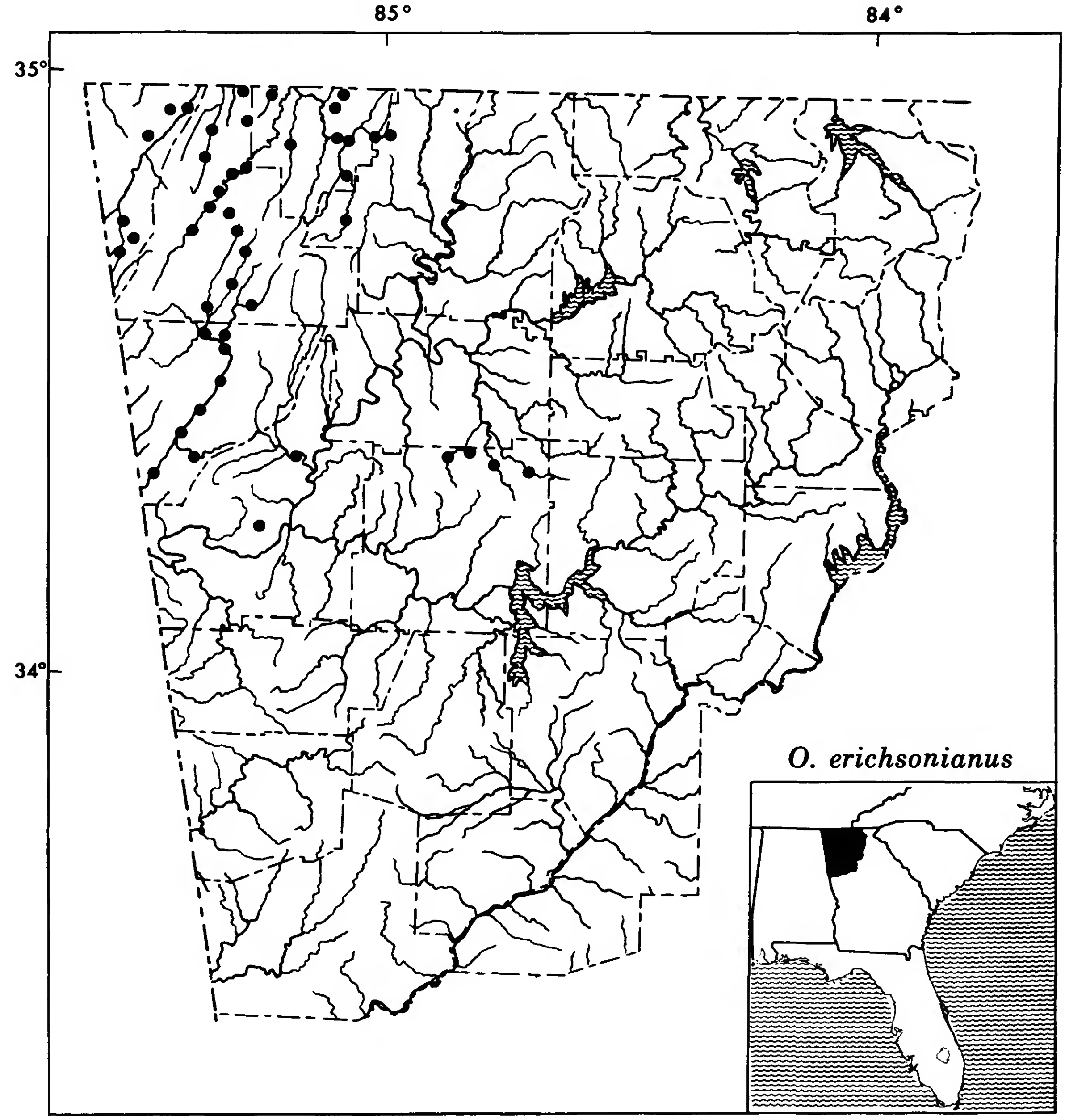


FIGURE 110.—Distribution of *Orconectes erichsonianus* in Georgia.

length to the width of the areola in the two basins is 4.2 to 7.5 and 3.9 to 5.7. The variations noted by Fitzpatrick (1967:148) in specimens throughout the range are slightly different from those included in the "Diagnosis" given herein of the species in Georgia: areola 4.66 to 5.32 (average 4.88) times as long as wide and constituting 24.9 to 34.5 (average 30.6) percent of entire length of carapace. Thus some of the Georgia specimens have proportionately broader and longer areolae than other members of the species outside of the state. The rostral margins, although always subparallel, are sometimes deflected laterally at the base of the marginal spines, resulting in the latter being positioned at an angle. The chelae exhibit little sexual dimorphism other than in the minute denticles on the opposable margins of the fingers: in the males they are arranged in a band, whereas in the females there is a single row. In young adults, there is scarcely any gap between the fingers, and there are relatively fewer tubercles discernible on the opposable margins, but in the larger individuals, especially the males, there is a distinct gap (Figure 111*e*), and the fixed finger bears a row of as many as 13 tubercles and the dactyl, 15. The mesial and dorsomesial surface of the palm may bear two to four, often irregular, rows of tubercles, the mesialmost consisting of eight to 12. The mesial surface of the carpus supports a single large acute or subacute tubercle that is rarely bifid, and a much smaller one may be situated proximal to it. The ventral surface of the merus of the cheliped bears a lateral row of one to five tubercles and a mesial one of eight to 11. The mesial process of the first pleopod of the first form male is also highly variable both in its relative length, falling short of or reaching as far distally as the tip of the central projection, and in the configuration of the distal extremity (Figure 111*a–d*). In specimens from the Middle and East forks of South Chickamauga Creek (Tennessee Basin), the distal extremity is truncate; elsewhere it tapers distally, and in one specimen from Armuchee Creek (Coosa Basin) it bears a preapical spine and a tubercle (Figure 111*c,d*). In a specimen from a tributary to Lookout Creek in Dade County, the apical part of the central projection is obscured in caudal aspect by the distal part of the mesial process (Figure 111*a*).

SIZE.—The largest specimen from Georgia is a female, collected in the East Fork of South Chickamauga Creek, that has a carapace length of 44.7 (postorbital carapace length 32.2) mm. Corresponding lengths of the smallest and largest first form males are 19.3 (14.0) and 43.5 (32.3) mm, and of the smallest female carrying eggs or young, 29.1 (21.2) mm.

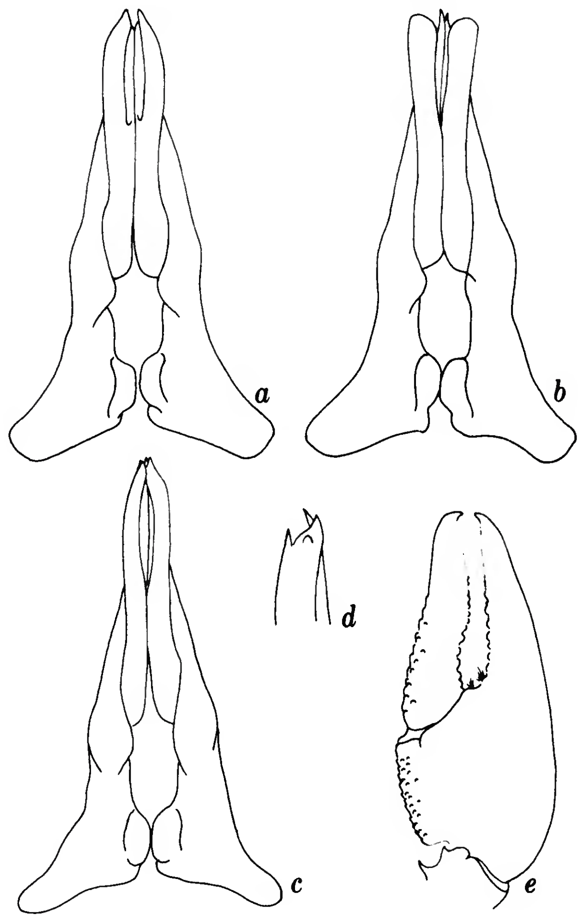


FIGURE 111.—*Orconectes erichsonianus*, variations (*a–c*, caudal view of first pleopods of first form male; *d*, caudal view of distal part of right first pleopod of first form male; *e*, dorsal view of distal podomeres of cheliped): *a*, *e*, Squirrel Town Creek (Lookout Creek drainage), Dade Co; *b*, South Chickamauga Creek at Ringgold, Catoosa Co; *c*, *d*, Armuchee Creek (Coosa River basin), Floyd Co.

LIFE HISTORY NOTES.—The life history of this crayfish has not been investigated in any part of its range. In Georgia (see "Seasonal Data"), first form males were found in March, April, and from August to October; ovigerous females were collected in April, and a single female (carapace length 29.1 mm; postorbital carapace length 21.2 mm) with 85 young was taken in May. Three of the ovigerous females had corresponding lengths of 29.7, 21.3 mm (carrying 99 eggs, 2.0–2.2 mm in diameter); 32.7, 23.7 mm (255 eggs, 1.9 mm); and 44.1, 33.2 mm (347 eggs, 1.8–1.9 mm). The latter two ovigerous females were preserved in the same container, and seven eggs became detached; whether all were from the same female or some were from each is not known. Two other ovigerous females, which were also preserved together, had lost so many eggs that recording a count of those attached would be almost meaningless.

Among available specimens collected throughout the range of the species, first form males are represented from every month of the year except February, May, and June. Almost certainly the absence of such males in February is an artifact of collecting, and I suspect that at least in early May some laggards from the spring molt from first to second form will be found. Indeed, Ortmann (1931:69) cited a first form male from Knox County, Tennessee, collected on 12 May. In view of the absence of breeding males in a number of collections made in June, it seems probable that the molt from form II to form I must occur in July and that males in the latter form are indeed rare, if they occur at all, in June. The only ovigerous females I have seen from any part of the range were collected in April, and the only female carrying young that I have observed was found in May.

Seasonal Data

Sex/stage	*J*	*F*	*M*	*A*	*M*	*J*	*J*	*A*	*S*	*O*	*N*	*D*	*?*
♂I			1	8				1	7	10			
♂II				22	6			9	3	3			
♀			1	11	3		2	16	9	8			1
♂j				10	7		2	23	21	6			
♀j			1	10	8			16	40	15			
♀ ovig				5									
♀ with young					1								

ECOLOGICAL NOTES.—*Orconectes erichsonianus* is a stream dweller, occupying, for the most part, creeks and rivers with a moderate current and a rock-littered bed. Hay (1902a:439) stated that it lives "in shallow burrows in soft mud, in shallow water, or in excavations under flat stones." According to Ortmann (1931:69), "it is found in large rivers and in creeks, sometimes in rather small ones . . . ." Bouchard (1976a:579) noted that it occurs in "lotic situations varying in size from small creeks to large rivers" but that most collections had been made in "small to medium sized streams where it occurs under rocks and in leaf litter." These observations are in accord with those made by me in Georgia. Whereas the species occurs more abundantly in areas of the stream other than in riffles, individuals also frequent shallow, swiftly flowing segments of the streams.

GEORGIA CRAYFISH ASSOCIATES.—This crayfish was collected with the following (number of times found together noted in parentheses): *Cambarus (C.) bartonii* (1), *C. (D.) latimanus* (9), *C. (D.) striatus* (11), *C. (H.) coosawattae* (1), *C. (H.) girardianus* (27), *C. (H.) longirostris* (2), *C. (L.) acanthura* (1), *C. (P.) coosae* (1), *C. (P.) extraneus* (13), *C. (P.) scotti* (10), *Orconectes forceps* (2), *Procambarus (O.) lophotus* (7), and *P. (Pe.) spiculifer* (1).

Orconectes forceps (Faxon)

FIGURES 19*c*, 107*b*, 108*c*, 112, 113, 232

Cambarus forceps Faxon, 1884:133; 1885a:119–121, 163, 168, 170, 174, 178, pl. V: fig. 4, pl. IX: fig. 5, 5′, 5a, 5a′.

Cambarus (Faxonius) forceps.—Ortmann, 1905a:109, 112, 115, 116, 128.

Cambarus (Faxonius) rusticus forceps.—Ortmann, 1931:66, 71–76, 78, 79, 81.

Faxonius forceps.—Creaser, 1933a:3 [by implication].

Faxonius (Faxonius) forceps.—Creaser, 1933b:10 [by implication].

Orconectes rusticus forceps.—Hobbs, 1942a:352 [by implication]; 1968b:K-13*, K-30, fig. 28d.—Anonymous, 1970c:50*, 52*.—Wharton, 1978:220*.

Orconectes (Orconectes) rusticus forceps.—Hobbs, 1942b:154 [by implication].

Orconectes forceps.—Fitzpatrick, 1967:143.—Hobbs, 1972b:98, 148*, figs. 77i, 80d; 1974b:29, fig. 137.—Bouchard, 1976a: 563, 574–576, 579, 581.

The list of references cited above is by no means a complete bibliography for the species but does include all of the synonyms, summary articles, records of the occurrence of the species in Georgia (indicated by asterisks), and illustrations.

Summary of Literature Pertaining to Georgia.—Although this crayfish was described in 1884, not until 1959 is there evidence that it was collected in Georgia. The only published localities (see below) recorded from the state appeared in 1970 in an anonymous report of a "Biological Investigation of Tennessee Basin Streams of Northwestern Georgia."

Diagnosis.—Rostrum with margins slightly or strongly concave laterally and bearing marginal spines or tubercles. Postorbital ridges terminating cephalically in spines or tubercles. Cervical spine well developed. Areola 2.8 to 4.4 (average 3.7) times as long as broad and constituting 30.8 to 34.9 (average 32.3) percent of entire length of carapace (40.4 to 43.4, average 41.9, percent of postorbital carapace length). Mesial surface of palm of chela shorter than dactyl and bearing at least 2 rows of tubercles, mesialmost consisting of 7 to 10, dorsal surface conspicuusly punctate; opposable margin of fingers strongly gaping, especially in larger individuals, and bearing row of rounded tubercles along proximal three-fourths and single row (sometimes staggered in males) of minute denticles along distal fourth; prominent tufts of setae often present at mesial base of fixed finger (usually absent in large males). Ventral surface of carpus of cheliped lacking distomedian spine or tubercle. Ischium of third pereiopod of first form male with hook overreaching basioischial articulation but not opposed by tubercle on basis. First pleopod of male reaching coxa of second pereiopod and with mesial process slightly shorter than central projection; former bowed with distal extremities often overlapping; central projections, constituting less than 0.5 length of appendages, subparallel and contiguous along most of length, distal parts not conspicuously deflected laterally; cephalic surface of appendage lacking shoulder at base of central projection. Female with annulus ventralis bearing deep transverse fossa across midlength; first pleopod present.

Color Notes (Figure 108*c*).—Basic coloration tan to straw with dark brown to black markings. Cephalic section of carapace with rostral margins and postorbital ridges dark brown; trilobed splotch covering much of mandibular adductor and midcaudal gastric area, and irregular horizontal dark line extending from ventral part of trilobed splotch to orbit; remainder of cephalic section with smaller dark markings, especially on rostrum and anterior part of gastric region. Thoracic section of carapace with conspicuous saddle caudally; horns extending anteriorly almost to level of midlength of areola, sometimes also with prominent irregular markings, subparallel to horns of saddle, situated more anteriorly on branchiostegites; areola with dark lines along branchiocardiac grooves converging anteriorly to apex, latter located on median line just posterior to cervical groove. Cephalic part of first abdominal tergum black, succeeding 4 with paired, dark, anteriorly situated dorsolateral splotches decreasing in size and intensity on more posterior terga; caudal parts of third, fourth, and fifth terga with paired, narrow transverse bars; sixth tergum with small dark flecks. First pleuron with large cream spot, second through sixth slightly darker than corresponding terga, sometimes set off from latter basally by undulating dark line. Cephalic section of telson with median dark patch flanked by lateral ones; caudal section with irregular flecks; lateral halves of both rami of uropods and caudal section of mesial ramus darker than remainder. Antennular and antennal peduncles mostly dark brown but distal podomere of latter pale dorsally; flagella reddish brown; antennal scale dark laterally and almost cream dorsolaterally, lamellar area dark laterally, fading mesially. Chelipeds with distal third of merus often almost black dorsally; carpus with conspicuous dark patch mesially and with similarly colored splotches dorsally; palmar area of propodus with dark mesial margin, irregular and anastomosing splotches dorsally, and with black wash at base of fixed finger; both fingers dark but becoming pale pinkish cream along distal third. Remaining pereiopods mottled from ischium distally. Ventral surface of body bluish cream.

In some individuals conspicuous dark markings

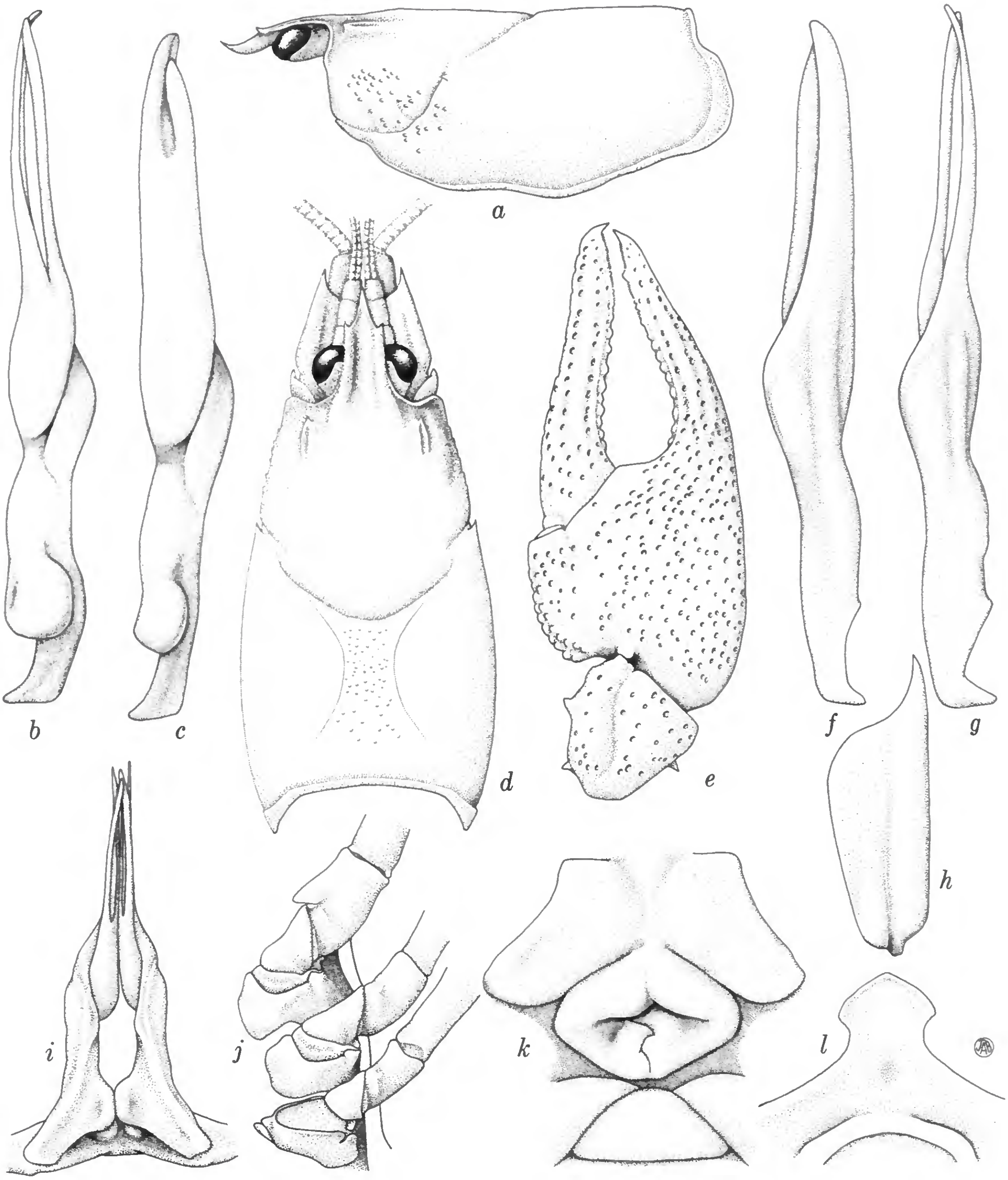


FIGURE 112.—*Orconectes forceps* (*c*, *f*, from second form male; *k*, *l*, from female from South Chickamauga Creek at Rte S819 in Graysville, Catoosa Co; all others from first form male from Little Chickamauga Creek at Ringgold, Catoosa Co): *a*, lateral view of carapace; *b*, *c*, mesial view of first pleopod; *d*, dorsal view of carapace; *e*, dorsal view of distal podomeres of cheliped; *f*, *g*, lateral view of first pleopod; *h*, antennal scale; *i*, caudal view of first pleopods; *j*, proximal podomeres of third, fourth, and fifth pereiopods; *k*, annulus ventralis; *l*, epistome.

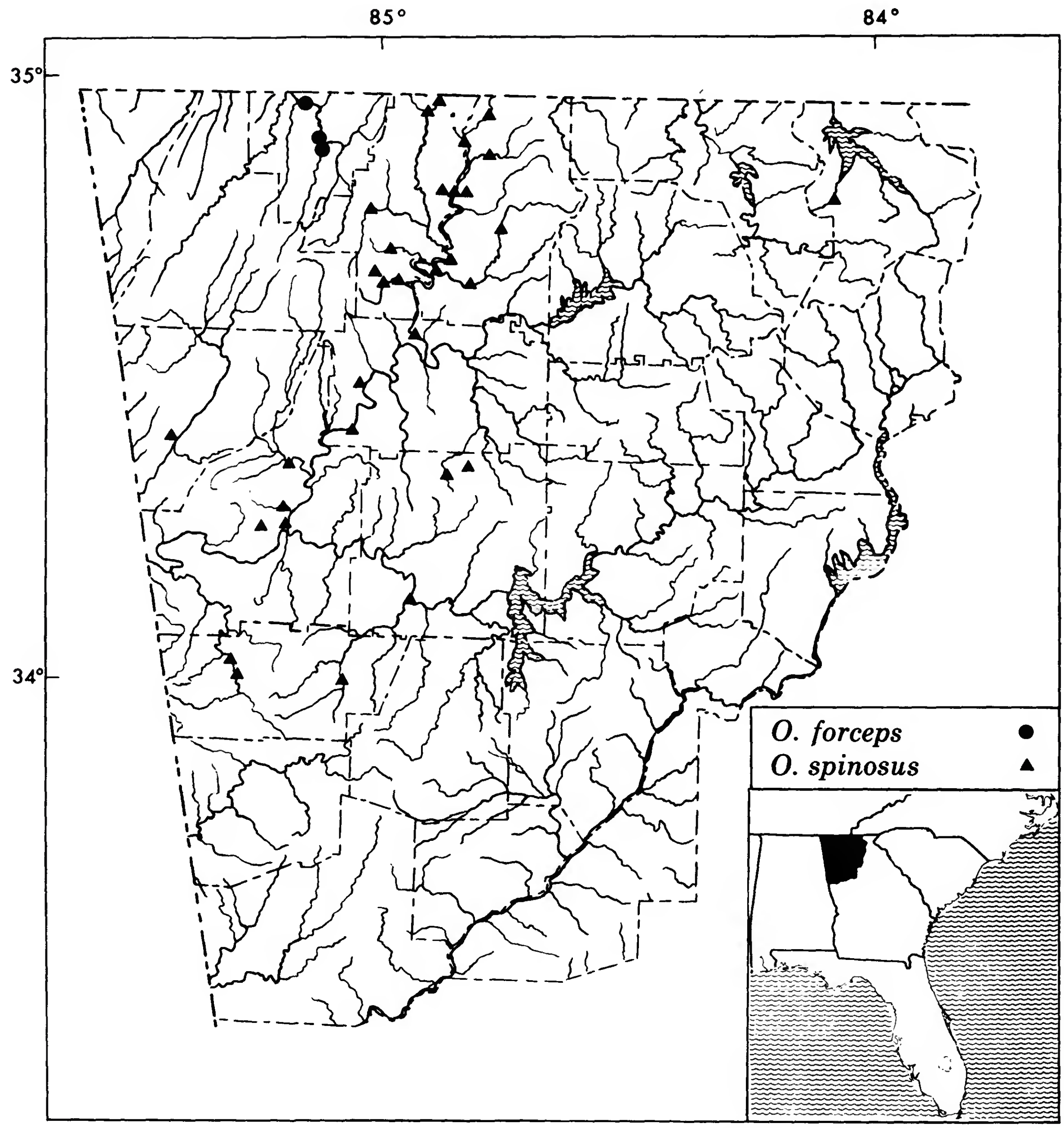


FIGURE 113.—Distribution of *Orconectes forceps* and *O. spinosus* in Georgia.

on carapace greatly reduced in intensity and size.

TYPES.—Syntypes, USNM 4880 (3♂I, 4♀), MCZ 3582 (♂I, ♀).

TYPE-LOCALITY.—Cypress Creek, Lauderdale County, Alabama.

RANGE.—Tennessee River drainage from southwestern Virginia downstream to Wayne County, Tennessee. In Georgia, it has been found only in the Ridge and Valley Province, where it occurs in the South Chickamauga Creek Basin in Catoosa County.

GEORGIA SPECIMENS EXAMINED.—I have examined

38 specimens from the following localities. *Catoosa County*: (1) South Chickamauga Creek at Rte S819 in Graysville (Anonymous, 1970c:52), 3♂II, 2♀, 2j♂, 30 Aug 1959, W. R. Taylor, R. H. Kanazawa, collectors; 3♂II, 2♀, 4j♂, 8j♀, 26 Aug 1969, E. T. Hall, Jr., M. W. Walker; (2) Little Chickamauga Creek just above confluence with South Chickamauga Creek near St Rte 2 at Ringgold (Anonymous, 1970c:50), 1♂I, 1♂II, 2♀, 1j♂, 3j♀, 26 Aug 1969, ETH, MWW; (3) South Chickamauga Creek at Rte S280, Ringgold, 5♂I, 1♀, 23 Oct 1977, R. W. Bouchard, J. W. Bouchard.

VARIATIONS.—So few specimens are available from Georgia that the variations noted probably do not adequately represent those actually existing. There is remarkable uniformity in most features. As noted in the "Diagnosis," however, the areola is rather variable in width, and the number of punctations across the narrowest part ranges from five to seven. The number of tubercles in the mesialmost row on the mesial surface of the palm of the chela ranges from seven to 10, that on the opposable margin of the fixed finger seven to nine, and on the corresponding surface of the dactyl nine to 11. The carpus of the cheliped always bears one large tubercle and usually there is a spiniform tubercle situated dorsomesially, which in larger specimens is sometimes reduced to a rudiment; rarely a small tubercle is present proximal to the major one. The dorsodistal surface of the merus is always provided with one spiniform tubercle, and occasionally there are two of them; the mesial and lateral rows of tubercles on the ventral surface that are characteristic of many crayfishes are usually each represented by a single, occasionally two, strong distal spine; the more proximal members of the two series, if present at all, are exceedingly small. Usually a small tubercle is present on the mesial surface of the ischium adjacent to the basioischial suture, but it is sometimes absent. The annulus ventralis varies chiefly in the breadth and depth of the transverse fossa and the relative height of its anterior wall.

SIZE.—The largest specimen available is a female in which the length of the carapace is 25.5 (postorbital carapace length 20.5) mm. The largest and smallest first form males have corresponding lengths of 24.8 (19.4) and 18.9 (14.2) mm, respectively. No ovigerous females or ones carrying young have been collected in Georgia.

LIFE HISTORY NOTES.—On the basis of the few specimens from Georgia, the only statement that can be made is that the single first form male that had recently molted (possessing an unincrusted exoskeleton that is weakly calcified) was collected on 26 August and the other five on 23 October. Elsewhere in the range of the species, first form males have been collected from March to June and from August to November. No collections available to me have been made in January, February, and December. Ovigerous females were found in March and April, and one female carrying young was taken in April.

ECOLOGICAL NOTES.—At the locality on South Chickamauga Creek,

> the stream, 200′ wide and average of 1′ deep . . . was brown-green in color . . . [and] included an impounded area and a riffle zone downstream from the dam. Areas sampled included those with quiet, swift, and very swift velocities. The stream bottom was sand overlaid with many stones varying in size from small to large; however, woody debris, twigs, leaves, roots of aquatic plants [*Justicia*] [were also present] . . . (Anonymous, 1970c:28).

The dissolved oxygen in bright sunlight measured 7.0 mg/l, and the temperature of the water was 21.5°C.

In the locality on Little Chickamauga Creek,

> the stream, some 35′ wide and 9″ deep, flowed with a moderate-swift velocity over bedrock on which sand, gravel, and stones had accumulated in some regions. Organisms were also obtained from leaves, logs, twigs, and other debris. . . . Water color was almost clear with a slight white discoloration (Anonymous, 1970c:26).

Bouchard (1976a:579) noted that this crayfish "occurs in [a] wide range of habitats from small streams to large rivers and impoundments . . . . [It is] more common in larger streams, especially in riffle areas under rocks . . . . [It] prefers streams flowing over limestone deposits."

GEORGIA CRAYFISH ASSOCIATES.—This crayfish has been found with *Cambarus (H.) girardianus* three times, and twice each with *C. (P.) extraneus* and *Orconectes erichsonianus*.

Orconectes spinosus (Bundy)

FIGURES 19*b*, 107*a*, 108*d*, 113, 114, 233.

Cambarus extraneus Hagen, 1870:74* [in part: "larger female" (fide Faxon, 1884:145*)].

Cambarus spinosus Bundy, 1877:173-174*.—Faxon, 1884: 148*; 1885a:84*-87, 114-117*, 119, 163*, 173, 174*, 178*, 179, pl. IX: fig. 7, 7', 7a, 7a'; ?1890:632; 1914:376, 419*.—Underwood, 1886:373*.—Adams, 1901:849.—Harris, 1903a:60*, 130*, 138, 144*, 146, 151, 152*, 154, 156, 159, 161; 1903b:602.—Ortmann, 1905a:109, 114*, 115*, 116, 128; 1913:334*, 335, 338, 341, 366, 377; 1931:70, 71, 82, 86, 87*, 88*, 89.—Fitzpatrick, 1967:148, 149.—Hart and Hart, 1974:88*.

Cambarus (Faxonius) spinosus.—Ortmann, 1905a:112.

Cambarus (Faxonius) juvenilis.—Ortmann, 1931:84, 86 [in part: records in the Tennessee River basin].

Orconectes spinosus.—Hobbs, 1942a:350-352 [by implication]; 1972b:86, 87*, 149*, figs. 68b,g, 69d; 1974b:32, 41*, fig. 146.—Anonymous, 1967a, tab. 3*; 1969a:(C-23, C-26, C-27, C-29, C-31)*; 1970b:(162, 163, 165, 168, 196)*.—Hart and Hart, 1974:21, 25, 51, 58*, 59, 63, 73*, 75, 87, 89, 90, 128, 134*, 136-138, 141.—Hobbs and Hall, 1974: 204*.—Bouchard, 1972:32, 36, 40, 42, 43, 50, 53, 59, 70, 72, 74-75*, 77, 80, 85, 86, 92, 108; 1976a:563, 575, 576, 580, 582.—Wharton, 1978:220*.

The above citations do not represent a complete bibliography for the species but do include all synonyms, descriptions, discussions of synonomy, and all references that I have found to its occurrence in Georgia; the latter are marked by asterisks.

SUMMARY OF LITERATURE PERTAINING TO GEORGIA.—The first recorded specimen of *Orconectes spinosus* from Georgia was one that was included in a lot of eight from the "Tennessee River, (near the borders of?) Georgia" (Hagen, 1870:74) identified as *Cambarus extraneus*. Faxon (1885a:84, 116) pointed out that this specimen was actually a member of *Cambarus spinosus* that had been described by Bundy (1877) from the "Etowah, Oostanaula, and Coosa Rivers, in the vicinity of Rome [Floyd County], Georgia, where it is extremely abundant, in company with *C. extraneus* [= *C. (P.) coosae*]." The locality in South Carolina cited by Faxon (1884:148; 1885a:116) and by subsequent authors is doubtful and should be confirmed, but there seems no reason to question his record from Alabama. Ortmann (1905a:115) pointed out that this crayfish had "crossed over [from the Tennessee River drainage] into the Gulf and Atlantic drainages in northern Georgia, South and North Carolina." The reference by him to the latter two states was based on Faxon's records (1884:148 and 1890:632). In the same paper, Ortmann (p. 112) assigned this crayfish to his subgenus *Faxonius*, and in 1913 (p. 334), he cited an additional locality in the Tennessee Basin in Tazewell County, Virginia; otherwise, there is little added to his discussion on the species presented in 1905. In Ortmann's summary of this and related species (1931:84-90), a confusion was initiated that even at this time has not been completely resolved. Specimens from most of the Tennessee Basin, along with *Cambarus putnami* Faxon (1884:131), were assigned to Ortmann's *Cambarus (Faxonius) juvenilis*; furthermore, those assigned by Faxon to *C. spinosus* from the "Tennessee River, near borders of Georgia" were considered as perhaps conspecific, "but this is entirely too indefinite." Continuing, he believed that

> *C. spinosus* Bundy (type-locality Rome, Floyd Co., Georgia, and also from Saluda River, South Carolina and Tar River, Rocky Mount, Edgecombe Co., North Carolina, according to Faxon) is still . . . a doubtful form, and requires further study on the basis of better material. It may be different from *juvenilis*.

Following Ortmann's conclusions, subsequent authors prior to 1974 accepted the relegation of Faxon's *C. putnami* as a synonym of *Orconectes juvenilis*, and although *O. spinosus* was recognized as a distinct species, the ranges were not at all clear. Recognizing the existing confusion in relation to the three taxa (and suspecting that *O. juvenilis* was perhaps a synonym of *Orconectes rusticus* because of the bladelike incisor region of the mandible) Hobbs (1974b) included all four species in his checklist. Bouchard (1976a:580-582) did much to clarify a part of the problem when he presented evidence that *O. juvenilis* is synonymous with *O. rusticus*, thus leaving the name *O. putnami* available for application to those populations occurring in the Green and Cumberland river basins. Furthermore, he also considered *O. spinosus* to be distinct from *O. putnami*, citing the range of the former to include the Tennessee and Coosa river systems and that of *O. putnami* in the Cumberlands to encompass "Russel [sic] Fork (Big Sandy River system), Kentucky and Cumberland River systems" (p. 580). He also tentatively included the New River system (p. 581) within the range of the latter. That further study of variations in these species is needed is evident from Bouchard's tentative identification of specimens from the New River system and his statements (pp. 580, 582) that research is needed to determine if *O. spinosus* and *O. putnami* are species complexes.

Prior to 1967, the only near-specific locality records of the occurrence of *O. spinosus* in Georgia were those cited by Bundy (1877:174) in the vicinity of Rome. Based upon my identifications, Anonymous (1967a, tab. 3) reported it from Holly Creek, 2 miles above the confluence with the Conasauga River in Murray County, and in 1969 from another locality on Holly Creek and from four others in the Conasauga Basin in Whitfield County or on the Murray-Whitfield County line. Four additional localities on the Conasauga River in Murray and Whitfield counties and one on the Etowah River in Bartow County were cited by Anonymous (1970b). Finally, Hart and Hart (1974) listed this species as hosts to four entocytherid ostracods (*Dactylocythere falcata*, *D. suteri*, *Entocythere elliptica*, and *Uncinocythere simondsi*) in four localities: one each in Chattooga, Murray, Polk, and Whitfield counties.

Hobbs and Hall (1974:204) reported that in the Conasauga River, *O. spinosus* was present in localities where the oxygen content of the water was measured at 6.0 and 3.6 mg/l but was absent downstream in one area where the oxygen concentration had dropped to 1.6 mg/l.

DIAGNOSIS.—Rostrum with subparallel margins bearing well-developed marginal spines or tubercles. Postorbital ridges terminating cephalically in spines or tubercles. Cervical spine strong. Areola 4.1 to 7.2 (average 5.5) times as long as broad and constituting 27.1 to 31.9 (average 29.4) percent of entire length of carapace (38.3 to 43.3, average 40.9, percent of postorbital carapace length). Mesial surface of palm of chela shorter than dactyl and bearing at least 2 rows of tubercles, mesialmost consisting of 7 to 11; opposable margin of fingers slightly gaping in larger individuals and bearing row of rounded tubercles along proximal two-thirds and band (males) or very narrow band or single row (females and some second form males) of minute denticles along distal half. Ventral surface of carpus of cheliped with distomedian spine. Ischium of third pereiopod of first form male with hook overreaching basioischial articulation and usually opposed by small tubercle on basis. First pleopods of male reaching coxae of first pereiopods and with mesial process distinctly shorter than central projection; mesial processes somewhat bowed with slightly flattened, acute distal extremities contiguous; central projections, constituting about 0.5 mesial length of appendages, subparallel and in contact along most of their length but with acute distal parts diverging laterally; cephalic surface of appendage with angular or subangular shoulder at base of central projection in first form males. Female with annulus ventralis bearing deep transverse fossa across midlength; first pleopod well developed.

COLOR NOTES (Figure 108*d*).—Carapace pale olive to tan with brown markings. Dorsal surface of rostrum brown or with narrow brown band situated immediately mesial to rostral ridges; elongate, oval median brown spot extending posteriorly from base of rostrum to or almost to broad dark band cephalic to cervical groove, band encompassing mandibular adductor region. Postorbital ridge flanked ventrolaterally by narrow dark line; antennal region pinkish cream and hepatic area with few dark splotches. Thoracic section of carapace bearing white cervical spine flanked dorsally and ventrally by small black spots or streaks; saddle present posteriorly, its bar with cephalomedian prominence; horns rudimentary but much expanded cephaloventrally, tapering almost to level of cervical spine; borders of posterior flange of branchiostegite pale olive. Abdominal terga also basically olive with brownish olive transverse band abutting vermilion posterior margins; first tergum almost entirely very dark green; remaining ones with submedian similarly colored spot flanked by paired dorsolateral ones and with cream spot immediately dorsal to base of pleura; pleura sometimes set off from terga by V-shaped markings continuous with bands on terga; latter edged anteriorly and posteriorly by dark green or black markings. Telson with paired

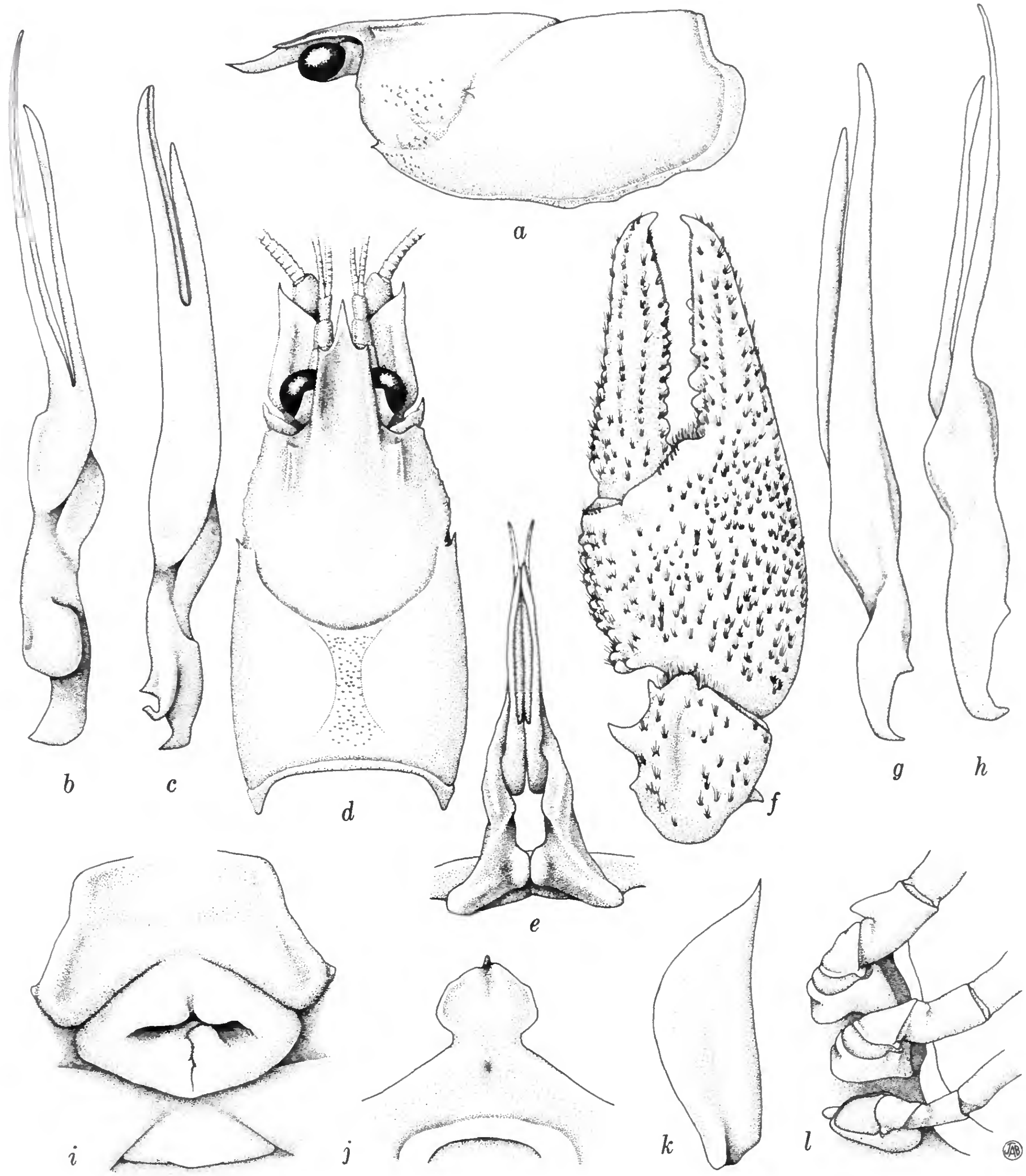


FIGURE 114.—*Orconectes spinosus* (*c*, *g*, from second form male from Coahulla Creek 13 air mi NNE of Dalton, Whitfield Co; *i*, from female, all others from first form male from Mill Creek at US Highway 41, 1.9 mi N of Interstate Hwy 75, Whitfield Co): *a*, lateral view of carapace; *b*, *c*, mesial view of first pleopod; *d*, dorsal view of carapace; *e*, caudal view of first pleopods; *f*, dorsal view of distal podomeres of cheliped; *g*, *h*, lateral view of first pleopod; *i*, annulus ventralis; *j*, epistome; *k*, antennal scale; *l*, proximal podomeres of third, fourth, and fifth pereiopods.

black spots at lateral bases of posterior section. Uropod deep olive, sometimes with both rami dark laterally and fading mesially. Antennular and antennal peduncles pale olive mottled with dark green, flagella brownish olive to tan. Third maxilliped olive with dark spots on distal podomeres. Cheliped also olive from midlength of merus distally and bearing cream spines on dorsodistal part of merus; prominent black spots on mesiodistal end of merus, at base of large spine on mesial side of carpus, on dorsal articular knob of propodus at base of dactyl, and another distolateral to latter spot; in addition, lateral side of propodus margined in black and broad black band present on fingers proximal to yellow distal ends, black bands often bleeding proximally along ridges of fingers. Remaining pereiopods pale olive, banded or spotted with darker olive. Sternal area of cephalothorax cream.

TYPES.—Syntypes, MCZ 3540 (2♂II, 2♀), MCZ 3541 (♂II, ♀), USNM 19779 (3♂II, 2♀).

TYPE-LOCALITY.—Etowah, Oostanaula, and Coosa rivers, in the vicinity of Rome, Floyd County, Georgia.

RANGE.—Streams in the Coosa and Tennessee river basins in Alabama, Georgia, North Carolina, Tennessee, and Virginia. In the Coosa Basin of Georgia, it occurs from the Conasauga watershed in Murray and Whitfield counties, and the Etowah system in Bartow and Polk counties downstream to Floyd County; although there are no records of its occurrence in this basin in Alabama, it is almost certainly present at least in Cherokee County. In the Tennessee Basin, it ranges from southwestern Virginia downstream through eastern Tennessee and northern Alabama to Hardin and Wayne counties, Tennessee. In the Tennessee Basin in Georgia, it has been collected in only one locality, a tributary of the Nottely River, 2.6 miles east of the Fannin County line on U.S. Highway 76, Union County. Thus it is confined to the Ridge and Valley and Blue Ridge provinces in this state.

GEORGIA SPECIMENS EXAMINED.—I have examined 428 specimens from 32 localities (Figure 113) in the following counties, number of localities in parentheses: Bartow (3), Chattooga (1), Floyd (4), Gordon (3), Murray (9), Polk (3), Union (1), and Whitfield (8).

VARIATIONS.—In addition to the range of variations in body proportions included in the "Diagnosis," there may be three to six punctations across the narrowest part of the areola, and the surface may appear sparsely or densely punctate. The spines on the carapace are generally more prominent in smaller individuals, but in occasional large ones they are equally as conspicuous and acute. The number of spines and tubercles on the cheliped exhibits a rather wide range of variation: the mesial surface of the ischium occasionally bears one small tubercle, but generally there is none; the ventrolateral row of spiniform tubercles on the merus consists of two to four, and the ventromesial row consists of six to nine; the mesial surface of the carpus is armed with a large spiniform tubercle, and usually two additional smaller ones (one situated proximally and the other dorsodistally); the mesial surface of the palm bears at least two rows of tubercles (mesialmost row consisting of seven to 11), and frequently other tubercles flank the rows; the opposable surface of the fixed finger bears a row of four to seven low rounded, usually corneous, tubercles in addition to one situated more distoventrally; the corresponding surface of the dactyl bears a row of four to nine tubercles similar to those on the fixed finger, and both fingers of larger males exhibit a comparatively broad band of minute denticles along the distal half or third. In smaller second form males and females the denticles are arranged in a single row or occasionally in a narrow band. The chela is frequently studded with conspicuous tufts of plumose setae that partially obscure both punctations and tubercles; these setae are most densely arranged above and below the proximal bases of the opposable surfaces of the fingers; in some individuals, however, the setae are comparatively inconspicuous even in crayfish that have recently molted. The ventral surface of the thoracic region is also sometimes conspicuously hirsute or sparsely setose. While most specimens collected in a single locality are similar in the degree to which the setae are developed, the hirsute individuals do not seem to be regionally restricted. The first pleopods of the male are remarkedly uniform, and all reach the coxa of the first pereiopod. The only conspicuous variation that has been noted in the annulus ventralis is in the depth and width of the transverse fossa.

SIZE.—The largest specimen collected in Georgia is a second form male obtained in Coahulla Creek, a tributary to the Conasauga River; it has a carapace length of 38.4 (postorbital carapace length 28.4) mm. Corresponding lengths of the smallest and largest first form males are 18.2 (12.9) mm and 37.1 (28.0) mm, and of the smallest ovigerous female, approximately (acumen broken) 22.5 (16.2) mm.

LIFE HISTORY NOTES.—First form males have been collected in Georgia in April and from August to October. Virtually no collections have been made from November through March (see "Seasonal Data"), and few specimens were collected from May to July. It is probable, however, that the molt in males from first to second form occurs during April and May and that few, if any, first form males are in the population during June and early July. Six ovigerous females were found during April. Data for the ovigerous females are as follows:

Carapace and postorbital carapace lengths (mm)	*Number of eggs*	*Diameter of eggs (mm)*
22.5(16.2)	89	1.8–1.9
23.2(16.8)	86	1.8–1.9
29.5(21.0)	163	2.1–2.2
30.8(22.5)	208	2.1–2.2
32.0(23.2)	214	2.1–2.2
35.9(25.8)	286	2.1–2.2

One female, collected on 1 May, had egg membranes still attached to the pleopods. Presumably the eggs had hatched and the young had recently left her.

Elsewhere in the range of the species, first form males have been collected also in March and November, and three were found on 24 July; all ovigerous females were found in April except for one collected in June.

Seasonal Data

Sex/stage	*J*	*F*	*M*	*A*	*M*	*J*	*J*	*A*	*S*	*O*	*N*	*D*	*?*
♂I				6				6	5	49			2
♂II				15	4	2	7	12		9			3
♀				8		6	12	15	4	50	1		4
♂j				2	1	3	35	77	1	1			1
♀j				2	1	3	14	56	1	3	1		
♀ ovig				6									

ECOLOGICAL NOTES.—Like its congeners in Georgia, this crayfish is a stream dweller, living in both small to large creeks and in rivers, but it has not been found in cascading brooks. Whereas it occurs in greater numbers in areas where the current is moderate to sluggish, or in eddies, it has also been found in riffles. It occurs both under rocks and in tree litter and does not shun accumulations of other types of debris.

GEORGIA CRAYFISH ASSOCIATES—This crayfish has been found with each of the following species (the number of times they have been collected together is noted in parentheses): *Cambarus (C.) bartonii* (2), *C. (D.) latimanus* (4), *C. (D.) striatus* (14), *C. (H.) fasciatus* (2), *C. (H.) manningi* (3), *C. (L.) acanthura* (8), *C. (P.) coosae* (25), *C. (P.) scotti* (1), *Procambarus (O.) lophotus* (3), and *P. (Pe.) spiculifer* (7).

Genus Procambarus

Astacus.—Harlan, 1830:464 [not Fabricius, 1775:413].

Subgenus *Cambarus* Erichson, 1846:95 [in part].

Cambarus—Girard, 1852:91 [in part].—Ortmann, 1905a:96 [not Erichson, 1846], [type-species, proposed therein, *Astacus Blandingii* Harlan, 1830:464; gender: masculine; proposed as typical subgenus by Ortmann, but type-species previously selected by Faxon, 1898:644, *Astacus Bartonii* Fabricius, 1798:407.]

Camborus.—Williamson, 1899:47 [erroneous spelling].

Procambarus Ortmann, 1905d:435, 437. [Type-species, by subsequent designation (Fowler, 1912:340), *Cambarus Digueti* Bouvier, 1897:225. Gender: masculine. Proposed as subgenus of *Cambarus*, elevated to generic rank by Hobbs, 1942a:341.]

Paracambarus Ortmann, 1906a:1. [Type-species, by monotypy, *Cambarus (Paracambarus) paradoxus* Ortmann, 1906a: 3. Gender: masculine. Proposed as subgenus of *Cambarus*, elevated to generic rank by Hobbs, 1942a:344, and reduced to subgenus of *Procambarus* by Hobbs, 1972a:10.]

Ortmannicus Fowler, 1912:34, 341. [Type-species, by original designation, *Astacus Blandingii* Harlan, 1830:464. Gender: masculine. Replacement name for Ortmann's subgenus *Cambarus*, utilized as generic name by Rhoades, 1944:114, and as subgenus of *Procambarus* by Hobbs, 1972a:2–5, 9.]

Cambarellus.—Creaser, 1933b:21 [lapsus for *Cambarus*].

Cambaru.—Goodnight, 1941:72 [erroneous spelling].

Ortmanmanicus—Hobbs, 1942a:342 [erroneous spelling].

Pracambarus.—Villalobos, 1953:352 [erroneous spelling].

Paracamburus.—Villalobos, 1953:354 [erroneous spelling].

Procambrus.—Sukô, 1961:37 [erroneous spelling].

procambarus.—Padgett, 1970:19 [lapsus calami].

Procambararus.—Hobbs III, Thorp, and Anderson, 1976:12 [erroneous spelling].

Procambasrus.—Huner, 1977:10 [erroneous spelling].

Procambaris.—Wharton, 1978:46 [erroneous spelling].

Subgenus *Girardiella* Lyle, 1938:76. [Type-species, by monotypy, *Cambarus Hagenianus* Faxon, 1884:141. Gender: feminine.]

Subgenus *Acucauda* Hobbs, 1972a:3–5. [Type-species, by original designation, *Procambarus fitzpatricki* Hobbs, 1971b:461. Gender: feminine.]

Subgenus *Austrocambarus* Hobbs, 1972a:2–5. [Type-species, by original designation, *Procambarus vazquezae* Villalobos, 1954:328. Gender: masculine.]

Subgenus *Capillicambarus* Hobbs, 1972a:3–4, 6. [Type-species, by original designation, *Cambarus (Cambarus) hinei* Ortmann, 1905c:401. Gender: masculine.]

Subgenus *Hagenides* Hobbs, 1972a:2–4, 7. [Type-species, by original designation, *Astacus advena* LeConte, 1856:402. Gender: masculine.]

Subgenus *Leconticambarus* Hobbs, 1972a:2–5, 7. [Type-species, by original designation, *Cambarus barbatus* Faxon, 1890:621. Gender: masculine.]

Subgenus *Lonnbergius* Hobbs, 1972a:2–4, 8. [Type-species, by original designation, *Cambarus acherontis* Lönnberg, 1895:6. Gender: masculine.]

Subgenus *Mexicambarus* Hobbs, 1972a:3, 4, 8. [Type-species, by original designation, *Cambarus (Cambarus) bouvieri* Ortmann, 1909:159. Gender: masculine.]

Subgenus *Pennides* Hobbs, 1972a:2–4, 10. [Type-species, by original designation, *Procambarus natchitochae* Penn, 1953:5. Gender: masculine.]

Subgenus *Remoticambarus* Hobbs, 1972a:3, 4, 11. [Type-species, by original designation, *Procambarus pecki* Hobbs, 1967b:2. Gender: masculine.]

Subgenus *Scapulicambarus* Hobbs, 1972a:2, 3, 5. [Type-species, by original designation, *Cambarus clarkii paeninsulanus* Faxon, 1914:369. Gender: masculine.]

Subgenus *Tenuicambarus* Hobbs, 1972a:3, 5, 12. [Type-species, by original designation, *Procambarus tenuis* Hobbs, 1950: 194. Gender: masculine.]

Subgenus *Villalobosus* Hobbs, 1972a:3, 5, 12. [Type-species, by original designation, *Paracambarus riojae* Villalobos, 1944:161. Gender: masculine.]

Subgenus *Distocambarus*, new subgenus [described herein].

DIAGNOSIS.—Antenna never with conspicuous fringe on mesial border. Third maxilliped with teeth on mesial margin of ischium. Mesial margin of palm of chela with none to many tubercles; lateral margin of fixed finger never bearing spiniform tubercles; opposable margin of dactyl occasionally with prominent excision. Areola broad to obliterated at midlength. Ischia of third and/or fourth pereiopods of male with hook. Coxa of fourth pereiopod of male with or without caudomesial boss, latter lacking basal setiferous pit ventrally. First pleopods of first form male symmetrical or asymmetrical, sometimes deeply withdrawn between bases of pereiopods and usually at least partially concealed by setae extending from ventrolateral margin of sternum; subcontiguous, contiguous, or partially overlapping basally, and terminating in 2 or more, usually 3 or 4 elements; presence of subterminal setae in many members of genus unique; terminal elements highly variable in form and disposition; if only 2 elements present (mesial process and central projection), shoulder present on distal third of cephalic surface of appendage, or central projection forming distally projecting triangular plate, or central projection arising from caudal margin of enlarged terminal region; if more than 2 elements present, central projection seldom bladelike, if so, directed laterodistally or lacking subterminal notch, and elements never bent caudally at angle of so much as 90 degrees. Female with annulus ventralis freely movable, although sometimes partially covered ventrally by caudally projecting prominences from sternal plate immediately cephalic to it; first pleopod usually present. Branchial count 17 + epipodite. (Slightly modified from Hobbs, 1974a:15–16.)

RANGE.—Middle and North America: Guatemala and Cuba to Minnesota and southern New England. In the United States, east of the continental divide and absent from mountainous and most foothill areas. Introduced into California, Hawaii, Japan, Spain, and several countries in Africa and Central America (see Huner, 1978: 193).

SPECIES.—Twenty-eight of the 148 currently recognized members of the genus have been found in Georgia, and almost assuredly, *Procambarus (Ortmannicus) leonensis* is present in the Aucilla or Ochlockonee watersheds in the southwestern part of the state. Six of the subgenera are represented, the numbers of species of each are enclosed in parentheses: *Distocambarus* (1), *Hagenides* (5), *Leconticambarus* (3), *Ortmannicus* (11), *Pennides* (5), and *Scapulicambarus* (3).

The following is presented to account for the total number of species stated above to be currently recognized. In his checklist of the North and Middle American crayfishes, Hobbs (1974b: 43–68) included all of the members of the genus that had been described when the manuscript was completed. Since then the following taxa have been added or are described herein: *Procambarus (Austrocambarus) oaxacae oaxacae* Hobbs (1973a:29); *P. (A.) oaxacae reddelli* Hobbs (1973a: 33); *P. (A.) sbordonii* Hobbs (1977b:201); *P. (Capillicambarus) brazoriensis* Albaugh (1975:1); *P. (Distocambarus) devexus*, new species; *P. (Girardiella) barbiger* Fitzpatrick (1978b:69); *P. (G.) cometes* Fitzpatrick (1978b:74); *P. (G.) connus* Fitzpatrick (1978b:76); *P. (G.) curdi* Reimer (1975:22); *P. (G.) hagenianus vesticeps* Fitzpatrick (1978b:64); *P. (G.) liberorum* Fitzpatrick (1978a:533); *P. (G.) pogum* Fitzpatrick (1978b:83); *P. (Hagenides) caritus*, new species; *P. (H.) talpoides*, new species; *P. (Leconticambarus) pubischelae deficiens*, new subspecies; *P. (Ortmannicus) erythrops* Relyea and Sutton (1975:8); *P. (O.) franzi* Hobbs and Lee (1976: 384); *P. (O.) geminus* Hobbs (1975a:1); *P. (O.) marthae* Hobbs (1975a:6); *P. (O.) medialis* Hobbs (1975a:10); *P. (Pennides) clemmeri* Hobbs (1975a: 19); *P. (Pe.) petersi*, new species; *P. (Pe.) roberti* Villalobos and Hobbs (1974:8); *P. (Scapulicambarus) strenthi* Hobbs (1977a:412); *P. (Villalobosus) xochitlanae* Hobbs (1975a:16).

REMARKS.—One of the greatest disappointments of my field efforts in the state has been my failure to rediscover LeConte's *Astacus angustatus*. Try as I may in streams in the sand hills of Georgia, I have not found any specimens that possess pleopods like those of his type specimen. If the species is still extant, I have no idea as to where next to search for it. It is also unfortunate, particularly in the absence of specimens identified by LeConte, that his description of *A. maniculatus* is not adequate to permit associating the name with any single species and it must therefore remain a nomen oblitum.

Much more work needs to be done in determining the relationships of *P. (H.) caritus* and *P. (H.) talpoides* and of *P. (L.) pubischelae deficiens* and the nominate subspecies.

To my knowledge there is no physiographic feature that separates the range of *P. (H.) truculentus* from that of *P. (H.) advena*, nor am I aware of any environmental factors that are responsible for their segregation. Surely somewhere along the narrow interval separating them, the two must share a hillside seepage area or a flatwoods section where the water table approaches the surface.

Intriguing also is the question of how *P. (Pe.) gibbus* maintains an apparently discrete gene pool when its range is located in the midst of that of one of its closest relatives where no obvious barrier separates them. How have *P. (Pe.) raneyi* and *P. (Pe.) spiculifer*, two species that vicariate for one another throughout much of their ranges, been able to adjust to sharing habitats in certain localities in the Altamaha Basin?

Is it possible that *P. (O.) leonensis* does not occur in Georgia even though it has been found abundantly in neighboring counties in Florida? Equally puzzling is the paucity of locality records for *P. (O.) a. acutus* in the state, for it has been found to be widespread in South Carolina and it is by no means rare in Alabama.

These problems, to say nothing of our limited knowledge of the life histories and especially of behavioral attributes of some of the more primitive species occurring in Georgia, need the attention of a number of patient investigators.

Key to Subgenera of *Procambarus* Occurring in Georgia

1. Two or more cervical spines present on each side of carapace . . ***Pennides***
   One or no cervical spine present on each side of carapace 2

2. Chela of male usually broadly triangular, strongly depressed, and always with cristiform row of tubercles on mesial margin of palm . . ***Hagenides***
   Chela elongate oblong to subrectangular, not strongly depressed, and never with cristiform row of tubercles on mesial margin of palm 3
3. First pleopod of male strongly inclined caudally and terminating in 2 parts flanked cephalically by well-defined hump. Annulus ventralis capable of motion through arc of about 90 degrees .... ***Distocambarus*** [*P. (D.) devexus*]
   First pleopod of male rarely strongly inclined caudally and always terminating in at least 3 parts. Annulus ventralis capable of motion through arc of no more than 45 degrees 4
4. First pleopod of male with subapical setae situated cephalically, never obscuring terminal elements; mesial process disposed distally, with apex often directed cephalodistally. Chela of first form male (unless regenerated) with mesial surface of palm bearded .... ***Leconticambarus***
   First pleopod of male with subapical setae situated cephalically and/or laterally, always partly obscuring terminal elements; mesial process variously disposed but never distally. Chela of first form male never with mesial surface of palm bearded 5
5. First pleopod of male with prominent cephalic angular or subangular shoulder situated far proximal to base of terminal elements .... ***Scapulicambarus***
   First pleopod of male without prominent cephalic angular or subangular shoulder situated far proximal to base of terminal elements .... ***Ortmannicus***

Subgenus *Distocambarus*, new subgenus

Diagnosis.—Body and eyes pigmented, latter small but well developed. Rostrum without marginal spines, tubercles, or median carina. Carapace with none to multiple cervical tubercles. Areola rather narrow, 8.9 to 13.2 (average 11.1) times as long as broad, and constituting 37.1 to 40.5 (average 38.9) percent of entire length of carapace (44.3 to 47.9, average 45.9, percent of postorbital carapace length). Ventral surface of ischium of third maxilliped obscured by dense mat of plumose setae. First 3 pairs of pereiopods without conspicuous brush of setae extending from basis to merus. First pair of pereiopods with ventral surface of merus densely tuberculate and corresponding surface of proximal part of both fingers with tubercles. Second pair of pereiopods with conspicuous brush of setae on carpus and propodus. Simple hook on ischium of third pereiopod only. Coxa of fourth pereiopod lacking caudomesial boss. First pleopods not contiguous at base, reaching coxae of third pereiopods, symmetrical, with proximomedian lobe but without proximomesial spur; cephalic surface with distinct shoulder near bases of terminal elements; subapical setae absent; shaft of appendage bent caudodistally near midlength at angle of approximately 40 degrees; terminal elements consisting

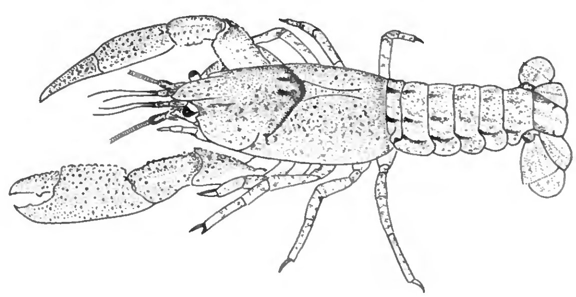


Figure 115.—Color pattern of *Procambarus (Distocambarus) devexus* from type-locality.

of broad, flattened, subtriangular mesial process directed distolaterally, and, in caudal view, obscuring part of corneous central projection; latter consisting of thin, strongly cornified, cephalically convex, lamelliform plate directed caudodistally; cephalic process represented by small rounded to acute knob on cephalodistal end of appendage and caudal elements lacking. Mesial ramus of uropod with distomedian spine premarginal. Female with annulus ventralis unique in genus in being capable of arclike motion in longitudinal axis of body; postannular sclerite covering caudal part of annulus when latter at caudal end of arc; first pleopod (with single exception, see below) rudimentary.

Type-Species.—*Procambarus (Distocambarus) devexus*, new species.

Gender.—Masculine.

List of Species.—Monotypic.

Etymology.—From the Latin *disto* (stand apart, be separate, differ) plus generic name *Cambarus*, alluding to the remote affinities of the single species to other crayfishes.

Habitat.—See "Ecological Notes" for *P. (D.) devexus*.

Procambarus (Distocambarus) devexus, new species

Figures 11*j*, 105, 115–117, 234

Diagnosis.—Same as that of subgenus *Distocambarus*.

Holotypic Male, Form I.—Body (Figure 116*a,k*) subovate, compressed laterally. Abdomen narrower than thorax (11.4 and 14.1 mm). Width of carapace slightly greater than depth at caudodorsal margin of cervical groove (14.1 and 13.4 mm). Areola almost 11 times as long as wide, with 2 punctations in narrowest part. Cephalic section of carapace about 1.7 times as long as areola, length of latter 37.5 percent of total length of carapace (44.4 percent of postorbital carapace length). Rostrum excavate dorsally, with slender convergent margins lacking spines or tubercles; dorsal surface punctate, acumen not clearly defined basally, and reaching anteriorly to base of ultimate podomere of antennular peduncle; subrostral ridge rather weak but evident in dorsal aspect along two-thirds length of rostrum from level of caudal margin of orbit. Postorbital ridge rather strong, swollen caudally, grooved dorsolaterally, and ending abruptly anteriorly, lacking spine or tubercle. Suborbital angle strong and subacute; branchiostegal spine very small but acute. Carapace punctate dorsally and dorsolaterally, rather weakly granulate laterally, tubercles somewhat larger in hepatic, ventral mandibular, and anteroventral branchiostegal regions than elsewhere except for 3 cervical tubercles on lateral part of branchiostegite. Abdomen subequal in length to carapace and not otherwise conspicuously reduced. Third through fifth pleura (Figure 117*a*) truncate ventrally and subangular caudoventrally. Cephalic section of telson with 2 spines in left and 3 in right caudolateral corners. Both lobes of proximal podomere of uropod with acute spine; mesial ramus with distolateral spine, well-developed median rib ending in premarginal acute distomedian spine; lateral ramus with short, fixed distolateral spine on anterior section flanked mesially by longer movable one, and with usual row of spines flanking proximal side of transverse suture. Cephalic lobe of epistome (Figure 116*g*), except for paired lobes laterally and small anteromedian projection, broadly rounded; margins little elevated, surface subplane, and main body with shallow fovea at cephalic apex of triangular depressed area; epistomal zygoma broadly arched, median part deep blue in color. Antennular peduncle with strong acute tubercle on ventral surface of basal podomere at about midlength. Antenna reaching third abdominal tergum, peduncle without spines; diameter of renal tubercle about half maximum width of coxal podomere bearing it. Antennal scale (Figure 116*j*) about 2.2 times as long as broad, greatest width distal to midlength, lamellar area slightly broader than twice width of thickened lateral part; latter terminating in spine, reaching level of base of distal podomere of antennular peduncle. Third maxilliped with basis, ischium, and peduncle of exopod bearing clusters of long plumose setae ventrally, largely obscuring surface of

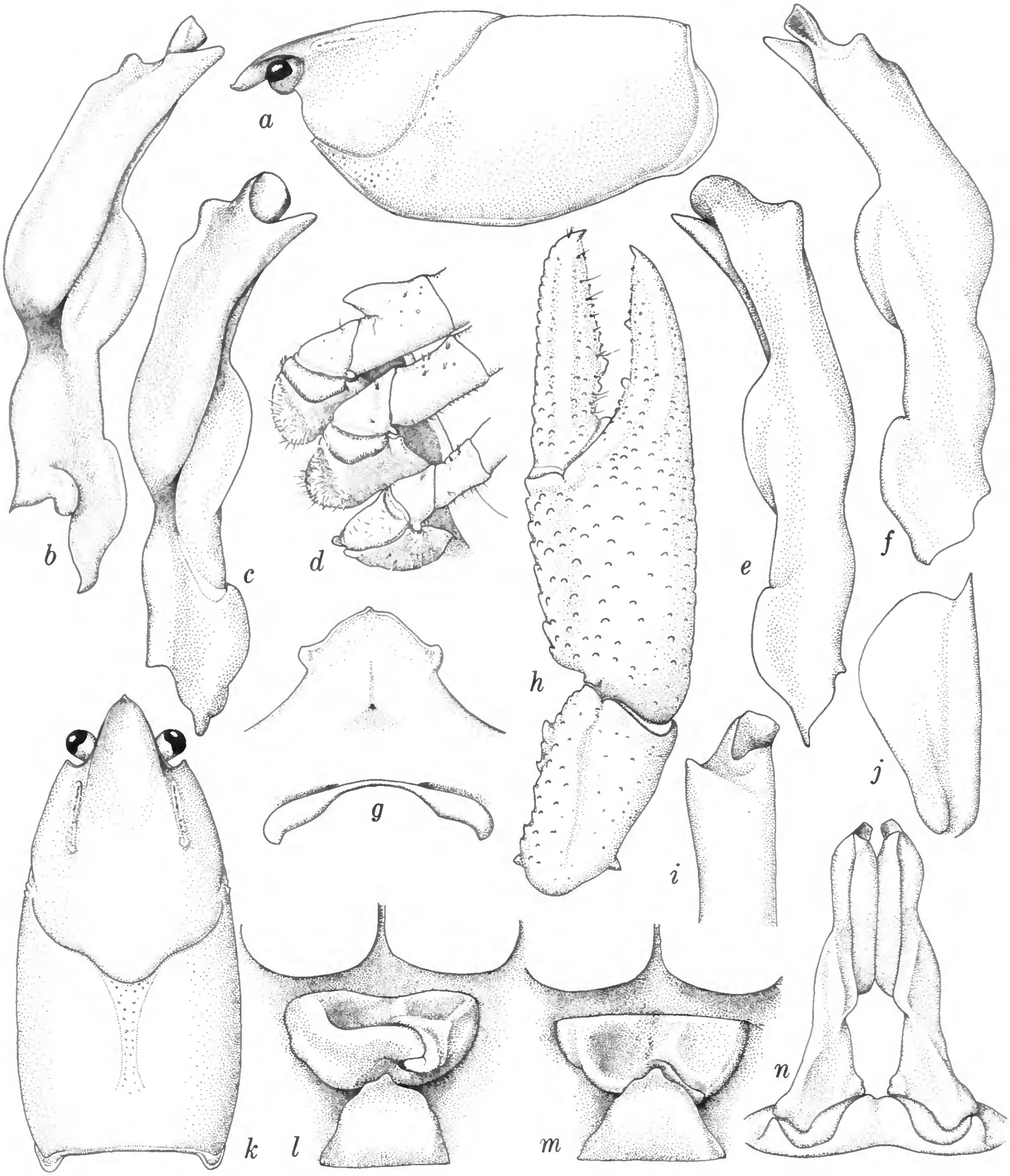


FIGURE 116.—*Procambarus (D.) devexus* (all from holotype except *c*, *e*, from morphotype, and *l*, *m*, from allotype): *a*, lateral view of carapace; *b*, *c*, mesial view of first pleopod; *d*, proximal podomeres of third, fourth, and fifth pereiopods; *e*, *f*, lateral view of first pleopod; *g*, epistome; *h*, dorsal view of distal podomeres of cheliped; *i*, cephalic view of distal part of left first pleopod; *j*, antennal scale; *k*, dorsal view of carapace; *l*, annulus ventralis in elevated position; *m*, same depressed beneath postannular sclerite; *n*, caudal view of first pleopods.

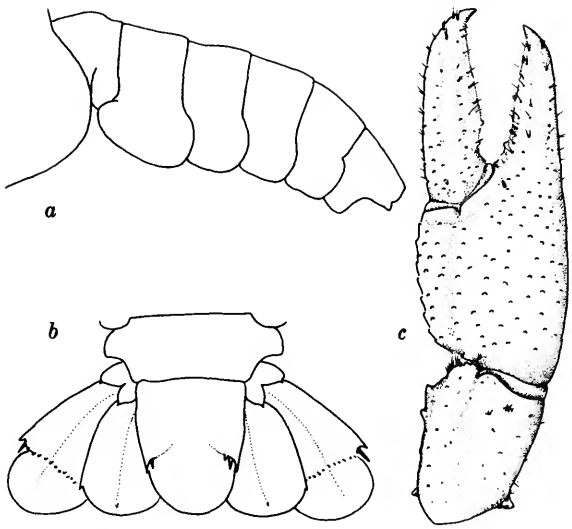


FIGURE 117.—*Procambarus (D.) devexus* (*a*, *b*, from holotype; *c*, from allotype): *a*, lateral view of abdomen; *b*, dorsal view of telson and uropods; *c*, dorsal view of distal podomeres of cheliped.

podomeres; distolateral extremity of ischium angular but not produced.

Right chela (Figure 116*h*) subovate in cross section but not strongly depressed. Entire surface of palm conspicuously tuberculate, with mesial surface bearing row of 7; tubercle on ventral surface opposite base of dactyl made relatively inconspicuous by other larger ones situated more proximally. Both fingers with comparatively low submedian longitudinal ridges dorsally and ventrally; ridges flanked along proximal half of length by tubercles and along distal half by setiferous punctations. Opposable margin of fixed finger with row of 9 (third from base largest) comparatively small compressed tubercles bearing rounded (basally) to acute (distally) corneous edges; larger tubercle present on lower level at base of distal third of finger, and narrow band of minute denticles, interrupted by more proximal tubercles, extending along almost entire length of finger; lateral margin of finger with row of tubercles, decreasing in prominence distally, along proximal half, replaced by row of setiferous punctations along distal half. Opposable margin of dactyl with row of 10 (9 on left) tubercles, third from base much larger than others, giving finger resemblance to that of members of subgenera *Acucauda* and *Girardiella*; minute denticles arranged as on fixed finger; mesial surface of finger with subserrate row of tubercles diminishing in size distally.

Carpus of cheliped conspicuously long, approximately twice as long as broad, bearing shallow oblique furrow dorsally, and with dorsomesial surface mostly tuberculate and dorsolateral largely punctate (small tubercles withdrawn in shallow to deep pits); mesial and mesioventral surfaces strongly tuberculate, 4 on former somewhat larger than others; lateral and ventrolateral surfaces more sparsely tuberculate; distoventral margin with well-developed tubercle on condyle and much smaller distomedian tubercle. Merus tuberculate along entire dorsal and ventral, as well as on distomesial and distolateral, surfaces; more proximal parts of latter two polished with few punctations; tubercles on ventral surface crowded and usual mesial and lateral rows hardly discernible. Ischium with row of 4 tubercles ventromesially flanked by 1 or 2 tubercles mesially and several laterally; dorsolateral margin with row of 5 tubercles flanked dorsally by few smaller ones.

Hook on ischium of third pereiopod only (Figure 116*d*); hook simple, overreaching basioischial articulation, and not opposed by tubercle on basis. Coxa of fourth pereiopod lacking caudomesial boss; that of fifth with small but clearly defined compressed ventromesial one, and with mesial process on anterior side of phallic papilla.

Sternum between third, fourth, and fifth pereiopods moderately deep and bearing conspicuous, mesially disposed fringe of plumose setae on ventrolateral margins adjacent to third and fourth; setae almost completely obscuring distal half of first pleopod.

First pleopods (Figure 116*b*,*f*,*i*,*n*) as described in "Diagnosis" of *Distocambarus*.

ALLOTYPIC FEMALE.—Excluding secondary sexual features, differing from holotype in following respects: postorbital ridges merging gently with surface of carapace cephalically; third through fifth pleura of abdomen rounded to subangular caudoventrally; cephalic section of telson with 2 spines in left and 1 in right caudolateral corner; lateral lobes of epistome not so strongly developed; antenna reaching first abdominal tergum; opposable margin of fixed finger of chela with row of 10 tubercles; minute denticles on both fingers arranged in single row; only 1 tubercle on mesial surface of carpus of cheliped obviously larger than others (Figure 117*c*); dorsolateral row of tubercles on ischium of cheliped consisting of 3 on right and 2 on left. First pleopods absent. (See "Measurements.")

Annulus ventralis movable through arc of 90 degrees. When depressed (Figure 116*m*), transverse cephalic margin almost straight, and lateral and caudal margins forming rather broad arc with much of caudal part hidden by strongly developed, elevated, and arched postannular sclerite; ventral face of annulus with broad, deep concavity dextrally and shallower one sinistrally; sinus originating near median line and forming arc across caudosinistral surface. When annulus elevated (Figure 116*l*), postannular sclerite obscuring very little of caudodorsal part of annulus, and surface bearing excavations directed anteriorly. Sternum cephalic to annulus lacking tubercles or posteriorly directed prominences.

Morphotypic Male, Form II.—Differing from holotype in following respects: acumen reaching midlength of ultimate podomere of antennular peduncle; pleura of fourth and fifth abdominal segments rounded caudoventrally; antenna, probably regenerated, not reaching caudal margin of carapace; mesial surface of palm of chela with row of 8 tubercles; opposable margin of fixed finger of right chela with row of 8 (9 on left) tubercles, that on lower levels situated at base of distal two-fifths of finger; minute denticles on opposable margins of both fingers arranged in single rows; opposable margin of dactyl of left chela with 11 tubercles; only 1 on mesial surface of carpus obviously larger than others; proximal tubercle on ventromesial surface of ischium of left cheliped bispinose; dorsolateral surface of ischium of both chelipeds with row of 4 tubercles. Hook on ischium of third pereiopod much reduced and not reaching basioischial articulation; boss on coxa of fifth pereiopod rudimentary; setal mats borne on ventrolateral margin of sternum less conspicuous and not obscuring part of first pleopod. (See "Measurements.") First pleopod (Figure 116*c*,*e*) resembling that of first form male in almost every detail except lacking sclerotization in slightly more inflated terminal elements.

Color Notes (Figure 115).—Background color of entire body pale tan to brown. Carapace marked with dark brown to black spots; paired ones in orbital region, along posterolateral side of postorbital ridges, and on mesial sides of mandibular adductor regions, latter spots, expanding and becoming more dilute caudally, joining dark line covering cervical groove. Dorsal and dorsolateral regions of carapace with small brown spots, latter anastomosing and becoming paler more ventrally. First tergum of abdomen with paired, subrectangular dark spots dorsolaterally, and spots on succeeding terga becoming progressively paler and smaller; undulating brown to black longitudinal line extending along bases of all pleura. Both pleura and terga with spots, many anastomosing. Telson with paired dark patches cephalolaterally and on caudolateral angles of cephalic section; slightly paler median stripe extending almost entire length. Basal podomere of uropod with brown margins; longitudinal ridges on both rami and distal margin of lateral ramus dark; remainder marked with anastomosing flecks. Antennular and antennal peduncles mottled in deep brown, distal podomere of antennal peduncle with similarly colored mesial and lateral borders; flagella of both appendages olive. Third maxilliped pale tan with brownish flecks. Cheliped pinkish cream to cream basally, darker along proximodorsal surface of merus, and coloration intensifying distally, spreading both ventromesially and ventrolaterally so that distal part of merus, carpus, and chela tan to light brown and studded with dark olive brown to black tubercles; fingers with pale tips (sometimes with reddish tinge); ventral surface of cheliped pale tan, sometimes suffused with orange. Remaining pereiopods with coloration much as that on cheliped, although darkest at distal end of merus and with dark spots. Ventral surface of body cream to pinkish cream.

Measurements (mm)

	Holotype	*Allotype*	*Morphotype*
Carapace			
Height	13.4	16.2	13.8
Width	14.1	18.0	15.2
Entire length	29.1	35.2	30.9
Postorbital length	24.6	29.6	25.8
Areola			
Width	1.0	1.4	1.0
Length	10.9	13.8	12.2
Rostrum			
Width	4.6	5.9	4.8
Length	6.1	7.2	6.7
Chela			
Length of mesial margin of palm	8.7	8.9	8.3
Width of palm	8.0	8.3	7.4
Length of lateral margin	22.4	21.8	21.0
Length of dactyl	12.0	12.6	11.4
Abdomen			
Width	11.4	15.1	12.2
Length	29.0	32.2	28.5

TYPES.—The holotypic male, form I, allotypic female, and morphotypic male, form II (numbers 148569, 148570, and 148571, respectively), are deposited in the National Museum of Natural History, Smithsonian Institution, as are the following paratypes: 7♂I, 3♂II, 3♀, 8j♂, and 16j♀.

TYPE-LOCALITY.—Marshy area under bridge within 200 meters south of and in the flood plain of the Broad River on State Route 17, Wilkes County, Georgia. There grasses, sedges, and low-growing Compositae are luxuriant in and bordering small pools of water around the bridge pilings and in depressions made by oversized tractor tires. At the edge of the right-of-way, a thicket of *Typha* sp., with entangling *Rubus* sp. and scattered *Salix nigra*, interrupts a wooded area supporting *Pinus* sp., *Platanus occidentalis*, *Liquidambar styraciflua*, and *Quercus* sp. Although a search was made in the wooded area and around the *Typha* thicket, no crayfish were found except under and in the immediate vicinity of the bridge. The juvenile specimens were obtained with the aid of a hand net in the pools, but all of the larger specimens were dug from burrows in the sandy clay soil.

RANGE.—Known only from the Piedmont Province in the Broad River basin in Oglethorpe and Wilkes counties, Georgia.

GEORGIA SPECIMENS EXAMINED.—I have examined 40 specimens from the following localities. *Oglethorpe County:* (1) roadside ditch adjacent to Goosepond Creek 2 mi E of St Rte 77 on Co Rd 195, 4♂II, 1♀, 3j♂, 6j♀, 2 Apr 1978, R. J. Dubois, D. J. Peters, J. E. Pugh, HHH, collectors. *Wilkes County:* (2) type-locality, 2♂II, 1j♂, 5j♀, 16 Apr 1977, C. E. Carter, C. W. Hart, Jr., JEP, HHH; 1♂II, 3j♂, 2j♀, 3 Oct 1977, T. A. English, Jr., HHH; 1♂I, 2♀, 5j♂, 3j♀, 2 Apr 1978, RJD, DJP, JEP, HHH; (3) seepage area adjacent to Susan Smith Branch about 2 mi W of St Rte 17 on unnumbered road, 1♀, 2 Apr 1978, RJD, DJP, JEP, HHH. The holotype, which is one of the males collected on 16 April 1977 and maintained alive in the laboratory, molted to first form during the first week of October 1977. By 1 November 1978, seven additional second form and juvenile males noted above had attained first form.

VARIATIONS.—The rostral margins in some specimens are less convergent than in others, resulting in a more spatulate appearance. The cervical tubercles may be reduced in size and number, and in some of the smaller specimens are not discernible. The number of tubercles on the several podomeres of the cheliped is slightly variable, but most seem to be associated with degree of maturity, the smaller specimens having fewer. In the adults, the mesial margin of the palm bears a row of seven to nine tubercles; except in regenerated or injured fingers, the opposable margin of the fixed finger of the chela, nine or ten; and the dactyl, 10 tubercles; the minute denticles on the opposable margins of the fingers of the chelae are arranged in a single row in females and second form males, but in first form males, at least two rows are present distally. Mirror images of the annulus ventralis occur, and whereas in most females the first pleopods are vestigial (represented by minute prominences) or absent, an occasional one is present.

SIZE.—The largest specimen available is the allotype, which has a carapace length of 35.2 (postorbital carapace length 29.6) mm. The corresponding lengths of the smallest and largest first form males available are 28.2 (24.0) mm and 31.3 (26.6) mm. Ovigerous females or ones carrying young have not been collected.

Life History Notes.—Virtually nothing is known of the life history of this crayfish. Only one first form male was collected in the field, that on 2 April; the remaining seven attained form I in the laboratory. The only clue as to when the egg-laying season occurs exists in the size range of specimens collected in April and October. During the latter, five juveniles with carapace lengths ranging from 7.4 to 11.9 mm were obtained, and among the specimens taken in April the corresponding range of lengths was 13.9 to 20.5 mm, thus suggesting that egg laying probably occurs in late spring and/or early summer. Two of the females collected on 2 April 1978 carried sperm plugs.

The holotype had a carapace length of 22.0 mm when collected as a juvenile on 16 April 1977. Upon molting to second form on 6 June 1977, the length increased to 23.9 mm, and following a second molt to second form on 12 August 1977, the length was 25.8 mm. On 5 October, it molted to first form, attaining a carapace length of 29.1 mm.

Ecological Notes.—On the basis of morphological characters in this crayfish, there is little reason to suspect that it might be largely restricted to burrows. Few features does it share with the other primary burrowers of the genus *Procambarus* known to occur in Georgia (cf. Figures 116*h*, 119*k*). To be sure, the carapace and appendages are comparatively aspinous, the rostrum lacks marginal spines or tubercles, the antennae are comparatively short, and the eyes are rather small. Unlike its primary-burrowing congeners that are found in the state, its areola is comparatively broad, the chelae are elongate and narrow (although resembling those of burrowers belonging to the subgenera *Acucauda* and *Girardiella*) instead of being broadly triangular. Whereas the carpus of the cheliped is conspicuously long and slender, it lacks the usual procurved spiniform tubercle on the mesial surface. The entire appendage appears rather ungainly to function in any capacity associated with constructing or inhabiting subterranean galleries. Nevertheless, I must conclude that this crayfish appears to be a primary burrower, but its young apparently frequent open water of ditches to a greater degree than do the young of the burrowing members of the subgenus *Hagenides* that also typically construct complex galleries.

The burrows located under the bridge at the type-locality were constructed in sandy clay soil in which rocks and chunks of asphalt (probably discarded during repairs of the bridge) made tracing the passageways exceedingly difficult. The tunnel systems constructed by the larger individuals were moderately complex, with two or three openings in and on the banks of the pools; below the surface, lateral galleries branched from the principal, gently sloping to subvertical, passageway that exceeded a meter in depth. The chimneys marking the openings to the surface were poorly formed, and, during my three visits to the type-locality, few bore signs of recent work by the occupants of the burrows. The colony there is probably a small one, for I saw fewer than two dozen chimneys on the occasions I attempted to collect specimens. In April 1978, attempts were made with a seine and dip net to obtain specimens from small pools connected to the large pool supporting a dense stand of *Typha* sp., but the only specimens found were young of *Procambarus (O.) acutus acutus*.

In a clay-bottomed, flooded ditch adjacent to Goosepond Creek in Oglethorpe County, several small second form males and juveniles were seined. Only two recently worked burrows were observed in the area, and from one of them we obtained a specimen of *Cambarus (D.) strigosus*; the individual in the other evaded capture.

Relationships.—My opinion of the remote affinities of this crayfish with other members of the genus are alluded to in assigning it to a monotypic subgenus. In many respects, it resembles members of the subgenus *Girardiella*: in the absence of a boss on the coxa of the fourth pereiopod, aspects of the chela, and the presence of a shoulder at the cephalic base of the cephalic process of the first pleopod of the male, as well as in the rather small eyes. The development of the setae on the third maxillipeds and distal podomeres of the second pereiopod are similar to those of members of the subgenus *Capillicambarus*, some representatives of *Leconticambarus*, and to certain members of the genus *Fallicambarus.* Despite these similarities, its closest affinities appear to me to be with members of the subgenera *Girardiella* and *Leconticambarus.* The absence of the marginal rostral spines, the tuberculate condition of the cheliped, the densely setose third maxilliped, the shoulder at the cephalic base of the terminal elements of the pleopod, and the small annulus ventralis as compared with the size of the postannular sclerite, are all typical of members of the three subgenera. The presence of a hook on the ischium of only the third pereiopod of the male and the absence of a boss on the caudomesial angle of the coxa are characteristic of some members of *Leconticambarus.*

Unique in this crayfish, however, are most features of the first pleopod which, in the first form male, is sharply bent near midlength, lacks any trace of a caudal process, and possesses a central projection that consists of a curved lamelliform plate, resembling that of some members of the Mexican subgenus *Villalobosus.* The long carpus of the cheliped is also distinctive as is the dorsal hinge of the annulus ventralis, which allows movement through an arc of as much as 90 degrees.

GEORGIA CRAYFISH ASSOCIATES.—*Procambarus (D.) devexus* has been collected with *Cambarus (D.) latimanus, C. (D.) strigosus,* and *P. (O.) a. acutus* twice each.

ETYMOLOGY.—From the Latin *devexus* (sloping), chosen because of the strongly sloping cephalodistal half of the first pleopod of the first form male.

REMARKS.—When first I saw small specimens of this crayfish in the field in April 1977, I was reasonably certain that they were members of *Cambarus (D.) latimanus*, but the chelipeds were so narrow that I decided to retain two small males alive. In examining the specimens upon my return to the museum, much to my surprise, not only were some of the females virtually mature, but I had not recognized them as belonging to the genus *Procambarus*! The two living males were accorded the best treatment that we could offer them, in the hope that eventually they would molt to first form. Both individuals molted during the summer months, but neither had attained first form when I left the museum in October to return to Georgia, determined to obtain a series of specimens including a first form male.

Upon arriving at the locality where this crayfish had been obtained in April, T. A. English, Jr., and I endeavored to make collections in the nearby Broad River, but it was at flood stage, resulting from heavy rains in the headwaters, so we returned to the pools under the bridge. Obviously the entire area had been subject to drought during the summer, for even the small *Typha* marsh was completely dry. Although water was in the shallow pools under the bridge, no insect larvae or nymphs were in them, suggesting that these pools too had been dry until a short time before our visit. When we attempted to excavate the few burrows that were marked by weathered chimneys exhibiting a modicum of recent work, we found that at depths of more than one meter the tunnel continued downward. A combination of large rocks obstructing digging, together with flooded excavations, resulted in our obtaining a single small male from one of the burrows, and five juveniles were collected with a hand net from one of the deeper pools. After several hours of digging and searching for chimneys in the adjoining wooded area, we abandoned our efforts but returned after dark, hoping that some crayfish might be in the pools. No activity of any kind was observed in them. Attempts were made the following day to locate other similar habitats, but neither in creeks nor in the burrows that were excavated did we find another specimen of the species.

Fortunately, during my absence from the museum, one of the males that had been obtained in April molted to first form, thus allowing me to prepare the above description.

Still dissatisfied with the small series of specimens, in company with R. J. Dubois, D. J. Peters, and J. E. Pugh, I returned to the flood plain of the Broad River in April 1978. Although there was little standing water in two of the three localities in which we found *P. (D.) devexus*, we obtained a few additional adults, including the only first form male that has been collected in the field, and juvenile specimens.

Subgenus *Hagenides*

Subgenus *Cambarus*.—Ortmann, 1905a:97 [in part; not Erichson, 1846:97].
Subgenus *Ortmannicus* Fowler, 1912:341 [in part].
Subgenus *Hagenides* Hobbs, 1972a:7 [type-species, *Astacus advena* LeConte, 1856:402].

DIAGNOSIS.—Body and eyes pigmented, latter usually small but well developed. Rostrum without marginal spines, tubercles, or median carina. Carapace without cervical spine. Areola 6.9 times as long as broad, to being obliterated along part of its length and constituting 33 to 42 percent of entire length of carapace. Ventral surface of ischium of third maxilliped not obscured by mat of long plumose setae. First 3 pairs of pereiopods without conspicuous brush of setae extending from basis to merus. Simple hooks on ischia of third or third and fourth pereiopods, latter only in *Procambarus geodytes*. Coxa of fourth pereiopod with caudomesial boss. First pleopods reaching coxae of second pereiopods (except in some members of *P. (H.) caritus*), asymmetrical, with proximomedian lobe, without proximomesial spur; cephalic surface without shoulder; subapical setae absent. Terminal elements of first pleopod of first form male represented by distally to caudally directed, acute, usually long mesial process; prominent beaklike or broad platelike central projection; cephalic process rarely well developed, often vestigial or lacking; and caudal element usually consisting of prominent caudal knob, although much reduced in *Procambarus pygmaeus*. Mesial ramus of uropod with distomedian spine acute, reduced to tubercle, or absent; if present, never extending beyond distal margin of ramus. (Slightly modified from Hobbs, 1972a.)

RANGE.—From the Atlantic coast of Georgia onto the Tifton and Vidalia uplands and southward into the peninsula and panhandle of Florida: in the peninsula to Alachua County, and, along the Saint Johns River, to Seminole County; in the panhandle, from the Ochlockonee and Saint Marks river basins in Leon and Wakulla counties westward to the eastern side of the Choctawhatchee Basin in Bay and southeastern Walton counties. In Georgia, it ranges south of the Fall Line Hills from the Savannah River to the Ochlockonee and Flint river basins.

GEORGIA SPECIES.—Of the nine species and subspecies assigned to the subgenus, five occur in Georgia: *Procambarus (Hagenides) advena, P. (H.) caritus, P. (H.) pygmaeus, P. (H.) talpoides,* and *P. (H.) truculentus.*

HABITAT.—All of the members of the subgenus except *P. (H.) pygmaeus* are primary burrowers that frequent seepage areas and flatwoods where the water table seldom retreats more than 0.5 meter below the surface. *Procambarus (H.) pygmaeus,* while an able burrower, has been found most frequently in beds of the sedge *Juncus repens,* occurring in pools, sluggish areas of streams, and in roadside ditches. Never have I collected it more than a few meters from clumps of this plant.

REMARKS.—Hobbs (1942b) recognized two species groups (*advena* and *rogersi*) in his *advena* Section [= Subgenus *Hagenides*] of the genus *Procambarus*, and in 1954 proposed a third, the monotypic *truculentus* Group. These groups are characterized chiefly on features of the first pleopod of the male.

The *advena* Group: First pleopod of male with mesial process and subtriangular, laterally compressed central projection arising from distal surface of shaft of appendage and directed caudodistally. Hooks on ischia of third or third and fourth pereiopods. Georgia representatives include *Procambarus (H.) advena, P. (H.) caritus, P. (H.) pygmaeus,* and *P. (H.) talpoides.*

The *truculentus* Group: First pleopod of male with mesial process and subtriangular, laterally compressed central projection arising from caudal surface of expanded distal end of shaft of appendage and directed caudally at approximately right angle. Hooks on ischia of third pereiopods only. *Procambarus (H.) truculentus* is the only member and, except for a questionable occurrence in "South Carolina," is apparently endemic in the state.

The *rogersi* Group: First pleopod of male with

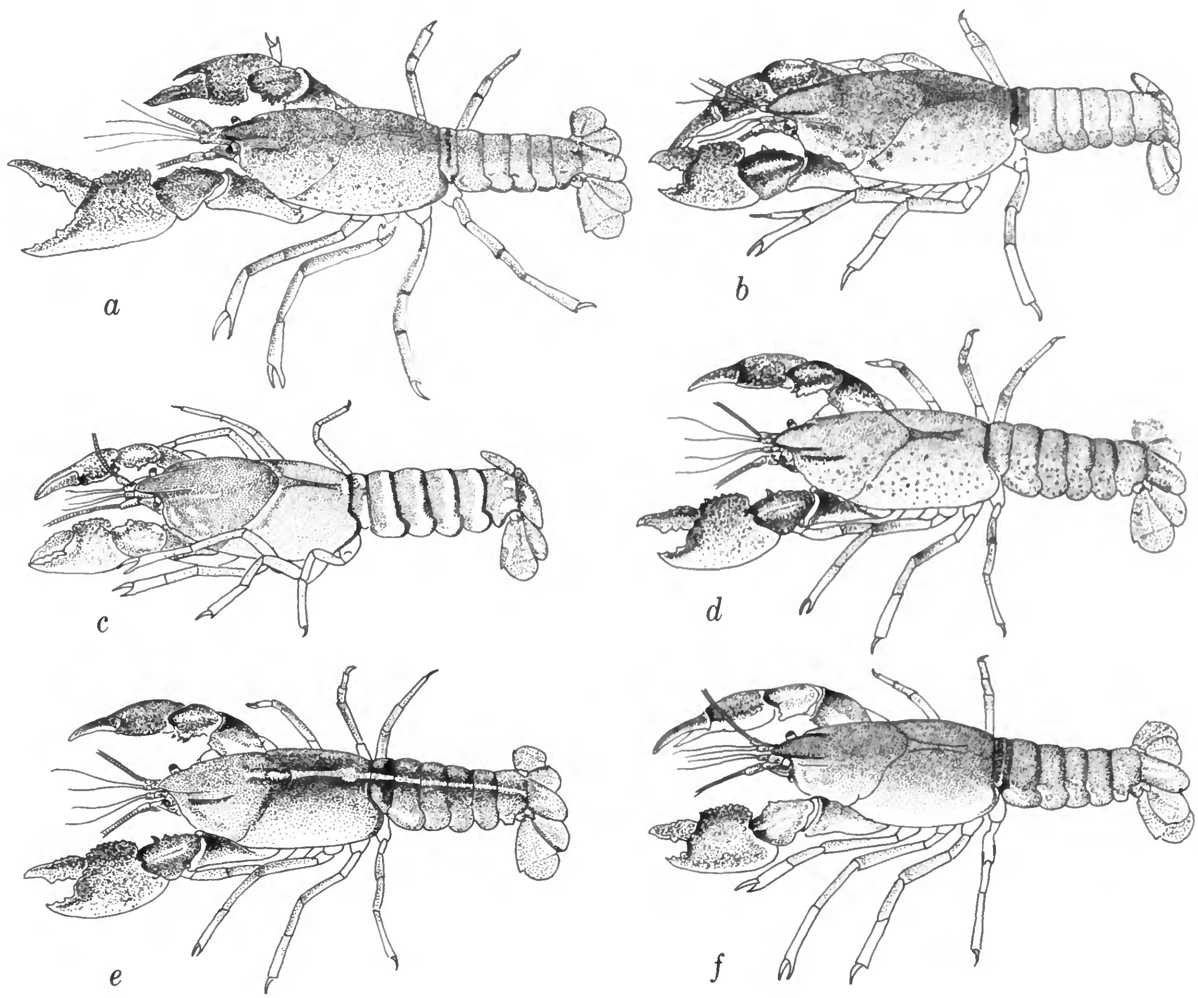


FIGURE 118.—Color patterns in members of subgenus *Hagenides: a, Procambarus (H.) advena* from 0.1 mi SW of Toombs Co line on St Rte 130, Montgomery Co; *b, P. (H.) caritus* from 6.1 mi W of McRae on US Hwy 280, Telfair Co; *c, P. (H.) pygmaeus* from 5.0 mi SW of Wilderness Church off US Hwy 82, Liberty Co; *d, P. (H.) talpoides* from 15.4 mi N of Fargo on US Hwy 441, Clinch Co; *e, P. (H.) talpoides* from 2.8 mi S of Coffee Co line on US Hwy 221, Atkinson Co; *f, P. (H.) truculentus* from 11 mi N of St Rte 292 on US Hwy 1, Emanuel Co.

mesial process and platelike, cephalocaudally compressed central projection arising from distal end of shaft of appendage and directed distolaterally. Hooks on ischia of third pereiopods only. This group is confined to the panhandle of Florida.

I have found the females and second form males of the Georgia representatives of the subgenus *Hagenides* to be difficult, and sometimes impossible, to identify. Although I believe that the majority of the records cited here are reliable, those localities listed for which no first form males are noted should be confirmed by securing breeding males in them.

On the basis of available data, the Oconee-Altamaha River system seems everywhere except in Montgomery County to delimit the range of *P. (H.) advena* from that of *P. (H.) caritus*, but I have discovered no physiographic or ecological feature that separates the ranges of the former and *P. (H.) truculentus*, and I can only surmise that the Oconee River separates the range of *P. (H.) truculentus* from that of *P. (H.) caritus*. Puzzling also is the absence of any recognizable barrier between the ranges of *P. (H.) caritus* and *P. (H.) talpoides*. They have been collected in the same locality in the southwestern part of Bacon County and in the eastern part of Coffee County, and only 0.5 mile apart in the western part of Wayne County. Although I have suspected that the two intergrade in the Satilla River Basin, I have no clear evidence that such occurs.

Attesting to the broader ecological tolerance of *P. (H.) pygmaeus*, its range virtually overlaps those of all of the other members of the subgenus in Georgia except that of *P. (H.) truculentus*.

Key to Georgia Members of Subgenus *Hagenides*

1. First pleopod of first form male with terminal elements directed caudally at approximately right angle to shaft of appendage .... **truculentus**
   First pleopod of first form male with terminal elements directed distally or caudodistally but never at more than 40-degree angle to shaft of appendage 2
2. First pleopod of first form male with caudal element very weakly inflated, and, in lateral view, base of bladelike central projection spanning about three-fourths diameter of distal part of appendage; color forest green with scarlet markings .... **pygmaeus**
   First pleopod of first form male with caudal element moderately to strongly inflated, and, in lateral view, base of beaklike or dentiform central projection spanning scarcely more (usually less) than one-half diameter of distal part of appendage; color variable but never green with scarlet markings 3
3. First pleopod of first form male with well-developed cephalic process .... **advena**
   First pleopod of first form male with cephalic process reduced or absent 4
4. Cephalic process vestigial, rarely absent; central projection beaklike and strongly arched cephalically, its cephalocaudal diameter approximately half corresponding distal diameter of appendage .... **talpoides**
   Cephalic process absent; central projection dentiform and weakly arched cephalically, its cephalocaudal diameter little, if any, greater than one-fourth corresponding distal diameter of appendage .... **caritus**

The *advena* Group

Procambarus (Hagenides) advena (LeConte)

FIGURES 17*f*, 118*a*, 119–121, 235

Astacus advena LeConte, 1856:402.—Hagen, 1870:9, 10.—Faxon, 1885a:12, 54.—Hobbs, 1972a:2, 7; 1974a:15.

Cambarus advena.—Hagen, 1870:31, 53, 86 [name only], 87, 98 [in part, Georgia only], 100 [in part], 107, pl. VII [♀ instead of ♂, form I]; not 86 [description = *P. (G.) hagenianus*], 101, 105, 106, pl. I: figs. 90–92 [figures, *P. (G.) hagenianus*].—Brocchi, 1875:27.—Faxon, 1884:113, 140; 1885a:8, 9, 17, 47–49, 54–56, 58, 158, 167, 173, 178; 1885b:358; 1914:412.—Underwood, 1886:366, 368.—Hay, 1899b:959, 961.—Ortmann, 1902:277, 279; 1905c: 403; 1905d:438.—Harris, 1903a:58, 68, 129, 150, 152.—Graeter, 1909:470.—Spandl, 1926:96.—Hobbs, 1938:65;

1940a:389, 393; 1942a:335; 1972a:2.—Hobbs and Villalobos, 1964:321.

Cambarus Carolinus.—Hagen, 1870:32, 74, 75, 87 [description only], 88 [in part, excluding specimens from Alabama and South Carolina], pl. III: fig. 165 (?).

Cambarus (Cambarus) advena.—Ortmann, 1905a:98, 100, 101, 104 [in part, by implication].

Cambarus (Ortmannicus) advena.—Fowler, 1912:341 [by implication].

Procambarus advena.—Hobbs, 1942a:340; 1942b:73–76, 84, 86, 92 [all in part]; 1954:110, 116; 1959:887 [in part], fig. 31.26; 1968b:K-8 [in part]; 1969a:118.—Villalobos, 1955: 38.—Hart and Hart, 1974:21 [in part], 28 [in part].

Procambarus (Hagenides) advena.—Hobbs, 1972a:7, figs. 2*e*, 8*a–g*; 1972b:50, 150 [in part], 154 [in part], figs. 5g, 41d; 1974b:48, fig. 194.—Hobbs and Bouchard, 1973:52 [by implication], 63.

This synonomy is believed to represent a complete bibliography for the species, and inasmuch as this crayfish is endemic in Georgia all references concern the state.

SUMMARY OF LITERATURE.—LeConte's (1856) description of *Astacus advena*, together with Hagen's (1870) concept of the species, left no doubt in the mind of the latter as to its distinctive features, and, following Girard (1852) in assigning the American species to the genus *Cambarus*, he employed the combination *Cambarus advena*. As pointed out by Faxon (1884, 1885a), unfortunately a transposition of the descriptions and most of the illustrations of his *Cambarus advena* and *C. Carolinus* (Erichson, 1846:96) occurred. Furthermore, in describing the first form male of the former, he chose a specimen purportedly (although highly unlikely—see Fitzpatrick, 1978b: 59) from Charleston, South Carolina, which was later designated as the "type" of *Cambarus hagenianus* (Faxon, 1884:141; 1914:366). It seems clear that when Hagen prepared his account of *C. advena* and *C. carolinus*, he had obviously misidentified specimens of the former as *C. carolinus*, and representatives of the species later described as *C. hagenianus* as *C. advena*, inadvertently transposing the Latin descriptions and all of his illustrations except that on plate VII. The synonomy cited above reflects this interpretation.

In addition to the female type in the Philadelphia Academy of Natural Sciences (there is no indication that he saw the female syntype that is now in the Museum of Comparative Zoology), the specimens available to Hagen consisted of

[1] a first form male (M.C.Z. No. 232) from Charleston, South Carolina ... [2] No. 3368, dry female from Georgia, L. Agassiz ... [3] No. 3367 ... a young female, also from Georgia ... [4] No. 230, young female specimens from Mobile, Ala ... [5] No. 275, a very young male from the same locality ... (Faxon, 1884:141), [6] No. 282, Georgia, Dr. Jones. Male. Fem. Spec. 6 ... [and 7] No. 1850, Georgia. Male. Spec. 1 (Hagen, 1870:87, 88).

Of these, the first is the type of *Procambarus (Girardiella) hagenianus*; the second and third are in all probability members of *P. (H.) advena*; the fourth and fifth are clearly members of the genus *Cambarus*; the sixth includes representatives of two species, *P. (H.) talpoides* and *P. (H.) pygmaeus*; and the seventh is apparently no longer extant. Thus, as indicated by Faxon (1885a), *P. (H.) advena* was known to occur only in Georgia. Uncertainty surrounds the source of the specimens from which Hagen's figures 51–54 were illustrated; however, I suspect that they were from the first form male of *Procambarus (H.) pygmaeus* included in the sixth lot just mentioned, "No. 282, Georgia. ..."

All of the references from 1885 until 1942 are based on Faxon's identifications of the material that was available to Hagen and add nothing except notes on the affinities of *P. (H.) advena* to other species. No new localities were cited for it until Hobbs (1942b:77) recorded its presence in Bryan County, Georgia (although the species occurs in the county, this report was based on the misidentification of specimens of *P. (H.) pygmaeus*; all other locality records cited by him for *P. advena* are referable to *P. (H.) talpoides*). Subsequent to that time, the only reliable records that have been reported are the following based on collections and identifications made by me: 7.6 miles southwest of Midway on State Route 38, Liberty County, Georgia (Hart and Hart, 1974:21), and 16.9 miles north of Darien on U.S. Highway 17, McIntosh County, Georgia (Hart and Hart, 1974:28), where it served as host to the entocytherid ostracods, *Ankylocythere ancyla* Crawford, *A. hobbsi* (Hoff, 1944), and *Entocythere elliptica*.

The several definitions of the range of the species offered by Hobbs (1942–1972) that included that part of Georgia south of the Altamaha River and northern Florida encompass that of *P. (H.) talpoides*, which is described herein. Not until 1974 did he note a range consistent with that recorded below.

The only record of the habitat of this species is that of LeConte (1856), who stated, "Hymeme vitam degit subterraneam. Aestate in fossis invenitur." This statement led Graeter (1909) to conclude that this crayfish is an inhabitant of cave waters, an assumption that was negated by Spandl (1926).

DIAGNOSIS.—Rostrum without marginal spines or tubercles. Carapace lacking cervical spines. Areola obliterated to 19.8 times as long as broad and constituting 35.6 to 39.7 (average 38.0) percent of entire length of carapace (40.5 to 45.3, average 43.6, percent of postorbital carapace length). Ventral surface of basis and ischium of third maxilliped not densely bearded. Male with mesial surface of palm of chela lacking beard but bearing cristiform row of 7 to 9 tubercles; hooks on ischia of third pereiopods only; coxa of fourth pereiopod with caudomesial boss. First pleopods of first form male asymmetrical, subcontiguous, and reaching coxae of second pereiopods, cephalic surface without prominent shoulder; preapical setae limited to few on cephalodistal border; mesial process tapering to acute apex and directed caudodistally; cephalic process consisting of short, straight, rounded to subacute corneous blade at cephalic base of prominent, corneous, subtriangular central projection, latter arising from distal surface of appendage and directed caudodistally; caudal knob somewhat inflated but falling far short of central projection. Female with chela as in male; annulus ventralis subovate in outline, longer than broad, and with cephalolateral elevations frequently, if not usually, tuberculate; first pleopod present.

MALE, FORM I.—(From restricted type-locality, Liberty County, Georgia.) Body (Figure 119*a,i*) subovate, compressed laterally. Abdomen narrower than thorax (11.2 and 15.2 mm). Width of carapace greater than depth at caudodorsal margin of cervical groove (15.2 and 13.6 mm). Areola 29 times as long as broad, with 1 punctation in narrowest part. Cephalic section of carapace 1.6 times as long as areola, length of latter 38.6 percent of total length of carapace (44.1 percent of postorbital carapace length). Rostrum excavate dorsally, with rather slender convergent margins lacking spines or tubercles; upper surface with few punctations between submarginal rows; acumen not clearly defined basally and reaching anteriorly to base of ultimate podomere of antennular peduncle; subrostral ridges moderately well developed and evident in dorsal view to base of acumen. Postorbital ridges rather strong, grooved dorsolaterally, and cephalic extremity subangular but lacking spines or tubercles. Suborbital angle absent. Branchiostegal spine very small. Carapace punctate dorsally and weakly tuberculate laterally except in hepatic, mandibular, and anteroventral branchiostegal regions, in them tubercles more conspicuous; cervical spine absent. Abdomen shorter than carapace (28.3 and 30.3 mm); pleura broadly rounded and subtruncate ventrally. Cephalic section of telson with 2 spines in caudolateral corner; caudal section rounded and narrow. Uropod with short acute prominence on both lobes of proximal podomere; mesial ramus with conspicuous distolateral spine and less prominent premarginal tubercle on median ridge; lateral ramus with usual row of spines flanking proximal side of transverse suture, lateralmost spine no larger than others in row. Cephalic lobe of epistome (Figure 119*h*) subpentagonal, with small cephalomedian projection; ventral surface weakly convex and margins slightly thickened and elevated ventrally; fovea indistinct, replaced by shallow median depression, and epistomal zygoma strongly arched. Antennular peduncle with strong acute tubercle near midlength of ventral surface of basal podomere. Antenna almost reaching caudal margin of carapace, peduncle without spines; diameter of renal tubercle greater than half maximum width of coxal podomere bearing it. Antennal scale (Figure 119*d*) about 2.4 times as long as broad, greatest width distal to midlength, lamellar portion about 1.6 times as wide as thickened lateral part, latter

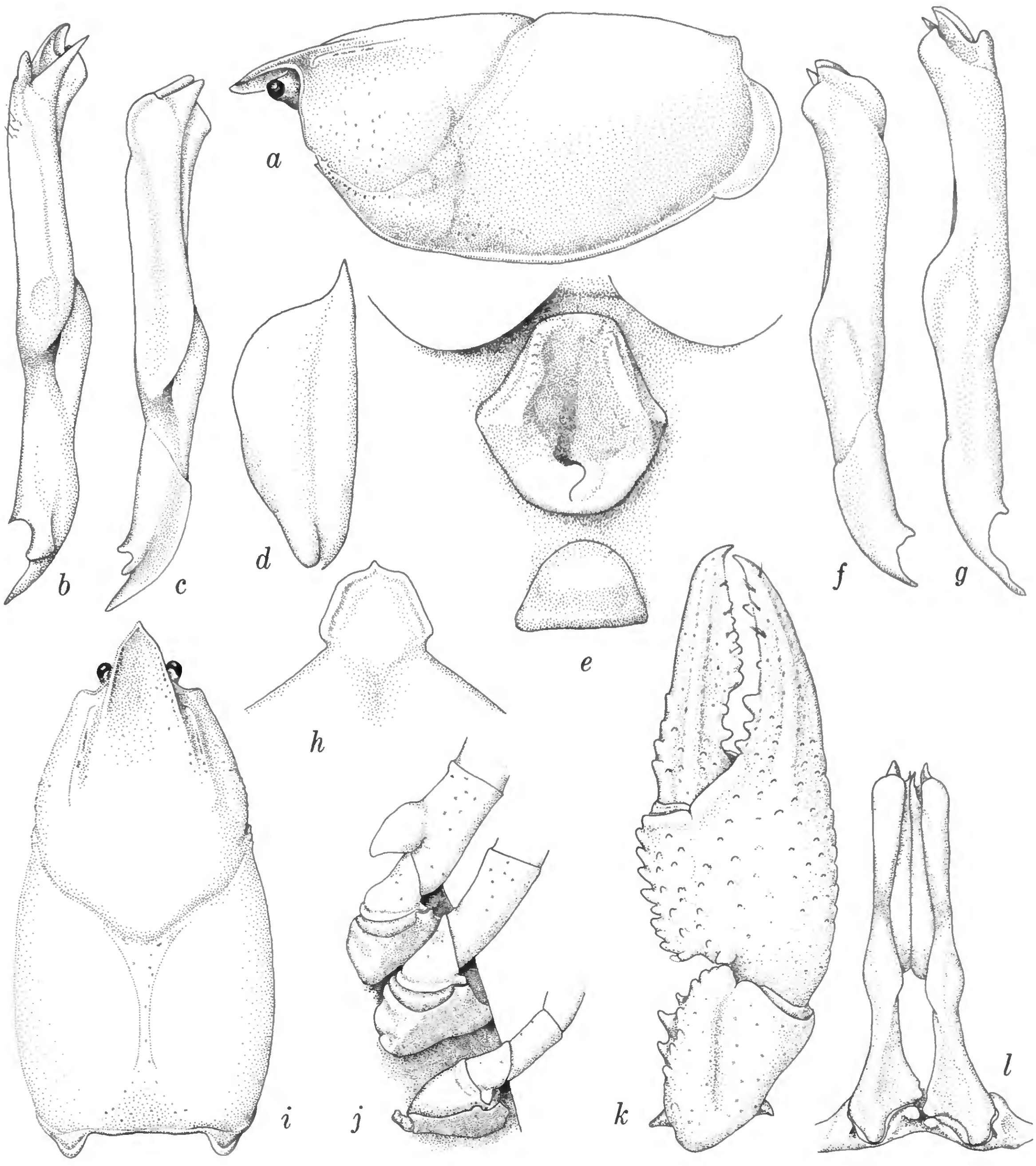


FIGURE 119.—*Procambarus (Hagenides) advena* (*c*, *f*, from male, form II; *e*, from female; *l*, from male, form I, from 7.6 mi W of Midway on St Rte 38, Liberty Co; all others from male, form I, from 2.5 mi W of Riceboro, Liberty Co): *a*, lateral view of carapace; *b*, *c*, mesial view of first pleopod; *d*, antennal scale; *e*, annulus ventralis; *f*, *g*, lateral view of first pleopod; *h*, epistome; *i*, dorsal view of carapace; *j*, proximal podomeres of third, fourth, and fifth pereiopods; *k*, dorsal view of distal podomeres of cheliped; *l*, caudal view of first pleopods.

terminating in strong spine. Third maxilliped with basis bearing conspicuous long, stiff, simple setae; ischium with distolateral tubercle, ventral surface with submarginal lateral row of short plumose setae, few clusters of similar setae in mostly naked proximolateral half, and 2 irregular rows of long stiff setae lateral to crista dentata.

Right chela (Figure 119*k*) subovate in cross section, strongly depressed. Mesial surface of palm with cristiform row of 9 (7 on left) tubercles subtended dorsolaterally by row of 5 squamous tubercles and similar ones scattered over dorsal surface and lateral margin of palm; ventral surface also with scattered squamous tubercles and punctations (latter replacing tubercles proximally and laterally), and strong tubercle opposite base of dactyl. Fixed finger with conspicuous median longitudinal ridge dorsally and ventrally, ventral one flanked by setiferous punctations, and dorsal ridge by squamous tubercles proximally and punctations along most of distal three-fourths; opposable margin of finger with row of 5 tubercles, third from base largest, along proximal two-thirds and tubercle present on lower level at base of distal fourth of finger; minute denticles, arranged in single row except proximal to second tubercle from base, extending from base of finger to corneous tip. Dactyl with dorsal and ventral surfaces similar to those of fixed finger although ridges less prominent; mesial surface with row of tubercles, decreasing in size distally, along proximal third of finger, giving way to punctations; opposable surface with row of 9 (left with 7, perhaps due to injury) tubercles, first and third from base larger than others, otherwise decreasing in size distally; single row of minute denticles extending between tubercles (beginning at third tubercle from base) and continuing to corneous tip of finger.

Carpus of right cheliped punctate dorsally, laterally, and ventrally, and tuberculate mesially; dorsal surface with shallow oblique furrow; dorsomesial margin with row of 7 tubercles; mesial surface with cluster of 7; and ventral surface with 2 on distal margin: 1 on ventrolateral articular knob and other on ventromesial angle.

Merus with dorsal surface bearing slightly irregular subserrate row of 15 (11 on left) tubercles, more distal member of which larger than more proximal ones; mesial and lateral surfaces sparsely punctate; and ventral surface with mesial row of 14 tubercles, and lateral one of 13 (left with 12 and 11, respectively), single tubercle between subdistal ends of rows. Ischium with row of 3 tubercles ventromesially.

Hook on ischium of third pereiopod (Figure 119*j*) only; hook inflated and extending proximally over distal part of corresponding basis. Coxa of fourth pereiopod with moderately strong boss caudomesially; that on fifth small and inconspicuous.

Sternum between third, fourth, and fifth pereiopods moderately deep and bearing fringe of plumose setae on ventrolateral margins.

First pleopods (Figure 119*b,g,l*) as described in "Diagnosis."

FEMALE.—(Liberty County, Georgia.) As in male, form I, except for secondary sexual characteristics and following: rostrum reaching midlength of ultimate podomere of antennular peduncle; ventrolateral part of branchiostegites more strongly tuberculate; lateral half of ventral surface of third maxilliped with short plumose setae more abundant; mesial margin of palm of chelae with row of 9 tubercles on right and 8 on left; opposable margin of dactyl of chela with row of 6 tubercles; carpus with cluster of 10 tubercles on mesial surface of right cheliped and 9 on left; merus with dorsal row of 12 and 15 tubercles, respectively, and ventrolateral row of 10; ischium with only 2 tubercles on ventromesial margin. (See "Measurements.")

Annulus ventralis (Figure 119*e*) slightly longer than broad, subovate, with broad, deep median depression (occupying three-fourth of its length) flanked by high, caudally diverging, anterolateral ridges, left ridge weakly tuberculate; caudal part of annulus forming somewhat flattened shelf; sinus originating dextrally in caudal extremity of depression and, following S-shaped course over shelf, ending on median line anterior to caudal margin of annulus. Postannular sclerite unadorned, strongly arched anteriorly and truncate posteriorly, its width approximately two-thirds and its length little less than half that of annulus.

MALE, FORM II.—(Liberty County, Georgia.)

Differing from first form male in only few minor respects: mesial margin of palm of chela with row of 8 tubercles; opposable margin of dactyl with 6; mesial surface of carpus with 10 tubercles in cluster; dorsal surface of merus with row of about 12, ventrolateral row of 7 on right and 6 on left, and ventromesial row of 10 and 13, respectively; ischium bearing row of 4 tubercles. Hook on ischium of third pereiopod greatly reduced, its free end not nearly reaching basioischial articulation, and bosses on coxae of both fourth and fifth pereiopods rudimentary. (See "Measurements.") First pleopod (Figure 119*c,f*) with mesial process and central projection markedly similar in shape to those of first form male, but cephalic process not evident although cephalodistal part of appendage produced in broad prominent excrescence; juvenile suture on basal part of shaft clearly defined.

Color Notes (Figure 118*a*).—Carapace almost uniformly mauve brown or olive brown, with small darker brown spots and flecks, fading ventrally to bluish gray, caudal flange dark blue. Abdomen mauve to brown with transverse darker brown bands (completely covering first tergum) on caudal fourth of second through fifth terga; pleura also brown without conspicuous markings although margins darker than central area of each. Sixth tergum with posteromedian dark spot. Telson with brown triangular area basally, flanked by paired, small, oblique cream spots abutting caudolateral margins of triangle; more caudal part becoming pale greenish blue matching uropods; ridges and articular areas of both telson and uropods dark blue. Antennular and antennal peduncles bluish gray, with darker lateral margins and bands at bases of articulations; flagella gray to pale tan. Chelipeds distal to ischium deep lavender to bluish gray dorsally, with most tubercles gray to black, fingers usually more brightly colored in shades of blue or lavender; major tubercles on carpus and propodus often pale lavender or blue and nearly always tipped with cream; ventral and ventrolateral surfaces of cheliped ranging from cream proximally to orange cream on fingers; distal extremities of fingers orange to yellowish tan. Remaining pereiopods with basal 2 podomeres cream, more distal ones bluish to lavender gray; color intensifying adjacent to articulations, and dactyls of fourth and fifth pereiopods distinctly blue or lavender. Ventral surface of body cream.

Measurements (mm)

	Male, form I	*Female*	*Male, form II*
Carapace			
Height	13.6	14.0	10.5
Width	15.2	14.3	10.7
Entire length	30.3	29.7	23.0
Postorbital length	26.5	25.7	20.0
Areola			
Width	0.5	0.4	0.4
Length	11.7	10.6	8.5
Rostrum			
Width	4.6	4.4	3.6
Length	5.1	5.0	4.2
Chela			
Length of mesial margin of palm	7.7	6.9	4.9
Width of palm	10.2	9.8	6.9
Length of lateral margin	23.5	20.5	14.2
Length of dactyl	15.0	13.1	8.4
Abdomen			
Width	11.2	11.3	8.5
Length	28.3	27.1	22.9

Types.—Syntypes, MCZ 3379 (♀), ANSP 321 (♀).

Type-Locality.—"Georgia inferiore" (LeConte, 1856:402). Restricted to 2.5 miles west of Riceboro, Liberty County, Georgia, by Hobbs (1974b:48).

Range.—Lower Coastal Plain Province of Georgia between the Savannah and Oconee-Altamaha rivers, where it is largely confined to the Vidalia Upland and Barrier Island Sequence districts.

Georgia Specimens Examined.—I have examined a total of 69 specimens as follows. *Bryan County*: (1) 1.5 mi NE of St Rte 204 on US Hwy 280, 1♀, 29 May 1969, E. T. Hall, Jr., HHH, collectors; (2) 1.9–2.0 mi S of Pembroke on St Rte 119, 1♀, 1j♀, 22 Jun 1975, D. J. Peters, J. E. Pugh, HHH; 1♂I, 20 Apr 1977, C. E. Carter, JEP, HHH; (3) 5.2 mi W of St Rte 119 on US Hwy 280, 1♀ with young, 22 Jun 1975, DJP, JEP, HHH. *Chatham County*: (4) 2.0 mi W of Pooler on US Hwy 80, 1♂II, 2♀, 29 May 1969, ETH, HHH.

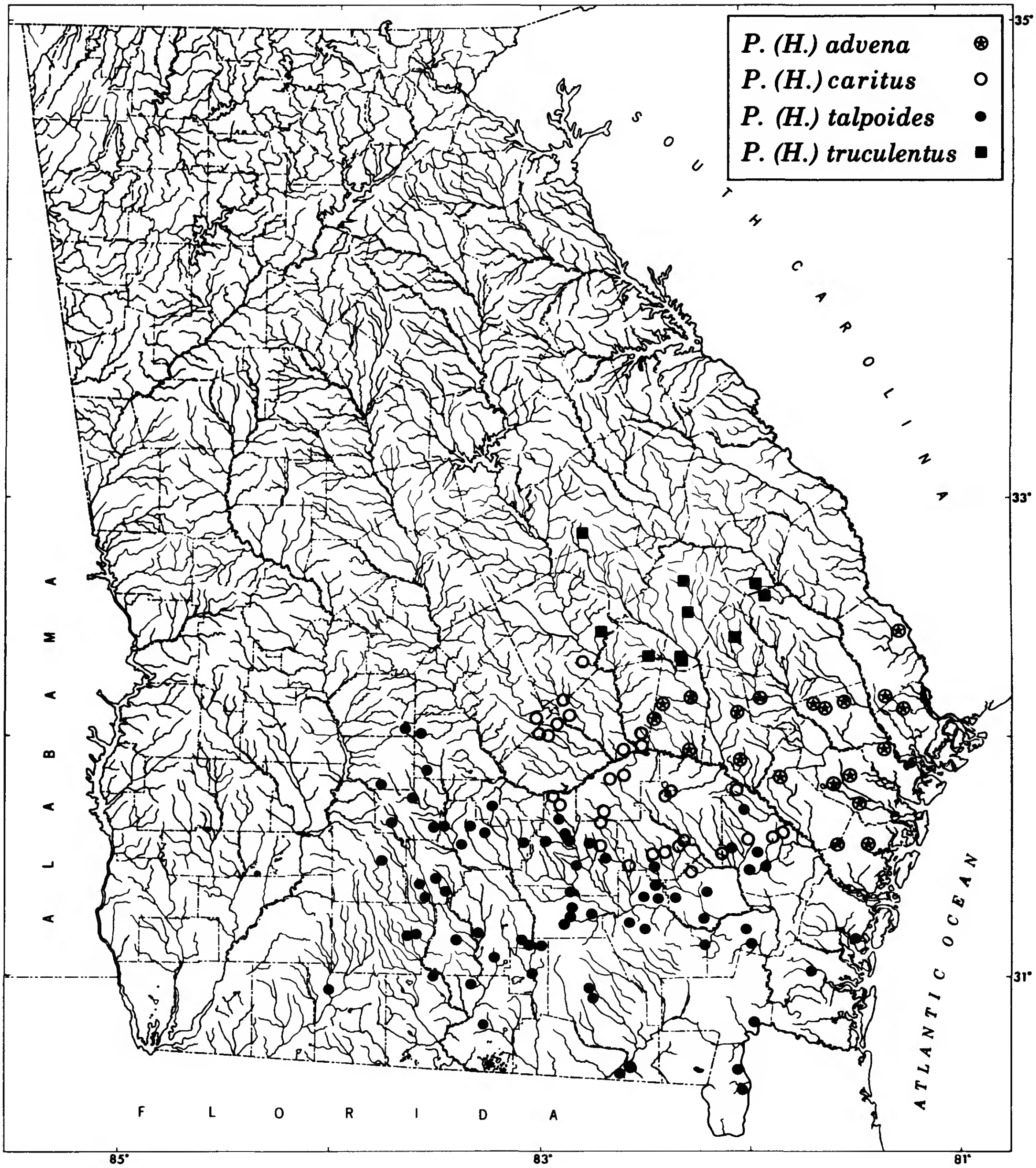


FIGURE 120.—Distribution of *Procambarus (H.) advena*, *P. (H.) caritus*, *P. (H.) talpoides*, and *P. (H.) truculentus* in Georgia.

Effingham County: (5) 3.1 mi NW of Chatham Co line on US Hwy 80, 1♀, 29 May 1969, ETH, HHH; (6) 3.9 mi S of Clyo on paved unnumbered road, 1♂II, 20 Apr 1974, DJP, HHH. *Evans County*: (7) 4 mi NW of Claxton at jct of St Rtes 129 and 169, 4♀, 2j♂, 3j♀, 30 May 1969, ETH, HHH. *Liberty County*: (8) Camp Stewart, 1♂II, 14 Aug 1943, L. W. Martin; (9) 2.5 mi W of Riceboro on unpaved road, 1♂I, 27 Feb 1945, N. T. Blount, HHH; (10) 7.6 mi W of Midway on St Rte 38, 1♂I, 2♂II, 11♀, 1j♂, 27 Feb 1945, NTB, HHH. *Long County*: (11) 10.1 mi NW of Ludowici on US Hwy 25, 1 ovig ♀, 17 Apr 1944, HHH; (12) 0.4 mi W of McIntosh Co line on St Rte 99, 1♀, 28 May 1969, ETH, HHH. *McIntosh County*: (13) 16.9 mi N of Darien on US Hwy 17, 4♀, 2j♀, 27 Feb 1945, NTB, HHH. *Montgomery County*: (14) 0.1 mi SW of Toombs Co line on St Rte 130, 1♂II, 1 ovig ♀, 20 Apr 1977, CEC, JEP, HHH. *Screven County*: (15) 3.3 mi SW of St Rte 79 on Rte 24, 1j♂, 1j♀, 18 Apr 1977, CEC, C. W. Hart, Jr., JEP, HHH. *Tattnall County*: (16) 0.5 mi NW of St Rte 169 on Rte 121, 1j♀, 27 May 1969, ETH, HHH; (17) 6.3 mi NE of Reidsville on US Hwy 280, 1♀, 21 Jun 1975, DJP, JEP, HHH. *Toombs County*: (18) within Vidalia, 1♂I, 1♀, 1 ovig ♀, 26 May 1969, ETH, HHH; (19) Montgomery-Toombs Co line on St Rte 130, 1♂II, 26 May 1969, ETH, HHH; (20) 2.9 mi W of St Rte 147 on Rte 107, 1♀ with young, 26 May 1969, ETH, HHH; (21) 3.1 mi W of Tattnall Co line on St Rte 292, 2♂II, 1♀, 1 ovig ♀, 1♀ with young, 20 Apr 1977, CEC, JEP, HHH; (22) 3.8 mi SE of Lyons on US Hwy 280, 1♂II, 1♀, 1j♀, 21 Jun 1975, DJP, JEP, HHH; (23) along Rocky Creek, 6 mi S of Lyons on US Hwy 1, 1♂II, 20 Apr 1977, CEC, JEP, HHH. *County Unknown*: (24) locality and dates unknown, 3♀ (MCZ 3367, 3368, 4964); syntypes, 2♀ (ANSP 321; MCZ 3379).

VARIATIONS.—Entirely too few specimens are available to determine whether or not the variations noted are individual ones or are perhaps associated with local or regional populations. The shape of the rostrum is quite variable, ranging from short and triangular to sublanceolate; the areola as noted in the "Diagnosis," although always comparatively narrow, exhibits a range of 19.8 times as long as broad to being linear. The number of tubercles and their disposition on the several podomeres of the cheliped are highly variable, although the cristiform row on the mesial surface of the palm, excluding regenerated appendages, consists of seven to nine. In the few available first form males, the terminal elements of the first pleopod are remarkably uniform (Figure 121). For the most part, the same is true of the annuli ventrales; however, in some females the cephalolateral walls are very weakly tuberculate, and in an occasional smaller individual the walls are scarcely elevated.

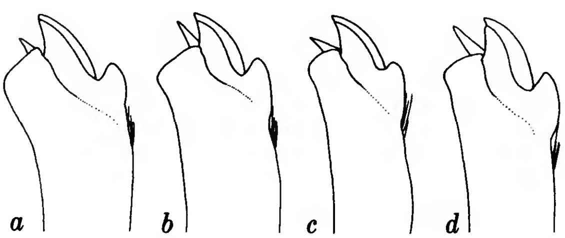


FIGURE 121.—*Procambarus (H.) advena*, variations in distal part of first pleopod of first form male (see "Specimens Examined" for precise localities): *a*, Liberty Co; *b*, Bryan Co; *c*, Effingham Co; *d*, Toombs Co.

SIZE.—The largest specimen available is a female having a carapace length of 38.1 (postorbital carapace length 33.4) mm. The smallest and largest first form males have corresponding lengths of 30.3 (26.4) mm and 33.6 (29.2) mm; those of the smallest ovigerous female or one carrying young are 21.1 (19.2) mm.

LIFE HISTORY NOTES.—First form males have been collected in February, April, and May; ovigerous females in April and May; and females carrying young in April, May, and June. In February, a female together with young less than one cm in total length were taken from a burrow. A first form male collected in April 1975 molted in the laboratory to second form on 5 October 1975. (See "Seasonal Data.")

The number of eggs carried by three females are as follows. The asterisk marks an instance in which a number of egg cases indicate more eggs had been present.

Carapace and postorbital carapace lengths (mm)	*Number of eggs*	*Diameter of eggs (mm)*
28.8 (24.9)	21*	1.9
29.2 (26.3)	72	2.0–2.1
32.5 (28.6)	85	2.0–2.1

One female with lengths of 30.3 (26.1) mm was carrying 30 second instar young; some may have been lost when the crayfish were being removed from the burrow.

ECOLOGICAL NOTES.—*Procambarus (H.) advena* is a primary burrowing species, spending the major part of its life in complex burrows. Most of the

Seasonal Data

Sex/stage	*J*	*F*	*M*	*A*	*M*	*J*	*J*	*A*	*S*	*O*	*N*	*D*	*?*
♂I		2		1	1								
♂II		2		5	2	1		1					
♀		15		1	10	3							5
♂j		1		1	2								
♀j		2		1	4	2							
♀ ovig				3	1								
♀ with young				1	1	1							

tunnel systems have at least three potential exits to the surface, which are marked by low, apparently carelessly constructed chimneys, one or more of which is usually plugged. The openings lead into a branching, and occasionally anastomosing, system of some 2 to 6 meters of passageways, at least one of which spirals downward below the annual low level of the water table. Inasmuch as the tunnels are largely confined to flatwoods or boggy areas where the water table is near the surface, few of the deep passages extend downward for more than 1.5 meters.

Unlike some burrowing crayfishes, members of this species have never been lured to the surface when I was attempting to capture them, and occasionally it has been necessary to excavate the entire system of tunnels before locating the crayfish at the end of one of the blind horizontal passageways; usually, however, when the burrow is disturbed, the crayfish retreats to the depth of the spiraling vertical tunnel, where it resists being removed.

Georgia Crayfish Associates.—This crayfish has been dug from burrows nearby those of *Faxonella clypeata* (2 times), *Procambarus (L.) barbatus* (13), *P. (O.) lunzi* (1), *P. (O.) seminolae* (2), and *P. (S.) troglodytes* (4). Occurring in streams adjacent to the burrows from which *P. (H.) advena* was obtained are *P. (H.) pygmaeus* (2), *P. (O.) enoplosternum* (1), *P. (O.) epicyrtus* (1), and *P. (O.) litosternum* (2).

Procambarus (Hagenides) caritus, new species

Figures 17*d*, 118*b*, 120, 122, 123, 236

Procambarus advena.—Hobbs, 1942b:77 [in part].—Hart and Hart, 1974:28 [in part].

Summary of Literature.—Records of the occurrence of *Procambarus advena* in Appling County, Georgia, by Hobbs (1942b) and in Laurens County by Hart and Hart (1974) are based on my erroneous determinations of specimens of the species described here.

Diagnosis.—Rostrum without marginal spines or tubercles. Carapace lacking cervical spine. Areola 13.7 to 30.5 (average 15.0) times as long as broad and constituting 34.8 to 38.4 (average 36.1) percent of entire length of carapace (38.9 to 44.7, average 41.3, percent of postorbital carapace length). Ventral surface of basis and ischium of third maxillipeds not densely bearded. Male with mesial surface of palm of chela lacking beard but bearing cristiform row of 6 to 9 tubercles; hooks on ischia of third pereiopods only; coxa of fourth pereiopod with caudomesial boss. First pleopods of first form male asymmetrical, contiguous, and reaching coxae of second or third pereiopods, cephalic surface without shoulder, and preapical setae limited to few on cephalodistal border; mesial process acute to rounded distally and directed caudodistally; cephalic process absent, its usual position marked by angle on corneous ridge along cephalolateral base of subtriangular central projection, latter strongly corneous, arising from cephalodistal surface of appendage and directed distally (weakly arched cephalically), exceeding tumescent caudal knob by less than half length of process. Female with chela as in male; annulus ventralis subelliptical in outline, longer than broad, and with multituberculate cephalolateral elevations; first pleopod present.

Holotypic Male, Form I.—Body (Figure 122 *c, h*) subovate, slightly compressed laterally. Abdomen narrower than thorax (9.8 and 12.7 mm). Width of carapace slightly greater than depth at caudodorsal margin of cervical groove (12.7 and 12.0 mm). Areola about 14 times as long as broad, with 1 punctation in narrowest part. Cephalic section of carapace 1.8 times as long as areola; length of latter 35.6 percent of total length of carapace (40.6 percent of postorbital carapace length). Rostrum excavate dorsally, with nonthickened convergent margins lacking marginal spines or tubercles; upper surface with widely

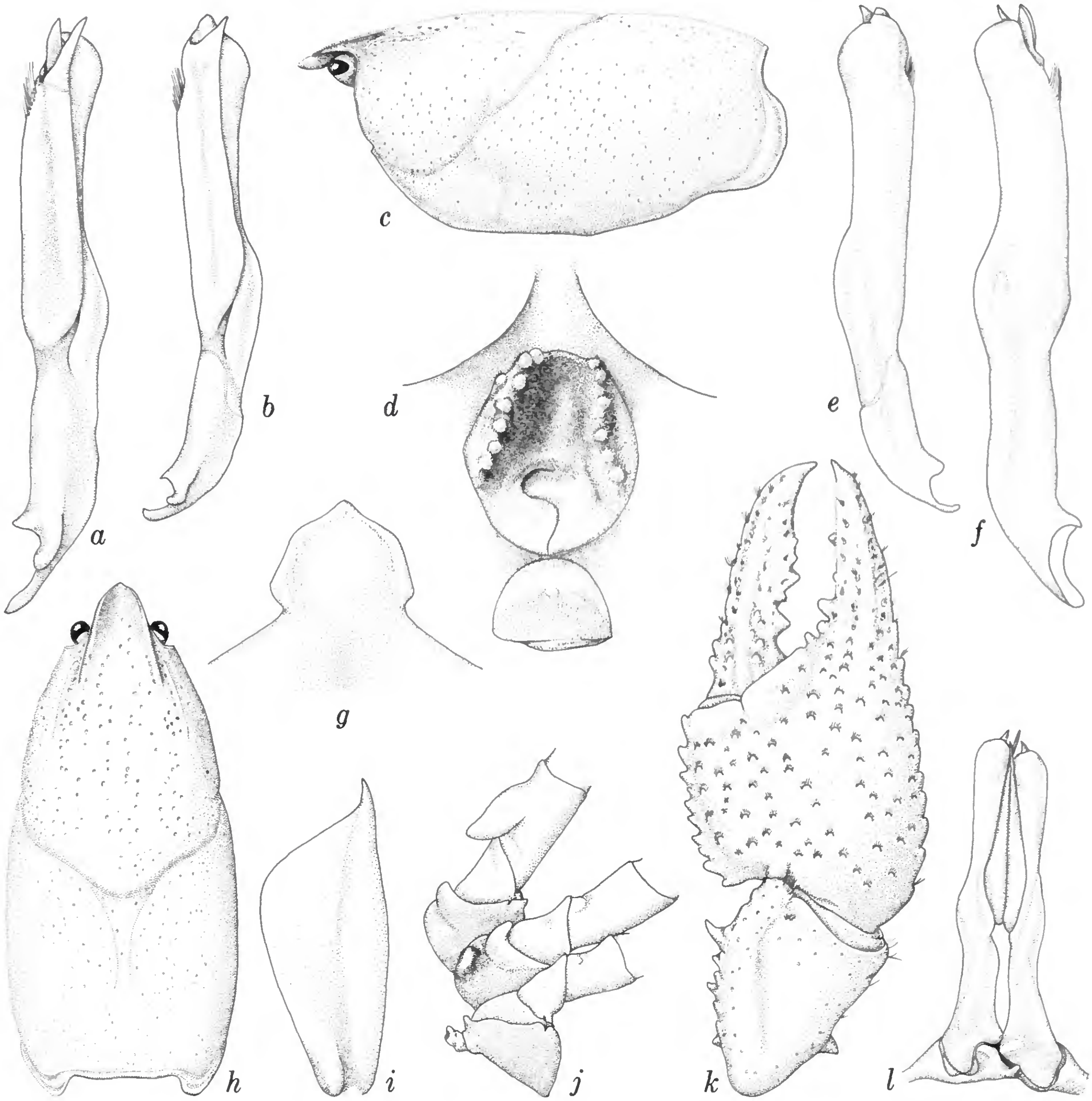


FIGURE 122.—*Procambarus (Hagenides) caritus* (all from holotype except *b*, *e*, from morphotype, and *d*, from allotype): *a*, *b*, mesial view of first pleopod; *c*, lateral view of carapace; *d*, annulus ventralis; *e*, *f*, lateral view of first pleopod; *g*, epistome; *h*, dorsal view of carapace; *i*, antennal scale; *j*, proximal podomeres of third, fourth, and fifth pereiopods; *k*, dorsal view of distal podomeres of cheliped; *l*, caudal view of first pleopods.

scattered tubercles between usual submarginal rows; acumen continuous with basal portion of rostrum and reaching anteriorly to base of ultimate podomere of antennule; subrostral ridges moderately well developed and evident in dorsal aspect for at least two-thirds length of rostrum. Postorbital ridge moderately strong, grooved dorsolaterally, and merging cephalically with carapace, lacking tubercle or spine. Suborbital angle obsolete. Branchiostegal spine very small. Carapace punctate dorsally and granulotuberculate laterally, cervical spine represented by very weak tubercle. Abdomen and carapace subequal in length (23.5 and 23.6 mm), pleura subtruncate ventrally. Cephalic section of telson with 1 spine in right and 2 in left caudal corners, caudal part rounded and rather narrow. Uropods with 2 short, acute prominences on basal podomere; mesial ramus with short distolateral spiniform tubercle but lacking spine or tubercle on median ridge; lateral ramus with usual row of small spines immediately proximal to transverse suture, lateralmost larger than others. Cephalic lobe of epistome (Figure 122*g*) resembling bell in outline, with cephalomedian projection, ventral surface slightly convex and margins somewhat thickened and elevated ventrally; fossa quite shallow and epistomal zygoma strongly arched. Antennule of usual form, with strong ventral spine near midlength of proximal podomere. Antennae broken but probably reaching almost to caudal margin of carapace; peduncle without spines. Antennal scale (Figure 122*i*) about 2.4 times as long as wide, greatest width distal to midlength, lamellar portion not greatly broader than thickened lateral part; latter terminating in strong spine. Third maxilliped with basis bearing conspicuous mesial tuft of long, stiff, simple setae; ischium, lacking distolateral spine, with submarginal lateral row of short setae, longer ones largely restricted to longitudinal series lateral to crista dentata, leaving most of broad ventrolateral area almost naked.

Right chela (Figure 122*k*) subtriangular, subovate in cross section, rather strongly depressed. Mesial surface of palm with cristiform row of 9 tubercles subtended dorsolaterally by row of 6 subsquamous ones, other squamous tubercles scattered over dorsal surface and lateral margin of palm and extending onto basal portions of fingers; ventral surface of palm mostly punctate with ventrolateral row of punctations, bearing tufts of conspicuously long setae, extending from base of palm almost to tip of fixed finger; ventromedian part of palm with scattered tubercles and very strong one opposite base of dactyl. Fixed finger with very sharply defined median longitudinal ridge dorsally and less well developed one ventrally, ridge flanked proximally by squamous tubercles and distally by conspicuous setiferous punctations; lateral margin of finger with row of squamous tubercles proximally, decreasing in size distally and near midlength replaced by setiferous punctations; opposable margin of fixed finger with 4 large tubercles in proximal half, third from base largest, and large tubercle on lower level at base of distal third of finger, row of minute denticles extending from proximal group of tubercles to corneous tip of finger. Dactyl with dorsal surface similar to that of fixed finger, mesial margin with few tubercles proximally, and ventral surface without tubercles but with setiferous punctations; opposable margin with row of 5 tubercles along proximal two-thirds of finger, first and third from base much larger than remaining ones, and single row of minute denticles extending from base of second major tubercle to corneous tip of finger.

Carpus of right cheliped punctate dorsally, laterally, and ventrally, and tuberculate mesially; dorsal surface with shallow oblique furrow; dorsomesial margin with row of small tubercles; mesial surface with row of 3 increasing in size distally; among small tubercles on ventral surface 2 large ones situated subterminally.

Merus with dorsal surface tuberculate, tubercles low and none spiniform; mesial and lateral surfaces mostly polished with few shallow setiferous punctations; ventral surface with lateral row of 9 tubercles (11 on left), 6 of which flanked by long stiff setae, and mesial row of 11 tubercles, rows not converging distally; distolateral extremity lacking spine. Ischium with row of 4 tubercles.

Hook (Figure 122*j*) on ischium of third pereiopod only; hook simple, heavy, curved, and extending proximally over distal portion of corresponding basis. Coxa of fourth pereiopod with prominent knoblike boss disposed obliquely vertically; that of fifth smaller and subacute.

Sternum between third, fourth, and fifth pereiopods rather shallow but bearing dense fringe of plumose setae on ventrolateral margins.

First pleopod (Figure 122*a,f,l*) as described in "Diagnosis."

ALLOTYPIC FEMALE.—Description of holotype applicable to allotype except for secondary sexual characters and following: cephalic section of telson with 1 spine in each caudolateral corner; left chela with only 3 tubercles on opposable margin of dactyl; ventral surface of merus of cheliped with ventrolateral row of 11 tubercles and ventromesial one of 12. (See "Measurements.")

Annulus ventralis (Figure 122*d*) only moderately deeply embedded in U-shaped sternum, subelliptical, longer than broad and with very high, multituberculate, cephalolateral ridges flanking deep median trough, from caudal part of which sinus originating, forming right hairpin turn to median line, there turning caudally and, in slightly sinuous curve, extending to caudal margin of annulus. Postannular sclerite as figured. First pleopod reaching midlength of annulus when abdomen flexed.

MORPHOTYPIC MALE, FORM II.—Except for following differences in cheliped and secondary sexual characters, description of holotype applicable to morphotype: mesial surface of palm of chela with row of 8 tubercles; opposable margin of dactyl with only 3; ventral surface of merus with 11 tubercles in both mesial and lateral rows. Hook on ischium of third pereiopod reduced to tubercle, and bosses on coxae of fourth and fifth pereiopods much less well developed.

First pleopod (Figure 122*b,e*) with shorter, more inflated mesial process and central projection, and latter lacking angular bend cephalically; juvenile oblique suture in proximal fourth of appendage.

COLOR NOTES (Figure 118*b*).—No features noted in the coloration of this crayfish serve to distinguish it from *P. (H.) advena* and *P. (H.) talpoides*.

TYPES.—The holotypic male, form I, allotypic female, and morphotypic male, form II, are deposited in the National Museum of Natural History, Smithsonian Institution, numbers 117598, 133678, and 116952, respectively, as are the paratypes consisting of 5♂I, 3♂II, 4♀, and 1 ovigerous ♀.

Measurements (mm)

	Holotype	*Allotype*	*Morphotype*
Carapace			
Height	12.0	13.1	11.0
Width	12.7	13.7	10.5
Entire length	27.0	27.5	22.8
Postorbital length	23.6	24.2	20.0
Areola			
Width	0.7	0.7	0.6
Length	9.6	10.0	8.5
Rostrum			
Width	3.9	3.9	3.5
Length	4.2	4.1	3.6
Chela			
Length of mesial margin of palm	6.3	5.7	4.1
Width of palm	8.3	8.2	6.1
Length of lateral margin	16.6	16.5	11.7
Length of dactyl	10.3	10.1	7.0
Abdomen			
Width	9.9	9.7	7.6
Length	23.7	25.2	19.3

TYPE-LOCALITY.—Seepage area, 3.7 miles west of Glenwood, Wheeler County, Georgia, on U.S. Highway 280. There the complex burrows were constructed in a sandy clay soil in a seep near a small stream tributary to Alligator Creek (Ocmulgee-Altamaha river basin). Although the seepage area was exposed to the sun, a wooded area supporting *Liriodendron tulipifera*, *Pinus* sp., *Quercus* sp., and *Magnolia* sp. was nearby.

RANGE.—This crayfish is endemic in Georgia, where it is largely confined to the western and southern part of the Vidalia Upland and the northern part of the Bacon Terraces districts. In Wayne County, it penetrates the Barrier Island Sequence District. Thus it has been found only in the Ocmulgee-Oconee-Altamaha and Satilla watersheds.

GEORGIA SPECIMENS EXAMINED.—I have examined 73 specimens collected from burrows in the following localities (those lots comprising the type series are marked with an asterisk). *Appling County*: (1) 3.0 mi S of Baxley on US Hwy 1, 4♂II, 3♀, 23 Aug 1937, HHH, collector; (2) 1.5 mi S of Baxley, 2♂II, 2♀, 2 Jan 1938, HHH. *Bacon County*: (3) vicinity of Alma, 1j♂, Sep 1949, C. Tuten; (4) 2.1 mi W of Appling Co line on St Rte 99, 2♂II, 1♀, 6 Oct 1977, T. A. English, Jr., HHH; (5) 3.1 mi W of Appling Co line on St Rte 99, 1♂II, 1♀, 6 Oct 1977, TAE, HHH; (6) 4.1 mi W of

Alma on St Rte 32, 1♂II, 1 ovig ♀, 1♀ with young, 6 Oct 1977, TAE, HHH; (7) 0.2 mi S of Coffee Co line on unnumbered road off St Rte 64 in extreme SSW corner of county, 1♂I, 5 Apr 1978, R. J. Dubois, D. J. Peters, J. E. Pugh, HHH. *Coffee County*: *(8) 3.6 mi S of Telfair Co line on US Hwy 441, 2♂I, 1♂II, 4 Apr 1978, RJD, DJP, JEP, HHH; (9) 5.1 mi E of US Hwy 221 on Rte S1730, 1♂I, 4 Apr 1978, RJD, DJP, JEP, HHH; (10) 6.1 mi S of Denton on US Hwy 221, 4j♀, 23 Jun 1975, DJP, JEP, HHH; (11) 8 mi N of Broxton on US Hwy 411, 2j♂, 6 Oct 1977 (molted to form I, on 29 Sep 1978 and late Oct 1978), TAE, HHH. *Dodge County*: *(12) 2.3 mi W of Telfair Co line on US Hwy 23, 1♂II, 22 Apr 1966, E. T. Hall, Jr., HHH; *(13) 1.2 mi S of Laurens Co line on US Hwy 441, 1♂I, 1♂II, 2♀, 4 Apr 1978, RJD, DJP, JEP, HHH; (14) 4 mi N of Chauncey on St Rte 165, 1♀, 21 Apr 1977, C. E. Carter, JEP, HHH. *Jeff Davis County*: *(15) 1.3 mi SW of Hazelhurst on US Hwy 221, 1♂I, 1♀, 1 ovig ♀, 23 Apr 1966, ETH, HHH; (16) 1.0 mi S of US Hwy 341 on Hwy 221, 2♂II, 2♀, 23 Jun 1975, DJP, JEP, HHH; (17) 0.8 mi S of Denton on US Hwy 221, 2j♂, 23 Jun 1975, DJP, JEP, HHH. *Laurens County*: (18) 20.6 mi S of US Hwy 80 on St Rte 19, 1♂II, 1♀, 20 Jun 1975, DJP, JEP, HHH. *Montgomery County*: (19) 1.4 mi N of Jeff Davis Co line on US Hwy 221, 1♂II (molted to form I, 7 Oct 1975), 8♀, 1j♂, 2j♀, 22 Jun 1975, DJP, JEP, HHH; 1♂II, 1j♀, 20 Apr 1977, CEC, JEP, HHH. *Telfair County*: *(20) 2.3 mi W of Helena, 1♂I, 23 Apr 1966, ETH, HHH; (21) 2.8 mi E of Milan on US Hwy 280, 2♂I, 2♀, 1j♀, 18 Apr 1974, DJP, HHH; 2♂I, 1j♀, 21 Apr 1977, CEC, JEP, HHH; (22) 3.4 mi E of St Rte 165 on US Hwy 280, 1♀, 21 Jun 1975, DJP, JEP, HHH. *Wayne County*: (23) 5.5 mi W of US Hwy 82 on St Rte 99, 1♂II, 1j♂, 6 Oct 1977, TAE, HHH; (24) 0.4 mi N of Jesup on US Hwy 25, 1♂II, 27 Mar 1939, HHH; (25) 1.9 mi N of Jesup on US Hwy 301, 1♂II, 23 Dec 1956, HHH; (26) 4.1 mi SE of St Rte 144 on Rte 169, 1♂II, 5 Oct 1977 (molted to form I, 28 Sep 1978), TAE, HHH; (27) 0.4 mi W of US Hwy 301 on Rte S1920, 2♀, 1j♂, 25 May 1979, G. B. Hobbs, HHH; (28) 2.4 mi N of St Rte 99 on Rte S1492, 3♂II (1 molted to form I, 22 Nov 1979), 1♀, 26 May 1979, GBH, HHH; (29) 8 mi NE of St Rte 99 on Rte S1492, 1♀, 26 May 1979, GBH, HHH; (30) 13.2 mi NW of Jesup on St Rte 169, 1j♀, 27 May 1979, GBH, HHH; (31) immediately E of Rte S605 on Rte S1491, 2♀, 1j♂, 1j♀, 27 May 1979, GBH, HHH. *Wheeler County*: *(32) type-locality, 1♂I, 1♀, 22 Apr 1966, ETH, HHH; *(33) 1.5 mi N of US Hwy 280 on Hwy 441, 1♂II, 1♀, 22 Apr 1966, ETH, HHH.

VARIATIONS.—There are few variations among the limited number of specimens available. The epistome of one is subrectangular, but that of two others from the same locality resembles that described and illustrated. The greatest range of differences occurs in the cheliped: mesial margin of palm with six to nine tubercles; opposable margins of fixed finger and dactyl with five and four, respectively, in most specimens; 11 to 13 tubercles in ventromesial row on merus, and nine to 13 in ventrolateral row; ischium with two to five tubercles. No variations seem to be peculiar to local populations, but specimens from the northwestern part of the range exhibit a more scabrous condition on the telson and uropods. See Figure 123 for variations in the first pleopod of first form males.

SIZE.—The largest specimen available is a fe-

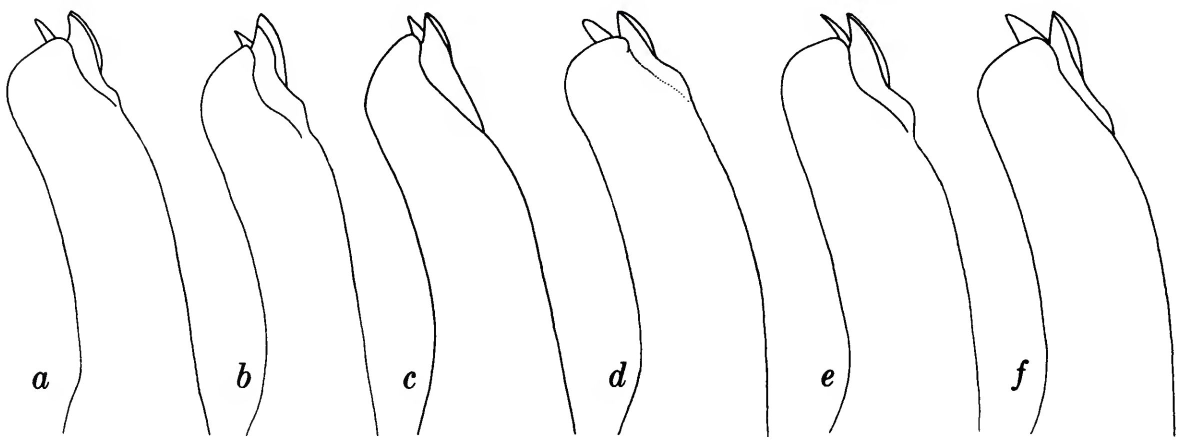


FIGURE 123.—*Procambarus (H.) caritus*, variations in first pleopod of male, form I. Altamaha Basin: *a*, Wheeler Co; *b*, *c*, Telfair Co; *d*, Montgomery Co. Satilla Basin: *e*, Jeff Davis Co; *f*, Bacon Co.

male having a carapace length of 34.8 (postorbital carapace length 30.3) mm. Corresponding lengths of the smallest and largest first form males are 25.6 (22.1) mm and 34.0 (29.9) mm, respectively, and of the smallest ovigerous female, 30.0 (26.2) mm.

LIFE HISTORY NOTES.—Ten of the first form males at hand were collected in April, and the remaining three that were obtained while in the second form, on 22 June 1975 and 5 and 6 October 1977 molted to first form in the laboratory on 7 October 1975 and 28 and 29 September 1978, respectively. One female, with a carapace length of 33.5 (postorbital carapace length, 28.0) mm and carrying 56 eggs and first instar young, was obtained on 23 April 1966. Another ovigerous female with corresponding lengths of 30.0 (26.2) mm and bearing 19 eggs was found on 6 September 1966, and in a nearby burrow there was another female measuring 34.4 (30.3) mm accompanied by an undetermined number of young, one of which had a carapace length of 9.6 mm. All of the eggs had diameters of 1.9 to 2.0 mm.

Seasonal Data

Sex/stage	*J*	*F*	*M*	*A*	*M*	*J*	*J*	*A*	*S*	*O*	*N*	*D*
♂I				10								
♂II	2		1	6	3	3		4		3		1
♀	2			15	6	4		3		2		
♂j					2	2			1	4		
♀j				4	2	4						
♀ ovig				1						1		
♀ with young										1		

ECOLOGICAL NOTES.—This crayfish has been found only in complex burrows in seepage areas along streams, in rolling pine woods, and in pine flatwoods, and there is every reason to believe that it is an ecological equivalent of the allopatric *P. (H.) advena* and *P. (H.) truculentus*, and the largely allopatric *P. (H.) talpoides*; the latter was collected with *P. (H.) caritus* in the extreme southwestern part of Bacon County (locality 7) and in the eastern part of Coffee County (locality 9). Notes on the burrows of *P. (H.) advena* and *P. (H.) talpoides* apply equally well to those of *P. (H.) caritus*. (See "Ecological Notes" under those species.)

RELATIONSHIPS.—This crayfish has its closest affinities with *P. (H.) advena* and *P. (H.) talpoides* and is so similar to both that it can be distinguished from them only on the basis of the secondary sexual characteristics of the first pleopod of the first form male and usually by the steep tuberculate cephalolateral ridges on the annulus ventralis. (See "Relationships" under *P. (H.) talpoides*.)

GEORGIA CRAYFISH ASSOCIATES.—The following crayfishes were collected from burrows, streams, or pools within a few meters of the burrows of *P. (H.) caritus* (the number of times they have been found together is indicated in parentheses): *Faxonella clypeata* (3), *Procambarus (H.) talpoides* (2), *P. (L.) pubischelae deficiens* (6), *P. (O.) acutus acutus* (1), *P. (O.) enoplosternum* (1), *P. (O.) seminolae* (6), and *P. (S.) howellae* (3).

ETYMOLOGY.—From the Latin *caritus* (lacking), so named because of the absence of a cephalic process on the first pleopod of the first form male.

Procambarus (Hagenides) pygmaeus Hobbs

FIGURES 17*c*, 102, 118*c*, 124, 237

Cambarus advena.—Hagen, 1870:87* ["Cat. No. 282, Georgia, Dr. Jones. Male. Fem. Spec. 6" (in part: both *P. (H.) pygmaeus* and *P. (H.) talpoides* present)].

Cambarus Carolinus.—Hagen, 1870: figs. 51–54.

Procambarus pygmaeus Hobbs, 1942b:13–15, 20, 30, 55, 66, 73–75, 83–88*, figs. 66–70, 296–304; 1954:110; 1959:885, 887*; 1962:279; 1968b:K-10*, fig. 16c.—Hobbs and Hart, 1959:149, 152, 158–160, 168–171, 173–176*, fig. 13.—Anonymous, 1967b, tab. 3*; 1967h, tab. 3*; 1973c:54*.—Wharton, 1978:220.*

Procambarus advena.—Hobbs, 1942b:77* [in part: Bryan County].

Procambarus (Hagenides) pygmaeus.—Hobbs, 1972a:7; 1972b: 50*, 152*, 154*, figs. 5j, 41e; 1974b:48–49*, fig. 196*a,c–g* [*b* is first pleopod of *P. (H.) geodytes* Hobbs, 1942b: 80].—Hobbs III, Thorp, and Anderson, 1976:3, 12, 28–29*, fig. 11.

The above citations are believed to constitute a complete bibliography of the species; those marked by an asterisk contain references to Georgia.

Summary of Literature Pertaining to Georgia.—The locality for the specimens available to Hagen (1870) is not known, but inasmuch as specimens of *P. (H.) talpoides* were accompanying them, it is likely that they were collected south of the Altamaha River. As pointed out when the species was first described (Hobbs, 1942b), the first specimens I saw and recognized as distinct from the closely allied "*P. advena*" (= *P. (H.) talpoides*) came from flowing water in a roadside ditch in Clinch County, Georgia. The most complete accounts of the species are that just cited and those of Hobbs and Hart (1959) and Hobbs III, Thorp, and Anderson (1976). Excerpts from Hobbs (1942b) are included below. The only specific new localities for this crayfish that have been cited since it was first described are those of Anonymous (1967b, 1967h, and 1973c). (See "Specimens Examined.")

Diagnosis.—Rostrum without marginal spines or tubercles. Carapace lacking cervical spines. Areola 20.0 to more than 50.0 times as long as broad and constituting 32.9 to 38.0 (average 36.0) percent of entire length of carapace (39.5 to 44.7, average 42.1, percent of postorbital carapace length). Ventral surface of basis and ischium of third maxilliped not densely bearded. Male with mesial surface of palm and chela lacking beard but bearing cristiform row of tubercles; hook on ischium of third pereiopod only; coxa of fourth pereiopod with prominent caudomesial boss. First pleopods of first form male asymmetrical, contiguous, and reaching coxae of second pereiopods, cephalic surface without angular shoulder and preapical setae limited to few on cephalodistal border; mesial process comparatively slender, acute, and directed caudodistally; cephalic process absent; central projection very prominent, bladelike, directed distally, and its base only slightly narrower in lateral aspect then shaft of appendage immediately proximal to it; caudal element vestigial. Female with chela as in male; annulus ventralis subcircular to subelliptical, with marginal elevation of almost uniform height (ventrally), broken only by broad cephalic notch and caudal area flanking sinus; first pleopod present.

Color Notes (Figure 118*c*).—(The color of this crayfish usually changes rapidly after capture. The bright green and scarlet coloration typical of the species in the wild changes, often within minutes, to olive and pale pinkish cream or tan). Cephalic section of carapace dark olive to forest green with at least 3 pairs of scarlet spots: 1 posterior to postorbital ridges, another across anterior margin of orbital and antennal regions, and third ventral to postorbital ridges on border of orbital and hepatic regions. Frequently rostral and postorbital ridges also scarlet. Branchiostegites olive to forest green, with paired oblique bands of scarlet flanking cervical groove, extending from areola to area of cervical tubercle; caudal and ventral ridges and flange of carapace black. Abdomen green, with broad transverse red band on each of first through fifth terga flanked caudally by narrow black band; sixth tergum with 3 prominent red spots posteriorly and very narrow marginal black band caudally. Pleura often with subcircular scarlet spot surrounding greenish cream center. Antennal and antennular peduncles olive green with flecks of scarlet, and flagella olive; antennal scale pale olive with dark lateral margin. Cheliped basically dark olive distal to base of distal two-thirds of merus; most tubercles almost black, articular knobs and ridges and few larger tubercles scarlet. Other pereiopods mostly pale olive, with distal parts of merus and carpus darker, and all scarlet at merocarpal and carpopropodal articulations. Ventral surface bluish to olive cream.

Types.—Holotype, allotype, and "morphotype," USNM 81285 (♂I, ♀, ♂II); paratypes, MCZ, USNM.

Type-Locality.—Roadside ditch 15.7 miles north of Fargo on U.S. Highway 41 (State Route 89), Clinch County, Georgia.

Range.—From the Tifton and Vidalia uplands in Georgia to the Atlantic coast (between the Suwannee and Savannah river basins), southward to Putnam County, Florida, and in the panhandle of the latter in Franklin, Gulf, and Liberty counties.

Specimens Examined.—I have examined a total of 328 specimens, 44 from Florida, and 284 from the following

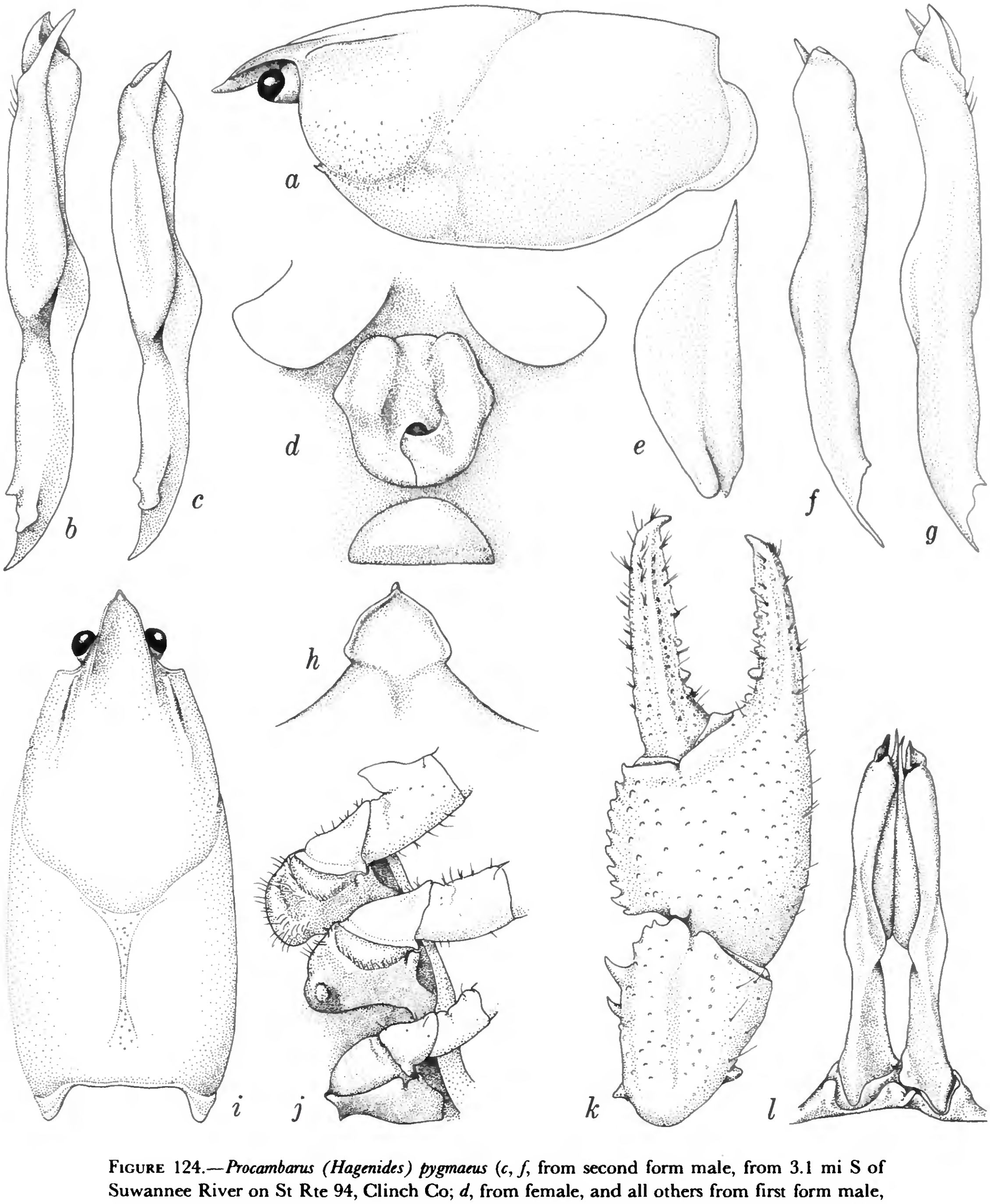


FIGURE 124.—*Procambarus (Hagenides) pygmaeus* (*c, f,* from second form male, from 3.1 mi S of Suwannee River on St Rte 94, Clinch Co; *d,* from female, and all others from first form male, from 15.4 mi N of Fargo on US Hwy 441, Clinch Co): *a,* lateral view of carapace; *b, c,* mesial view of first pleopod; *d,* annulus ventralis; *e,* antennal scale; *f, g,* lateral view of first pleopod; *h,* epistome; i, dorsal view of carapace; *j,* proximal podomeres of third, fourth, and fifth pereiopods; *k,* dorsal view of distal podomeres of cheliped; *l,* caudal view of first pleopods.

localities in Georgia. *Atkinson County*: (1) Pudding Creek at US Hwy 441 N of Pearson, 1j♂, 26 Sep 1972, E. T. Hall, Jr., W. D. Kennedy, HHH, collectors; (2) Pudding Creek at St Rte 135, 15.2 mi SW of Douglas, 1♂I, 3♀, 23 Mar 1959, R. H. Gibbs; (3) 0.2 mi W of US Hwy 221 on St Rte 64, 2♂I, 2♂II, 9♀, 6 Apr 1978, R. J. Dubois, D. J. Peters, J. E. Pugh, HHH. *Berrien County*: (4) Withlacoochee River at St Rte 76 (Anonymous, 1967b, tab. 3), 1♀, 1j♂, 1j♀, 11 Mar 1966, D. Schultz; 1♂II, 1j♂, 2j♀, 24 Jun 1975, DJP, JEP, HHH. *Bryan County*: (5) about 1 mi W of Ways Station (Richmond Hill), 1♀, 1 ovig ♀, 15 Jul 1939, E. H. Blount, HHH; (6) 7.9 mi W of US Hwy 17 on St Rte 67, 1♂II, 1♀, 28 May 1969, ETH, HHH; (7) Mill Creek 1.2 mi N of Ellabelle, 5j♂, 27 Dec 1971, G. K. Williamson; (8) 1.9-4.7 mi SW of Pembroke on St Rte 119, 1♂I,.1♂II, 1♀, 2j♀, 27 Dec 1971, GKW; 1♂I, 2♀, 3j♂, 5j♀, 22 Jun 1975, DJP, JEP, HHH; 2♂I, 5♂II, 2♀, 2j♀, 20 Apr 1977, C. E. Carter, JEP, HHH. *Candler County*: (9) Fifteen Mile Creek at St Rte 46, 6♂I, 6♂II, 12♀, 1j♂, 2j♀, 21 May 1980, Univ. of Tennessee Regional Faunas Class. *Charlton County*: (10) 7.9 mi S of Brantley Co line on US Hwy 301, 1♂II, 2j♂, 2j♀, 23 Aug 1965, J. E. Cooper, M. R. Cooper; (11) Okefenokee Swamp, 1♂II, 5♀, 2j♂, 2j♀, 15 Apr 1941, C. B. Obrecht. *Chatham County*: (12) headwaters of Little Ogeechee River, 1♂I, 1♀, Nov 1968, R. W. Heard III. *Clinch County*: (13) type-locality, 2♂I, 4♂II, 9♀, 21j♂, 16j♀, 27 Oct 1938, F. N. Young, Jr., HHH; (14) 5 mi NE of Homerville on US Hwy 441 (Hobbs, 1942b:86), 1♀, 2j♂, 7 Aug 1939, HHH; (15) 7.6 mi N of Fargo on US Hwy 441 (Hobbs, 1942b:86), 4♀, 27 Oct 1938, FNY, HHH; 1j♂, 29 Mar 1977, H. K. Wallace, HHH; (16) Suwannee River off St Rte 177 near entrance to Stephen Foster St Park, 3♂II, 19 Oct 1972, B. A. Caldwell, R. M. Gaddis; (17) 15 mi N of Fargo on US Hwy 441, 1j♀, 25 May 1941, G. B. Hobbs, HHH; 1♂I, 2♂II, 2♀, 1j♂, 2j♀, 1 ovig ♀, 29 Mar 1977, HKW, HHH; (18) 3.1 mi S of Suwannee River on St Rte 94, 1♂I, 2♂II, 2♀, 3j♂, 4j♀, 30 Mar 1977, HKW, HHH; (19) 3 mi S of Homerville off US Hwy 441, 1♂I, 1♂II, 3♀, 4 Nov 1967, J. J. Sullivan. *Coffee County*: (20) Seventeen Mile Creek at US Hwy 441, N of Douglas, 1♂II, 1j♂, 13 Sep 1972, RMG, M. W. Walker; 1j♀, 18 Oct 1977, BAC. *Effingham County*: (21) Ebeneezer Creek, 4.0 mi NW of Clyo, 1♀, 1 Oct 1972, GKW. *Jeff Davis County*: (22) Whitehead Creek 7.8 mi SW of Hazelhurst on US Hwy 221, 1♂I, 1♀, 3j♀, 23 Apr 1966, ETH, HHH. *Liberty County*: (23) Raccoon Branch about 2 mi N of Flemington, 1♂II, 1j♀, 28 May 1969, ETH, HHH; (24) Gouldins Creek about 5 mi S of Wilderness Church on unnumbered road, 1j♂, 2j♀, 27 May 1969, ETH, HHH. *Long County*: (25) Goose Run Creek 7.7 mi NW of McIntosh Co line on St Rte 99 near Ludowici, 1♂I, 2♂II, 3♀, 28 May 1969, ETH, HHH; 1♀, 18 Dec 1971, GKW. *McIntosh County*: (26) Buffalo Creek 6.5 mi W of US Hwy 17 on St Rte 251, 1♂I, 1♂II, 1♀, 2j♂, 3j♀, 28 May 1969, ETH, HHH. *Telfair County*: (27) 8.5 mi W of McRae on US Hwy 280, 1j♀, 21 Apr 1977, CEC, JEP, HHH. *Tift County*: (28) Ty-ty Creek at Worth Co line on US Hwy 82, 2♂I, 3♂II, 2♀, 5j♂, 6j♀, 24 Mar 1966, ETH, HHH; (29) Alapaha River at Irwin Co line on St Rte 35, 2♀, 2j♂, 4j♀, 25 Sep 1972, ETH, WDK, HHH. *Ware County*: (30) Satilla River at Rte S598, 5 mi N of Waycross, 1j♂, 13 Sep 1967, DS; (31) 18.2 mi SW of Waycross on US Hwy 84, 1♂II, 2j♂, 1j♀, 28 Sep 1972, ETH, WDK, HHH. *Wayne County*: (32) 0.5 mi N of Jesup on US Hwy 25 (St Rte 38), 1♀, 1j♂, 1j♀, 31 Dec 1938, HHH; 1♂I, 3♀, 27 Mar 1939, HHH. *Locality Unknown*: "Georgia," 1♂I, MCZ 282.

VARIATIONS.—There appears to be remarkable uniformity among the available material from Georgia. As indicated by Hobbs (1942b:85), the rostra of the specimens from Clinch County are more lanceolate than those of most specimens collected elsewhere in the range. The ratio of the areolar length to that of the carapace is slightly higher in some, if not most, adults occurring north of the Altamaha River than in those south of it. Whereas most populations lack spines on the ventral surface of the basal segment of the antennular peduncle, some individuals from Wayne County possess a well-developed one.

SIZE.—The largest specimen available is a female, reared in the laboratory, with a carapace length of 27.0 (postorbital carapace length 22.8) mm; the largest collected in the field are a second form male and a female, each with corresponding lengths of 23.5 (21.2) and 23.5 (20.1) mm, respectively. The smallest first form male has comparable lengths of 16.7 (14.0) mm, and those of the smallest ovigerous female 21.1 (17.8) mm.

LIFE HISTORY NOTES.—First form males have been collected from March to June and from October to December. Ovigerous females were found in March and July in Georgia and in May in Liberty County, Florida. The smaller (see "Size") of the two measured carried 23 eggs with diameters of 1.7 to 1.8 mm; the other, having a carapace length of 22.2 (postorbital carapace length 19.1) mm bore 28 eggs with diameters also of 1.7 to 1.8 mm.

Unfortunately, few data were maintained on a population kept in the laboratory in the Smithsonian Institution from April 1966 to May 1972 at a temperature range of 20 to 23 degrees C. The original male and female were collected on 27 April 1966, from Ty-ty Creek on U.S. Highway 82 on the Tift-Worth county line. The following

April a clutch of eggs was produced and hatched in May; 11 young eventually reached maturity. The same female laid again in October 1967, but these eggs did not develop. A third clutch of eggs was produced by her between 1 and 3 March 1968; these eggs hatched on 18 March, and the young left the mother between 23 and 25 March (no further data were recorded on these young).

Among the 11 offspring that hatched in May 1967, one male molted to first form in November at an age of six months. In February 1968, one of the females produced eggs that failed to develop but another produced a brood in late February; a female from the latter laid eggs that hatched in December 1968. The last individual of this brood died on 10 May 1972, at an age of approximately 3.5 years. Thus it seems possible, if not probable, that two broods of young may be produced by a single female during at least one year of its existence, that the female may be no more than 10 months old when the first clutch of eggs is produced, and that the offspring may live for at least three years. In all probability males live for about the same length of time.

Seasonal Data (Florida and Georgia)

Sex/stage	*J*	*F*	*M*	*A*	*M*	*J*	*J*	*A*	*S*	*O*	*N*	*D*	*?*
♂I			7	8	3	1				2	2	1	1
♂II			9	13	16	1		1	2	7	3	1	
♀			15	21	23	2	1	1	2	14	15	3	
♂j			14	7	8	4		4	7	21	1	6	
♀j			16	8	14	7		2	5	18		3	
♀ ovig			1		1		1						

Ecological Notes.—As has been pointed out by Hobbs (1942b:87) and Hobbs and Hart (1959: 176), *P. (H.) pygmaeus* probably should be classified as a secondary burrower. Even though the complexity of the tunnel systems of some of its burrows is equal to that of other members of the subgenus, this crayfish demonstrates a distinctly less restrictive tie to a subterranean habitat. Not only was it first found in open water but also it occurs in rooted vegetation in permanent bodies of flowing water. Invariably, where it has been found, whether in open water or in burrows, the sedge *Juncus repens* was in the vicinity. The fact that *P. (H.) pygmaeus* is apparently always associated with this plant would seem to limit its vagility and thus cause it to have as restricted a range as do its primary burrowing relatives. On the contrary, it is more widespread than any member of the subgenus. That both the crayfish and *J. repens* invade lotic habitats raises the probability of their being moved passively, not only downstream but across rivers as well; perhaps such occurred in *P. (H.) pygmaeus* traversing the Altamaha River, a stream that acts as a barrier to several species of crayfishes, including two members of the subgenus *Hagenides*.

The broad spectrum of habitats utilized by the crayfish associates listed below, together with the comparatively large range of *P. (H.) pygmaeus*, supports the conclusion that it has a much broader ecological tolerance than do the other members of the subgenus *Hagenides*. Also supporting this conclusion was my success (unique to me) in rearing three generations of this crayfish in nonaerated aquaria in my office between 1966 and 1972.

When first collected, all individuals are colored as indicated under "Color Notes," the greens and scarlet being typical of the plant with which they are associated. Individuals brought into the laboratory, however, soon lose the brilliant coloration; the green areas become dull greenish or bluish gray, and the scarlet markings fade to pale pinkish cream or gray, a transition from being one of the most spectacularly colored crayfishes to one that is rather drab and unattractive. On at least one occasion (29 March 1977 while I was collecting in Clinch County, Georgia), a small brightly colored individual changed to the drab form in less than one hour, and returning it to a container in which *Juncus repens* was present did not cause it to regain the original coloration, even after several weeks. To date I have no evidence that the crayfish feeds upon the plant.

In commenting on the discovery of this crayfish, Hobbs (1942b:87) stated:

> A glance at a specimen of *pygmaeus* would give the impression that it was a very small, highly colored specimen of *P. advena*. Finding this new species was a surprise, for it had been only a short distance back that I had dug *P. advena* [=

P. (H.) talpoides] from burrows in a roadside ditch, and to find two so nearly related forms so close together was at least unusual. Even more astounding was the fact that *pygmaeus* was not dug from burrows but was taken from flowing water. Judging by the method used in collecting them [with coffee sieve and dip net], they must have been out crawling under the vegetation and over the bottom of the ditch and stream. Since most of my collecting was done at night I was unable to ascertain whether these specimens had burrows in the bottom of the ditch and stream or whether they were true open water forms. . . . It has been noted that every locality from which this species has been taken is in swampy terrain. . . . For some time I was unable to find this species burrowing, and this seemed unusual in view of the fact that its relatives are all primary burrowers. Specimens have now been taken from burrows in nearly all of the localities cited. . . . These burrows are fully as complex as those of the other members of . . . [the subgenus *Hagenides*], having a number of side passages and sometimes several openings over which are moderately well constructed chimneys. Most of the burrows I have seen were in soft muck very close to the edge of the water or in recently dried up ditches.

Georgia Crayfish Associates.—Collected with this crayfish in one or more localities were (the number of times they were found together is indicated in parentheses): *Faxonella clypeata* (1), *Procambarus (H.) advena* (2), *P. (H.) talpoides* (1), *P. (L.) barbatus* (7), *P. (L.) p. pubischelae* (5), *P. (O.) enoplosternum* (2), *P. (O.) epicyrtus* (2), *P. (O.) fallax* (2), *P. (O.) litosternum* (3), *P. (O.) lunzi* (4), *P. (O.) seminolae* (21), *P. (Pe.) spiculifer* (4), *P. (S.) howellae* (1), *P. (S.) paeninsulanus* (3), and *P. (S.) troglodytes* (8).

Procambarus (Hagenides) talpoides, new species

Figures 17e, 118*d,e,* 120, 125–127, 238

Cambarus advena.—Hagen, 1870:87* ["Cat. No. 282, Georgia, Dr. Jones. Male. Fem. Spec. 6" (in part: both *P. (H.) talpoides* and *P. (H.) pygmaeus* present)].—Hobbs, 1942c: 56, pl. 2: figs. 10, 11; 1945a:67.

Procambarus advena.—Hobbs, 1942b:15, 20, 30, 45, 73–80* [in part], 84 [in part], 86 [in part], 87, 92 [in part], 106, 145, 170, figs. 56–60; 1945a:69, fig. 15; 1945b:250, 258*, 260, fig. 27; 1954:117; 1959:887 [in part]; 1966b:70*; 1968b:K-8* [in part], fig. 16a.—Hoff, 1944:341*, 345*, 356*.—Hart, 1959:201*, 203*.—Momot and Gall, 1971:363.—Hobbs and Hall, 1974:202.—Hart and Hart, 1974:(21 [in part], 22, 27, 28 [in part], 86, 87, 90)*.—Burgess and Franz, 1978:161, 167.

Procambarus (Hagenides) advena.—Hobbs, 1972b:50, 150, 154 [in part].

The above is believed to be a complete bibliography of the species, and those citations marked with an asterisk contain references to the occurrence of this crayfish in Georgia.

Summary of Literature.—The first reference to this crayfish was based on a collection from Georgia containing two species (*P. (H.) pygmaeus* and *P. (H.) talpoides*) and reported by Hagen (1870) as members of *Cambarus advena*. Hobbs (1942c, 1945a), in presenting an account of the morphology of the first pleopod of North American crayfishes, depicted the first pleopod of a specimen of this species that he identified as *advena*. In 1942(b), he diagnosed the species, illustrated several of its characters, listed a number of new county records in Florida and Georgia, compared specimens from over its range, and presented a rather lengthy ecological discussion, parts of which are quoted here under "Ecological Notes." In his account of the *rogersi* Group, Hobbs (1945b) pointed out the affinities of *P. (H.) rogersi* to his *P. (H.) advena* and illustrated the first pleopod of the latter. In the key to the crayfishes of the southeastern United States (Hobbs, 1968b), the range cited for *P. (H.) advena* mistakenly encompasses that of *P. (H.) talpoides*. The blue phase of *P. (H.) advena* mentioned by Momot and Gall (1971) was observed by me in *P. (H.) talpoides*, not in *P. (H.) advena* as I informed them. Hobbs and Hall (1974) reported that in preliminary experiments conducted by Hobbs to determine the lower limits of oxygen concentration that could be tolerated by several species, this crayfish dies at concentrations of 1.3 to 2.3 mg/l as do the other species tested, but it lives for a distinctly longer time. In most of the localities for entocytherids cited by Hoff (1944) *P. (H.) talpoides* (identified by Hobbs as *P. advena*) served as host. The specific localities reported by Hart (1959) and Hart and Hart (1974) were based on collections that were listed only by counties in Hobbs (1942b). Other references contain no new data on the species.

DIAGNOSIS.—Rostrum without marginal spines. Carapace lacking cervical spine. Areola 10.1 to more than 30 (average 18.3) times as long as broad and constituting 34.8 to 39.8 (average 38.0) percent of entire length of carapace (40.7 to 45.1, average 43.1, percent of postorbital carapace length). Ventral surface of basis and ischium of third maxilliped not densely bearded. Male with mesial surface of palm of chela lacking beard but with cristiform row of 6 to 9 tubercles; hook on ischium of third pereiopod only. First pleopods of first form male asymmetrical, contiguous, and reaching coxae of second pereiopods, cephalic surface without prominent shoulder, and preapical setae usually limited to few on cephalodistal border; elongate, tapering mesial process acute to rounded distally and directed caudodistally; caphalic process very small (usually subtriangular) to vestigial, rarely absent; central projection, arising from distal surface of appendage, corneous, subtriangular, much larger than other elements (spanning half anterior-posterior diameter of distal end of shaft), and directed caudodistally; and caudal knob prominent, tumescent, but not reaching nearly so far distally as central projection. Female with chela as in male; annulus ventralis subelliptical in outline, at least as long as broad, cephalolateral elevations rather weak or absent and rarely with tubercles; first pleopod present.

HOLOTYPIC MALE, FORM I.—Body (Figure 125*c,h*) subovate, compressed laterally. Abdomen narrower than thorax (9.6 and 12.8 mm); width of carapace greater than depth at caudodorsal margin of cervical groove (12.8 and 11.9 mm). Areola 14.1 times as long as broad, with 2 punctations across narrowest part. Cephalic section of carapace 1.6 times as long as areola, length of latter 37.8 percent of total length of carapace (42.7 percent of postorbital carapace length). Rostrum excavate dorsally, with little-thickened convergent margins lacking spines or tubercles; upper surface with widely scattered punctations between submarginal rows; acumen continuous with basal portion of rostrum and reaching anteriorly to midlength of penultimate segment of antennular peduncle; subrostral ridges moderately well developed and evident in dorsal aspect for two-thirds length of rostrum. Postorbital ridges moderately strong, grooved dorsolaterally, and cephalic extremity merging subangularly with carapace but lacking tubercles or spines. Suborbital angle absent. Branchiostegal spine rudimentary. Carapace punctate dorsally and tuberculate laterally; cervical spine absent. Abdomen shorter than carapace (22.7 and 26.2 mm), pleura broadly rounded and subtruncate ventrally. Cephalic section of telson with 1 spine in right and 2 in left caudolateral corners; caudal section rounded and narrow. Uropod with short, acute prominence on both lobes of basal podomere; mesial ramus with small distolateral spiniform tubercle and acute premarginal tubercle on median ridge; lateral ramus with usual row of small spines immediately proximal to transverse suture, lateralmost larger than others. Cephalic lobe of epistome subpentagonal (Figure 125*g*), in outline, without obvious cephalomedian projection, ventral surface slightly convex and margins weakly thickened and elevated ventrally; fovea represented by broad, shallow depression, and epistomal zygoma somewhat strongly arched. Ventral surface of antennular peduncle with spine slightly distal to midlength of basal segment. Antenna almost reaching caudal margin of carapace; peduncle without spines; coxa with diameter of renal tubercle almost as great as median length of podomere. Antennal scale (Figure 125*i*) about 2.6 times as long as broad, greatest width distal to midlength, lamellar portion about 1.5 times as wide as thickened lateral part; latter terminating in strong spine. Third maxilliped with basis bearing conspicuous mesial tuft of long, stiff, simple setae; ischium with distolateral tubercle, ventral surface with submarginal lateral row of short setae, longer ones largely restricted to 2 longitudinal series lateral to crista dentata, and most of broad lateral area almost naked.

Right chela (Figure 125*k*) subovate in cross section, strongly depressed. Mesial surface of palm with cristiform row of 6 tubercles (3 with knobs at proximal base) subtended dorsolaterally by row of 5 subsquamous tubercles and similar ones scattered over dorsal surface and lateral

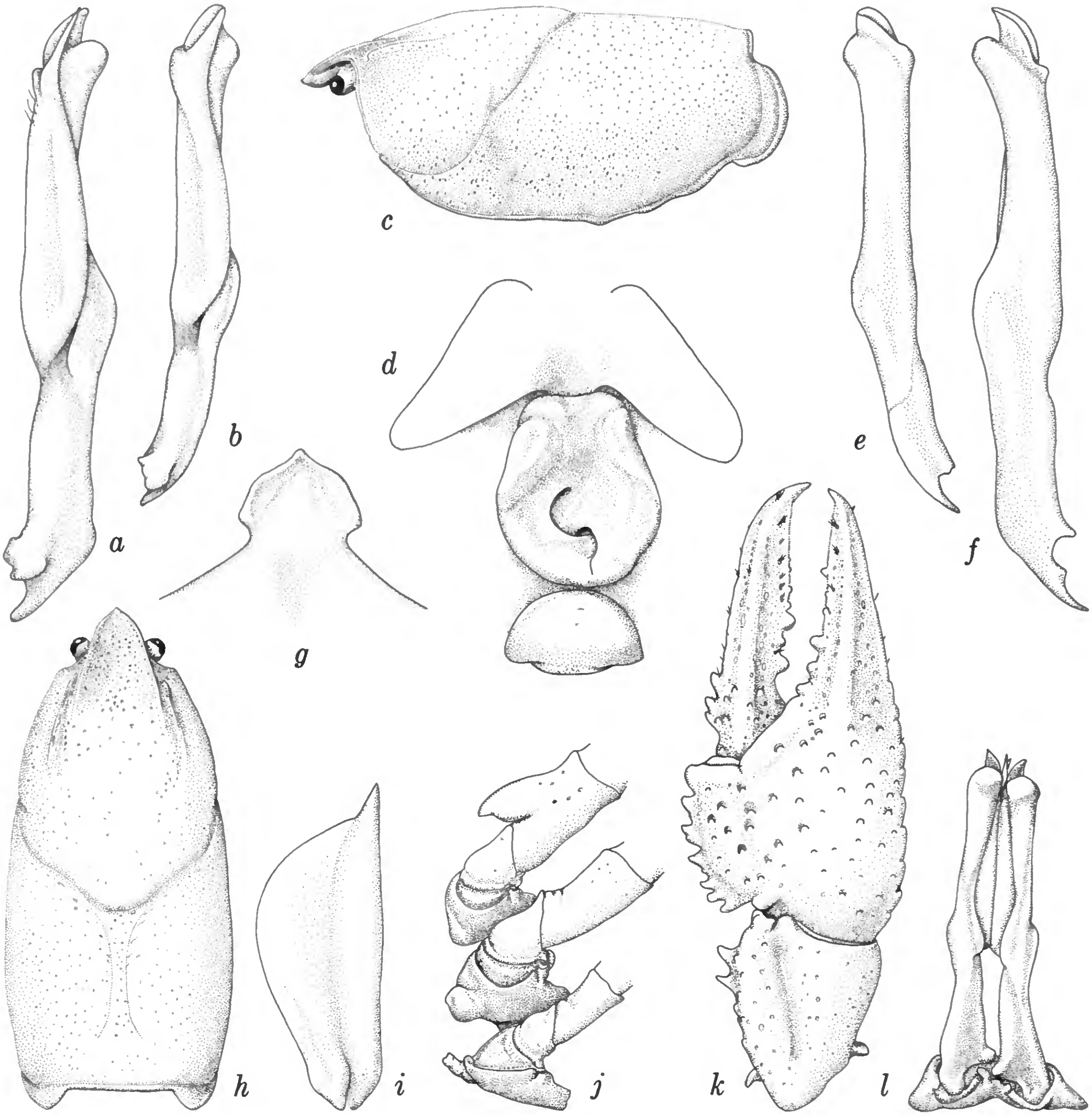


FIGURE 125.—*Procambarus (Hagenides) talpoides* (all from holotype except *b*, *e*, from morphotype, and *d*, from allotype): *a*, *b*, mesial view of first pleopod; *c*, lateral view of carapace; *d*, annulus ventralis; *e*, *f*, lateral view of first pleopod; *g*, epistome; *h*, dorsal view of carapace; *i*, antennal scale; *j*, proximal podomeres of third, fourth, and fifth pereiopods; *k*, dorsal view of distal podomeres of cheliped; *l*, caudal view of first pleopods.

margin of palm; ventral surface of palm mostly punctate with ventrolateral row of punctations, several bearing tufts of conspicuously long setae, extending from base of palm almost to tip of fixed finger; ventromedian portion of palm with scattered tubercles and very strong one opposite base of dactyl. Fixed finger with sharply defined median longitudinal ridge dorsally and less well developed one ventrally, ridge flanked proximally by squamous tubercles and by conspicuous setiferous punctations along most of its length; lateral margin of finger with row of squamous tubercles proximally, decreasing in size distally, and near midlength replaced by setiferous punctations; opposable margin of fixed finger with 5 tubercles in proximal half, third from base largest, and large tubercle on lower level at base of distal two-fifths of finger, row of minute denticles extending from between basal tubercles distally to corneous tip of finger. Dactyl with dorsal surface similar to that of fixed finger, mesial margin with 3 tubercles proximally, and ventral surface without tubercles but with setiferous punctations; opposable margin with row of 7 tubercles along proximal two-thirds of finger, first and third from base larger than remaining ones, and single row of minute denticles as on dactyl.

Carpus of right cheliped punctate dorsally, laterally, and ventrally, and tuberculate mesially; dorsal surface with shallow oblique furrow; dorsomesial margin with row of small tubercles; mesial surface with irregular row of 5 tubercles increasing in size distally; among small tubercles on ventral surface, 2 larger ones situated subterminally.

Merus with dorsal surface tuberculate, tubercles low and distal 2 spiniform; mesial and lateral surfaces mostly polished with few shallow, setiferous punctations; ventral surface with lateral row of 9 tubercles (11 on left), 3 of which flanked by long stiff setae, and mesial row of 11 (12 on left) tubercles, rows not converging distally; distolateral extremity lacking spine. Ischium with row of 3 tubercles.

Hook on ischium of third pereiopod (Figure 125*j*) only; hook simple, heavy, curved, and extending proximally over distal portion of corresponding basis. Coxa of fourth pereiopod with prominent knoblike boss disposed vertically; that of fifth, smaller, subacute, and compressed laterally.

Sternum between third, fourth, and fifth pereiopods moderately deep and bearing dense fringe of plumose setae on ventrolateral margins.

First pleopods (Figure 125*a,f,l*) as described in "Diagnosis."

Allotypic Female.—As in holotype, except for secondary sexual characters and following: rostrum almost reaching distal end of penultimate segment of antennule; subrostral ridges evident in dorsal aspect for two-fifths (right) and two-thirds (left) length of rostrum; cephalic lobe of epistome asymmetrical but similar to that of holotype and with weak cephalomedian projection; antenna reaching caudal margin of carapace; mesial margin of palm of chela with cristiform row of 8 tubercles subtended by row of 4, squamous tubercles elsewhere on palm strongly depressed and those on lateral margin of fixed finger restricted to basalmost portion; opposable margin of finger with row of 6 tubercles on right and left members, fourth and third from base largest, respectively; that of dactyl with row of 6 tubercles on right (7 on left); mesial surface of carpus with irregular row of 4 tubercles; ventral surface of merus of right and left chelipeds with 9 and 10 tubercles in lateral row and 13 and 12 in mesial row, respectively; ischium with row of 4 tubercles. (See "Measurements.")

Annulus ventralis (Figure 125*d*) only moderately deeply embedded in U-shaped sternum, subelliptical in outline, but with truncate cephalic margin, comparatively flat, and cephalolateral ridges low, with only rudiments of multiple tubercles; sinus originating almost on median line at about midlength, and, extending dextrally in semicircle, crossing median line before turning sharply in sinistral arc and then caudally, almost reaching caudal margin of annulus. Postannular sclerite as figured, almost as broad as maximum width of annulus. First pleopod reaching midlength of annulus.

MORPHOTYPIC MALE, FORM II.—Differing from holotype in following respects: rostrum subtriangular, with almost evenly convergent margins; cephalic lobe of epistome asymmetrical, resembling that of allotype; cephalic section of telson with 2 spines in each caudolateral corner; mesial margin of palm of chela with row of 8 tubercles on right (9 on left); opposable margin of dactyl with 5 tubercles; mesial surface of carpus with row of 3; ventral surface of merus with lateral row of 12 tubercles on right cheliped and mesial one of 10; ischium with row of 3 tubercles; ischium of third pereiopod with hook tuberculiform; bosses on coxae of fourth and fifth pereiopods greatly reduced in size. (See "Measurements.")

First pleopod (Figure 125*b,e*) with cephalic process and caudal knob poorly differentiated.

COLOR NOTES (Figure 118 *d,e*).—Cephalic section of carapace with dorsomedian area dark brown, flanked by steel blue areas covering much of rostrum, postorbital ridges, lateral gastric, dorsal hepatic, and mandibular adductor regions; posterior orbital and most of hepatic regions bluish brown with cream tubercles; branchiostegites dark brown and areola almost black; caudal ridge and flange also almost black. Abdominal terga and pleura olive brown, with caudal margins edged in very dark brown; pleura delimited from terga basally by faint shallowly scalloped line. Telson and uropods mostly olive, former with lateral fourths of cephalic section darker than median half; lateral half of mesial ramus of uropod and median keel on lateral ramus similarly dark. Antennular and antennal peduncle pinkish tan mottled in steel blue, flagella very pale, ringed in olive. Antennal scale also pinkish tan to cream with blue lateral margins. Chelipeds largely steel blue dorsally from distal two-thirds of merus through carpus; oblique furrow on latter and tips of tubercles on both pinkish cream (some tubercles white tipped); palm and lateral half of fixed finger pale pinkish tan with steel blue tubercles; dactyl and mesial half of fixed finger blue, both with yellowish tips; tubercles on opposable margins of fingers white. (Pinkish background studded with blue tubercles rendering lavender cast to chelae). Remaining periopods with basal podomeres through ischium cream, otherwise pale lavender, and distal parts of merus and carpus darker than other areas. Ventral surface of body with pinkish lavender suffusion. Eggs cream to burgundy in color.

Some individuals with cobalt blue suffusing entire carapace, abdomen, and chelipeds, thus entire animal more distinctly blue than lavender. In most individuals, both carapace and abdomen marked with dark spots, and in some individuals (Figure 118*e*), narrow, pale, median longitudinal stripe extending caudally from midgastric region across sixth abdominal tergum.

Measurements (mm)

	Holotype	*Allotype*	*Morphotype*
Carapace			
Height	11.9	15.1	9.4
Width	12.8	15.8	10.3
Entire length	26.2	31.9	20.0
Postorbital length	23.2	28.2	17.6
Areola			
Width	0.7	0.7	0.5
Length	9.9	12.3	7.5
Rostrum			
Width	4.1	5.4	3.1
Length	4.0	5.2	3.3
Chela			
Length of mesial margin of palm	5.8	6.5	3.9
Width of palm	8.5	10.4	5.7
Length of lateral margin	17.0	19.5	11.2
Length of dactyl	11.2	13.1	5.9
Abdomen			
Width	9.5	12.0	7.4
Length	24.0	30.7	19.2

TYPES.—The holotypic male, form I, allotypic female, and morphotypic male, form II, are deposited in the National Museum of Natural History, Smithsonian Institution, numbers 115002, 115018, and 133347, respectively, as are the paratypes (limited to specimens from Alachua County, Florida): 8♂I, 6♂II, 14♀, and 5j♂.

TYPE-LOCALITY.—Burrows along Hogtown Creek just southwest of the junction of 13th (U.S.

Highway 441) and Boundary streets in Gainesville, Alachua County, Florida.

RANGE.—Coastal Plain Province from the Satilla River system westward to Tift County, Georgia, and southward to Thomas County, Georgia, and Alachua and Putnam counties, Florida. In Georgia it occurs in the Tifton Upland, Bacon Terraces, Okefenokee Basin, and Barrier Island Sequence districts, between the Ocmulgee-Altamaha and Flint rivers.

SPECIMENS EXAMINED.—I have examined a total of 421 specimens (69 from Florida, 352 from Georgia) from 92 localities in the following states and counties (numbers of localities in parentheses). FLORIDA: Alachua (2), Clay (3), Duval (2), Nassau (4), Putnam (1). GEORGIA (Figure 120): Atkinson (5), Bacon (6), Ben Hill (1), Berrien (4), Brantley (3), Brooks (1), Camden (1), Charlton (3), Clinch (3), Coffee (7), Colquitt (3), Cook (1), Crisp (1), Dooly (1), Echols (1), Glynn (1), Irwin (6), Lanier (2), Lowndes (2), Pierce (4), Thomas (1), Tift (4), Turner (3), Ware (8), Wayne (5), Wilcox (2), and Worth (1).

VARIATIONS.—Uncertain as to the range and limits of variation of LeConte's *Astacus advena*, in treating the crayfishes of Florida (1942b), I assigned specimens of the crayfish described here to that species. Not until 1945, when I collected a first form male from the area of the LeConte Plantation in Liberty County, Georgia, could any assessment of his species be made, and the acquisition of more material was mandatory to determine its range. Even now, *P. (H.) advena* and its allies are poorly represented in collections. On the bases of my present understanding of the *advena* Group, most of the previous observations made on variations (Hobbs, 1942b:76–77) are applicable to *P. (H.) talpoides* rather than to *P. (H.) advena*, although the specimens from Appling County are herein assigned to *P. (H.) caritus*.

Most of the few variations that have been noted seem to be sporadic ones involving slight differences in sizes and numbers of tubercles on the various podomeres of the cheliped, none correlated with a restricted part of the range. There appears to be a trend, although far from absolute, toward a narrower areola in populations along the eastern part of the range, and in one specimen from Putnam County the areola is linear along much of its length; however, collected with this crayfish was another in which the areola was 24 times as long as broad. In specimens from and in the vicinity of the type-locality, the areola ranges from 8.9 to 17.4 times as long as broad. Nowhere else have representatives been encountered with broader areolae. Variations in the first pleopod of first form males from different parts of the range are illustrated in Figure 126. Most distinctive among them is Figure 126*a*, depicting the pleopod of the single male available from Thomas County, Georgia. This is the only male assigned to the species that lacks a trace of the cephalic process on the pleopod. The annuli ventrales are highly variable, and the greatest differences in them occur in the degree of development of the cephalolateral regions. In most specimens from Florida and adjacent parts of Georgia, these areas are flattened or rather low, but in the upper Suwannee and in the Satilla basins, they are somewhat elevated and in some individuals also weakly tuberculate, approaching the type of annulus characteristic of the closely allied *P. (H.) caritus*.

SIZE.—The largest specimen available is an ovigerous female from Ware County, Georgia, with a carapace length of 39.9 (postorbital carapace length, 35.6) mm. The corresponding lengths of the smallest and largest first form males are 22.5 (20.0) mm, and 33.1 (29.2) mm, respectively, and that of the smallest female carrying eggs or young, 26.3 (22.9) mm.

LIFE HISTORY NOTES.—Fifty-two first form males are available (4 second form males molted to first form in the laboratory) from throughout the range of the species; these were collected in February, March, April, May, October, and December. Ovigerous females were found in March, April, and October, and females carrying young in March, May, and October. Several of the ovigerous females were maintained alive in the laboratory, and the numbers of eggs carried by them are not known, but the numbers borne by the others are shown in Figure 127. The diameter of the eggs ranges from 1.8 to 2.1 mm.

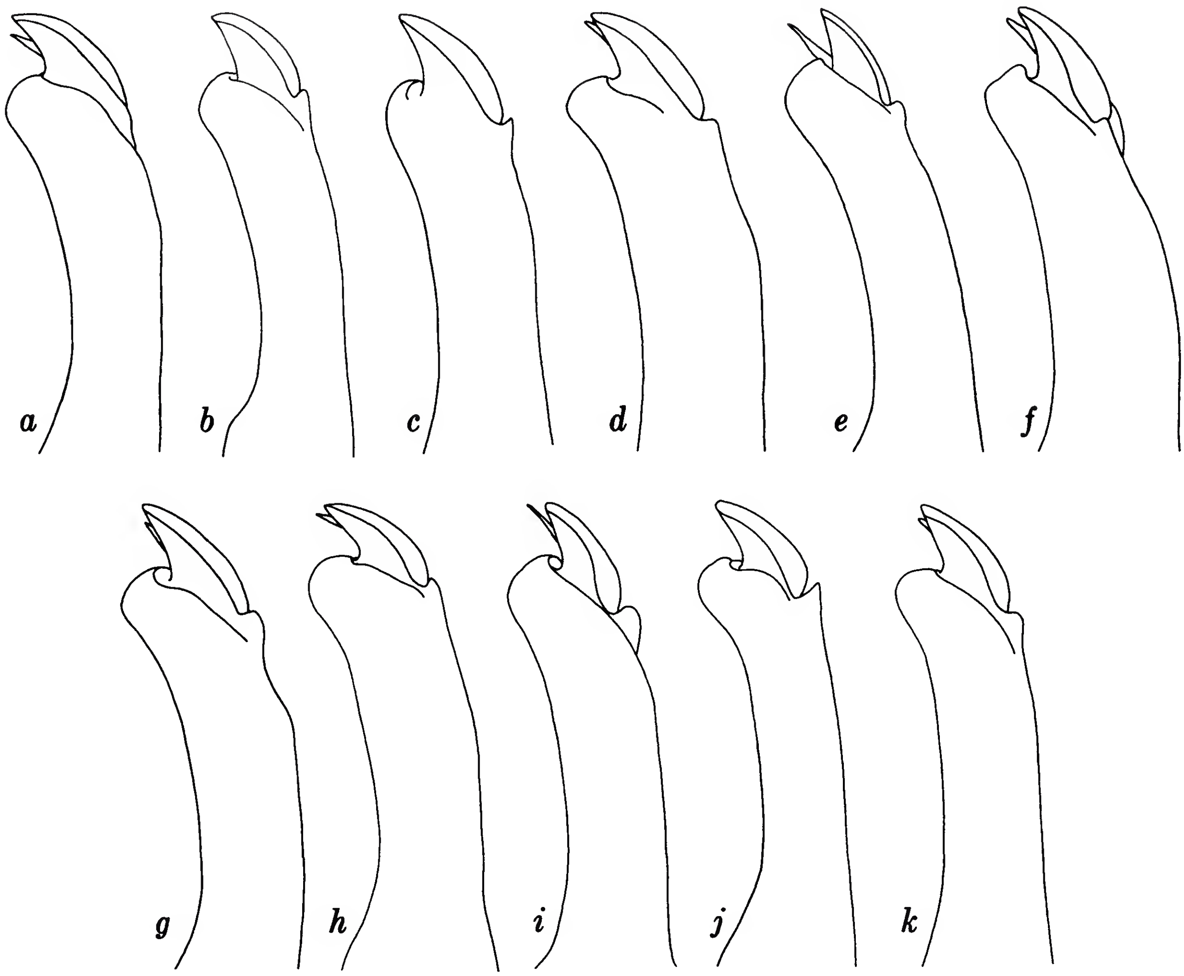


FIGURE 126.—*Procambarus (H.) talpoides*, variations in left first pleopod (lateral view) of male, form I. Ochlockonee Basin: *a*, Thomas Co. Suwannee Basin: *b*, Worth Co; *c*, Ben Hill Co; *d*, Cook Co; *g*, *h*, Lowndes Co. Satilla Basin: *e*, Glynn Co; *f*, Pierce Co; *i*, Brantley Co. Saint Johns Basin (Florida): *j*, *k*, Clay Co.

Seasonal Data (Florida and Georgia)

Sex/stage	*J*	*F*	*M*	*A*	*M*	*J*	*J*	*A*	*S*	*O*	*N*	*D*	*?*
♂I		1	9	27	2					4		4	1
♂II		1	9	45	14	3		2	4	18		3	2
♀			23	57	18	6	1	1	5	18	2	5	1
♂j			13	21	2	3			1	1	5		
♀j			3	40	5					2	2		
♀ ovig			4	28						1			
♀ with young			1		1					1			

ECOLOGICAL NOTES.—The burrows of this crayfish were described by Hobbs (1942b:78-79) as being

. . . beautifully constructed and, though rambling, are very elaborate with numerous galleries. They are made either in some plastic soil or in sand underlain by plastic material, and in the latter case the passage through the upper sand is plastered with mud brought from the deeper part of the burrow. Usually there are several large chambers, some that are interspersed along the runways and others

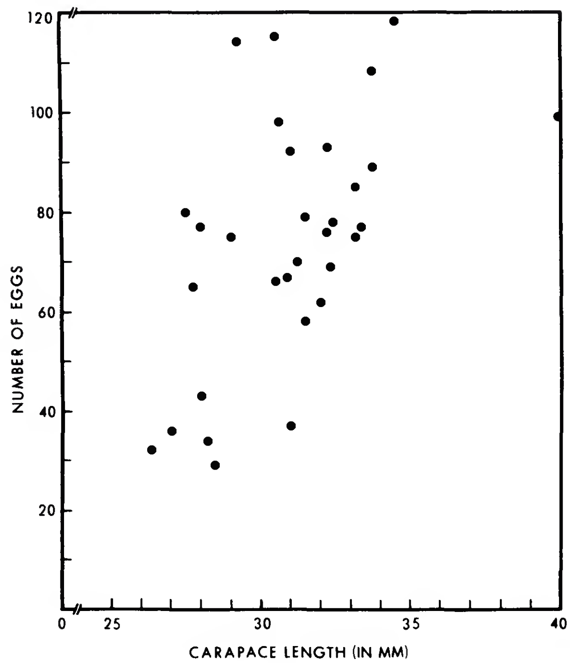


FIGURE 127.—*Procambarus (H.) talpoides*, number of eggs borne by ovigerous females.

placed at the terminals of the several passages. It is not uncommon to find a chamber with three or four passages leading away from it. In every burrow there is at least one passage which spirals downward a few inches to two or three feet to a "cellar" below the water table. This passage is usually near one of the chimneys of the ramifying structure. I have often found nuts, large pebbles, grass, and sticks in the passages and chambers.

The chimneys of these burrows are always carefully constructed and in their excellent masonry often approach the chimneys of *C. diogenes*. I have seen them extending five or six inches above the ground level and consisting of neatly formed, round pellets about five-sixteenths of an inch in diameter. Often a single crayfish will construct three or four of these chimneys from its single complex of passageways . . . [that extend for as much as] six to eight feet horizontally . . . .

A single soil class does not seem to determine the distribution of the species, for I have found it in clay, sandy clay (so hard that it felt like sandstone to my hands), sandy muck, loam, and even in seepage areas in which a black soil was predominant. Available subsurface groundwater seems to be a *sine qua non* in determining the distribution; streams and permanent open bodies of water seem to be as barren of this species as do the "Black-jack" ridges. Specimens are sometimes frequent along creeks but are confined to seepage areas well above the normal stream level. The water table in most of the localities I have collected is probably variable, and at times may cover the mouth of the burrows. In some localities where this is obviously the case, the groundwater in dry seasons may descend more than two feet below the surface.

Although *P. advena* [= *P. (H.) talpoides*] occurs chiefly in the flatwoods, it cannot be regarded as a typical flatwoods species: it is apparently just as successful in seepage areas along small streams in a region of high pine and rolling hammock lands.

These observations were based largely upon colonies of this crayfish in the northeastern part of Florida, but for the most part they are applicable to the species in Georgia as well. The chimneys are by no means always neatly constructed, and, in general, there are fewer chimneys marking a burrow housing a male than those inhabited by a female. In most instances I have endeavored to unearth the crayfish from burrows marked by chimneys that show evidence of recent work by the crayfish. Perhaps such a selection is the cause of my obtaining a disproportionately larger number of females than one might expect. It seems probable to me that the female of the species is a far more industrious digger than is the male. If this is true, one is tempted to conclude that these crayfish do have a home burrow to which they return following an assumed foray above the surface, although I do not recall ever having seen an adult individual outside of its lair.

In apparent contrast, G. K. Williamson collected a first form male, a second form male, and five juveniles of *P. (H.) talpoides* from Buffalo Creek, Brantley County, Georgia. When I received the specimens I immediately asked whether or not the stream was at flood stage when he collected them. Although the water was not high, he stated that the specimens had been obtained by "netting under logs and in shallow pools," and I suspect that the two adults, at least, were routed from beneath overturned logs at the water's edge. Oftentime, this crayfish, in constructing a tunnel complex, will utilize a felled log as the ceiling of one or more of the galleries.

Like other burrowing crayfishes, *P. (H.) talpoides* frequently "plugs" its tunnels from below, occasionally filling one or even all of the horizontal passageways near the surface. If the subsoil is similar in texture and color to that near the surface, the old runways are not discernible; frequently I have attempted to excavate a burrow marked by one to three chimneys only to discover that the passages to all of them had been filled and I failed to find the open gallery currently occupied by the crayfish. Never have I found two adult individuals sharing a single burrow.

In contrast to observations on *P. (H.) advena* (see above), Hobbs (1942b:79) indicated that

> almost any sort of commotion at the mouth of the burrow seems to attract [this crayfish] to the surface of the water. Recently I have found that in most instances, particularly in dry weather, when the burrow is disturbed the crayfish either retreats into the deep chamber or was already there. If the passage to this chamber is located, the water thoroughly agitated, and then allowed to remain still, the crayfish usually climbs up the passage to the surface of the water.

In collecting specimens in Georgia, awaiting the appearance of the crayfish at the surface of water in the burrow is often futile, and almost all of the specimens I have were obtained by dissecting the various runways until the animal was found.

RELATIONSHIPS.—*Procambarus (H.) talpoides* has its closest affinities with *P. (H.) advena* and *P. (H.) caritus.* Not only are there marked similarities in their morphology, but the three seem to be ecological equivalents in their respective ranges. The chief differences in them seem to be in the secondary sexual characters that are most distinct in the first pleopod of the first form male and, to a lesser degree, in the annulus ventralis. The central projection of the first pleopod is proportionately much larger and extends farther distally beyond the more tumescent caudal knob in *P. (H.) advena* and *P. (H.) talpoides* than it does in *P. (H.) caritus.* The cephalic process is much better developed in *P. (H.) advena* than is its vestigial (rarely absent) homologue in *P. (H.) talpoides.* The annulus ventralis of *P. (H.) talpoides*, in general, has comparatively low, often flattened cephalolateral walls flanking the central depression, whereas in the other two the walls are typically strongly elevated, and in *P. (H.) caritus* usually strikingly tuberculate.

CRAYFISH ASSOCIATES.—In Florida it was found with the following species: *P. (L.) pubischelae pubischelae*, *P. (O.) seminolae*, and *P. (S.) paeninsulanus.* In Georgia, the following crayfishes were collected from burrows, streams, or pools within a few meters of the burrows of *P. (H.) talpoides* (the number of times they were found together is noted in parentheses): *Faxonella clypeata* (3), *Procambarus (H.) caritus* (2), *P. (H.) pygmaeus* (1), *P. (L.) pubischelae deficiens* (5), *P. (L.) p. pubischelae* (17), *P. (O.) seminolae* (26), *P. (Pe.) spiculifer* (1), and *P. (S.) paeninsulanus* (3).

ETYMOLOGY.—From the Latin *talpa* (mole) in combination with *oides* (like), alluding to the extensive horizontal burrows constructed by this crayfish.

The *truculentus* Group

Procambarus (Hagenides) truculentus Hobbs

FIGURES 17*b*, 118*f*, 120, 128, 129, 239

Procambarus truculentus Hobbs, 1954:111–118, figs. 1–13; 1959: 887; 1968b:K-11, fig. 16h.—Hart and Hart, 1974:21, 90.
Procambarus (Hagenides) truculentus.—Hobbs, 1972a:7; 1972b: 49, 152, 154, figs. 5i, 41c; 1974b:49, fig. 201.—Hobbs III, Thorp, and Anderson, 1976:3, 12, 29–31, fig. 12.

These citations are believed to constitute a complete bibliography of the species, and all of the articles refer to its occurrence in Georgia.

SUMMARY OF LITERATURE.—This crayfish was first collected in 1934, but not until 20 years later was it described and reported from five localities in Bulloch, Emanuel, and Jenkins counties, Georgia. No additional information was added to our knowledge of the species until Hart and Hart (1974) reported its occurrence in Treutlen County, where it served as a host to two entocytherid ostracods: *Ankylocythere ancyla* and *Entocythere internotalus.* The account of the species presented by Hobbs III, Thorp, and Anderson (1976) contains no new data and was largely extracted from the information presented with the original description.

DIAGNOSIS.—Rostrum without marginal spines or tubercles. Carapace lacking cervical spines. Areola 8.8 to 16 (average 13.0) times as long as broad and constituting 36.0 to 38.7 (average 37.3) percent of entire length of carapace (41.1 to 44.2,

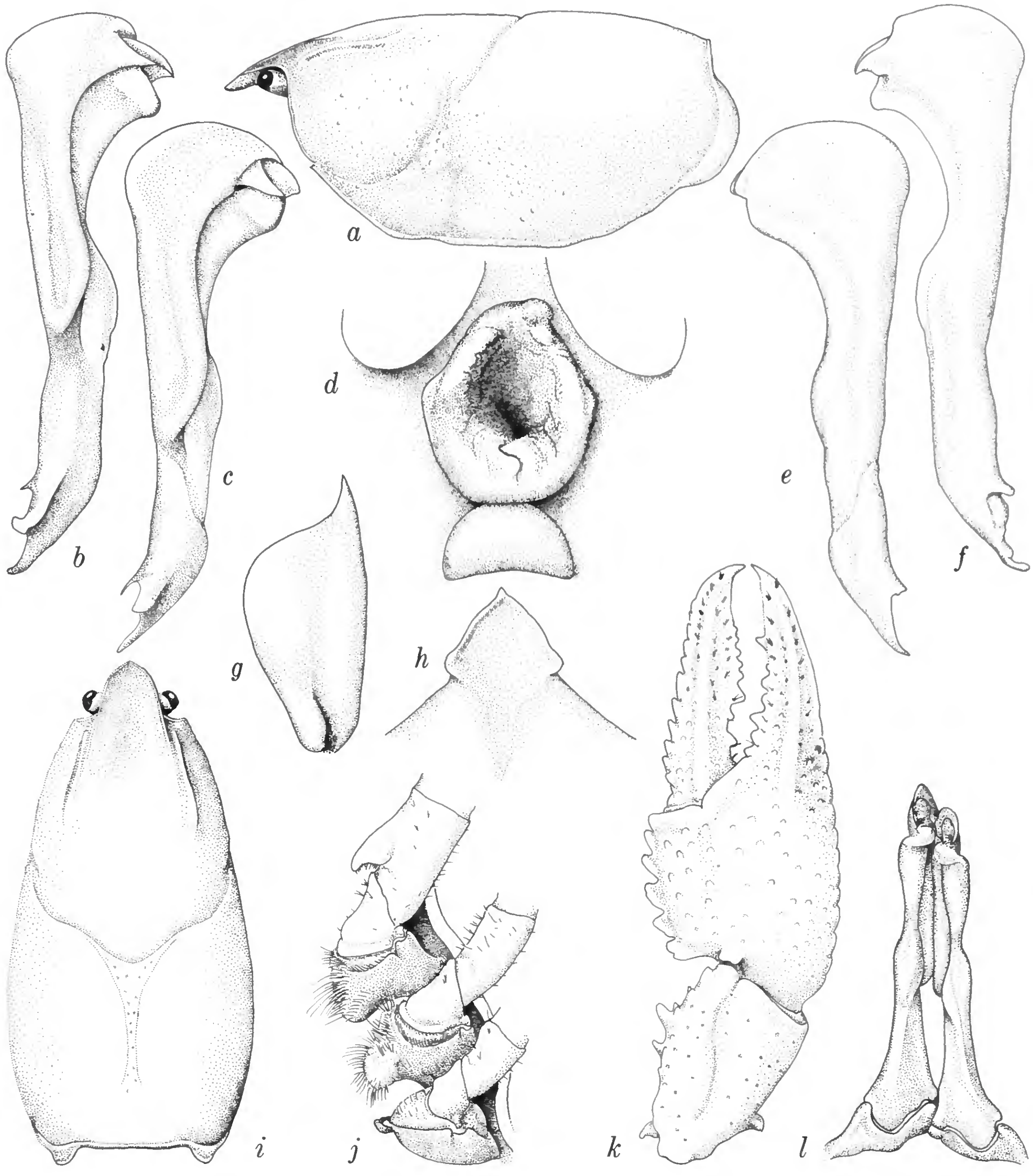


FIGURE 128.—*Procambarus (Hagenides) truculentus* (all from holotype except *c*, *e*, from morphotype, and *d*, from allotype): *a*, lateral view of carapace; *b*, *c*, mesial view of first pleopod; *d*, annulus ventralis; *e*, *f*, lateral view of first pleopod; *g*, antennal scale; *h*, epistome; *i*, dorsal view of carapace; *j*, proximal podomeres of third, fourth, and fifth pereiopods; *k*, dorsal view of distal podomeres of cheliped; *l*, caudal view of first pleopods.

average 42.6, percent of postorbital carapace length). Ventral surface of basis and ischium of third maxilliped not densely bearded. Male with mesial surface of palm of chela lacking beard but bearing cristiform row of tubercles; hook on ischium of third pereiopod only; coxa of fourth pereiopod with caudomesial boss. First pleopods of first form male asymmetrical, contiguous, and reaching coxae of second pereiopods, cephalic surface without shoulder or preapical setae; mesial process acute, directed caudally and usually entirely obscured in lateral aspect by central projection; cephalic process absent; central projection, also caudally directed, corneous, beaklike, and arising from caudal surface of expanded distal part of appendage; caudal knob, flanking proximocaudal base of central projection, variable in shape but always somewhat inflated. Female with chela as in male; annulus ventralis subcircular to elliptical in outline, very deeply embedded in sternum, and cephalolateral elevations lacking well-developed tubercles; first pleopod present.

COLOR NOTES (Figure 118*f*).—Ground color of carapace grayish tan to dark brown; cephalic section lighter than thoracic region, latter suffused with dark green and fading ventrally through bluish or mauve gray to pale gray or buff along ventral margin. Cervical groove, margins of rostrum, and postorbital ridges bluish green. Abdomen grayish buff to brown, with nondescript markings in cream and dark gray or brown; pleura pale mauve to tan, with or without light greenish gray line along base; telson and uropods with lateral parts and tips like pleura, otherwise colorless, with grayish green to brown splotches. Ground color of chelae and pereiopods buff to pale pinkish tan and bearing greenish blue to dark brown markings (particularly dorsally flanking articulations); tubercles on chela bluish green to purplish black, same color on dorsal surface of dactyl and on dorsomesial half of fixed finger; tubercles on mesial surface of palm dark basally but with cream to pinkish cream tips; lateral and ventral areas of chela light orange buff with pink suffusion; tubercles on opposable margins of fingers cream. Remaining pereiopods pinkish cream or greenish gray, with color intensified on dorsal surfaces of merus and carpus. Ventral part of body pinkish to bluish cream, with pale tan to gray setae.

TYPES.—Holotype, allotype, and morphotype, USNM 95670, 95671, 97672 (♂I, ♀, ♂II); paratypes, MCZ, TU, USNM.

TYPE-LOCALITY.—Seepage area 11 miles north of Lyons on U.S. Highway 1, Emanuel County, Georgia.

RANGE.—The Vidalia Upland District of Georgia, between the Oconee and Ogeechee rivers. There is one first form male in the Smithsonian collection with a questionable label "South Carolina," but other locality data are lacking.

GEORGIA SPECIMENS EXAMINED.—I have examined a total of 48 specimens from the following localities. *Bulloch County*: (1) 14.2 mi S of Millen on US Hwy 25, 1♂II(molted to form I in laboratory in October), 2♂II, 3♀, 17 Apr 1944, HHH, collector. *Candler County*: (2) adjacent to Wolfe Creek, about 6 mi S of Metter on St Rte 129, 1♀, 30 May 1969, E. T. Hall, Jr., HHH. *Emanuel County*: (3) type-locality, 1♂II, 6♀, 23 Aug 1937, HHH; 3♀, 9 Jun 1940, HHH; 6♀, 7 juv, 18 May 1941, G. B. Hobbs, HHH; 3♀, 25 May 1941, GBH, HHH: 1♂II(molted to form I in laboratory in November), Aug 1941, HHH; (4) 6.8 mi S of Swainsboro on US Hwy 1, 2j♂, 2j♀, 15 Jun 1934, J. S. Rogers, R. E. Bellamy, HHH; (5) 5.5 mi NE of Swainsboro on St Rte 56, 1♂II, 1♀, 4 May 1945, HHH; (6) 11 mi N of St Rte 292 on US Hwy 1, 1♂I, 20 Apr 1977, C. E. Carter, J. E. Pugh, HHH. *Jenkins County*: (7) 9.2 mi S of Millen on US Hwy 25, 1♂II, 1♀, 27 Mar 1939, H. H. Wallace, HHH. *Laurens County*: (8) 14.5 mi SE of East Dublin on St Rte 29, 1j♀, 22 Apr 1966, ETH, HHH. *Treutlen County*: (9) 19.5 mi SE of Dublin on St Rte 29 (Hart and Hart, 1974:21, 90), 1♂I, 1♀, 1 ovig ♀, 22 Apr 1966, ETH, HHH. *Washington County*: (10) 7.3 mi N of Johnson Co line on St Rte 15, 1♂II, 26 Apr 1966, ETH, HHH.

VARIATIONS.—Most of the variations noted are in the number of spines and tubercles on the chelipeds—7 to 10 occur in the cristiform row along the mesial margin of the palm. The basal segment of the antennule may or may not bear a spine on the ventral surface. The variations observed in the first pleopod of the first form male are illustrated in Figure 129. The cephalolateral ridges of the annulus ventralis may or may not bear weak tubercles, and in some specimens they end abruptly in a single tuberculiform prominence; the area covered by the median excavation

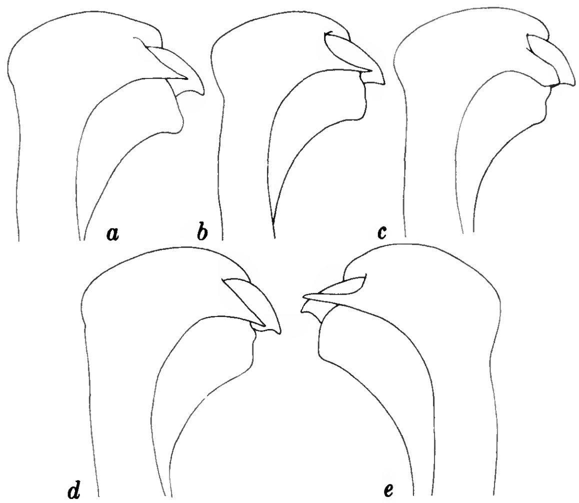


FIGURE 129.—*Procambarus (H.) truculentus*, variations in distal part of first pleopod of male, form I: *a*, holotype; *b*, Emanuel Co; *c*, Bulloch Co; *d*, South Carolina (?); *e*, Treutlen Co.

of the annulus is quite variable. Too few specimens are available, except from the type-locality, where there is considerable diversity, to detemine the extent of individual differences within members of the several known local populations.

SIZE.—The largest specimen available is a female having a carapace length of 34.6 (postorbital carapace length, 31.1) mm. The corresponding lengths of the smallest and largest first form males are 28.4 (25.2) mm and 32.0 (28.3) mm, respectively, and of the only known ovigerous female, 26.6 (23.2) mm.

LIFE HISTORY NOTES.—Of the five known first form males, the collecting date of that from South Carolina is not known; two were obtained in April, and the other two, collected in April and August as second form males, molted in the laboratory to first form in October and November, respectively. A single ovigerous female (carapace length 26.6 mm), bearing 30 eggs, each with a 2.1 mm diameter, was dug from a burrow in April. On

May [18, 1941] more than a dozen burrows were examined, and all of them contained females with young approximately 10 mm in length (from tip of rostrum to tip of telson). [Seven young that were preserved have carapace lengths of 4.9 to 6.1 mm. Four juveniles collected on 15 June 1934 have carapace lengths of 6.3 and 7.9 mm.] At this time no males could be found (Hobbs, 1954:117).

Seasonal Data

Sex/stage	*J*	*F*	*M*	*A*	*M**	*J*	*J*	*A*	*S*	*O*	*N*	*D*	*?*
♂I				2									1
♂II			1	3	1			2					
♀			1	4	10		4	6					
♂j							2						
♀j				1			2						
♀ ovig				1									

* + 7 juveniles.

ECOLOGICAL NOTES.—*Procambarus (H.) truculentus*, like most of the members of the subgenus *Hagenides*, frequently occurs in colonies in which each member constructs its own burrow, consisting of a branching system of galleries with two or more openings to the outside and at least one passageway that penetrates the water table.

Unlike some of the more astute burrowing species, *P. truculentus* may be attracted to the surface of the water in the burrow thus obviating the necessity for laborious digging. Most of my specimens were collected by opening the mouth of a burrow with a spade and vigorously roiling the water. After this was done other burrows were similarly opened. After a number of them had been so treated . . . the crayfish were often seen at the surface of the water, lying in a horizontal position with one of the branchiostegites exposed, and thus relatively easily caught with the hand . . . .

The soil in the localities from which most of the specimens were taken is a black muck, and supports a dense growth of wire grasses, pitcher plants, and other bog-inhabiting plants. The water table fluctuates from the surface to about two feet below it (Hobbs, 1954:117).

GEORGIA CRAYFISH ASSOCIATES.—Collected from burrows adjacent to those of this crayfish (the number of times they were found together is noted in parentheses) was *Procambarus (L.) barbatus* (3), and from streams within a few meters away were *Faxonella clypeata* (2), *P. (O.) enoplosternum* (2), and *P. (O.) litosternum* (1).

Subgenus *Leconticambarus*

Subgenus *Cambarus*.—Ortmann, 1905a:97 [in part; not Erichson, 1846:97].

Subgenus *Ortmannicus* Fowler, 1912:241 [in part].

Subgenus *Ortmanmanicus*.—Hobbs, 1942a:342 [in part; erroneous spelling].
Subgenus *Leconticambarus* Hobbs, 1972a:7 [type-species, *Cambarus barbatus* Faxon, 1890:621].

DIAGNOSIS.—Body with or without pigment; eyes well developed but pigmented area in Floridian troglobitic *P. (L.) milleri* Hobbs (1971a:115) much reduced. Rostrum with or without (Georgia members) marginal spines or tubercles, lacking median carina. Carapace with or without cervical spine or tubercle. Areola 2.5 to 13 times as long as broad and constituting 27 to 36 percent of entire length of carapace. Ventral surface of ischium of third maxilliped obscured by dense mat of long plumose setae. First 3 pairs of pereiopods without conspicuous brush of setae extending from basis to merus. Palm of chela with small subsquamous to squamous tubercles, those on mesial surface frequently obscured in first form male by conspicuous mat of plumose setae. Usually simple, occasionally bituberculate, hooks present on ischia of third or third and fourth pereiopods. Coxa of fourth pereiopod usually with well-developed, occasionally weak (rarely absent), caudomesial boss. First pleopods of first form male reaching coxae of third, rarely second, pereiopods, asymmetrical, with or without proximomedian lobe, and often (Georgia members) with proximomesial spur; setae along cephalodistal margin in sloping row or in cluster situated distinctly cephalic to central projection; terminal elements consisting of caudodistally to cephalodistally directed slender or massive mesial process, small rounded to acute cephalomesially situated cephalic process, prominent caudal knob or process, and usually small dentiform central projection. Mesial ramus of uropod with distomedian spine acute or reduced to tubercle but never extending beyond distal margin of ramus. Female with annulus ventralis comparatively narrow, only slightly wider than postannular sclerite except in *P. barbatus*, in which cephalolateral portions expanded in flared tuberculate prominences; first pleopod present. (Modified from Hobbs, 1972a.)

RANGE.—From the Perdido and Escambia

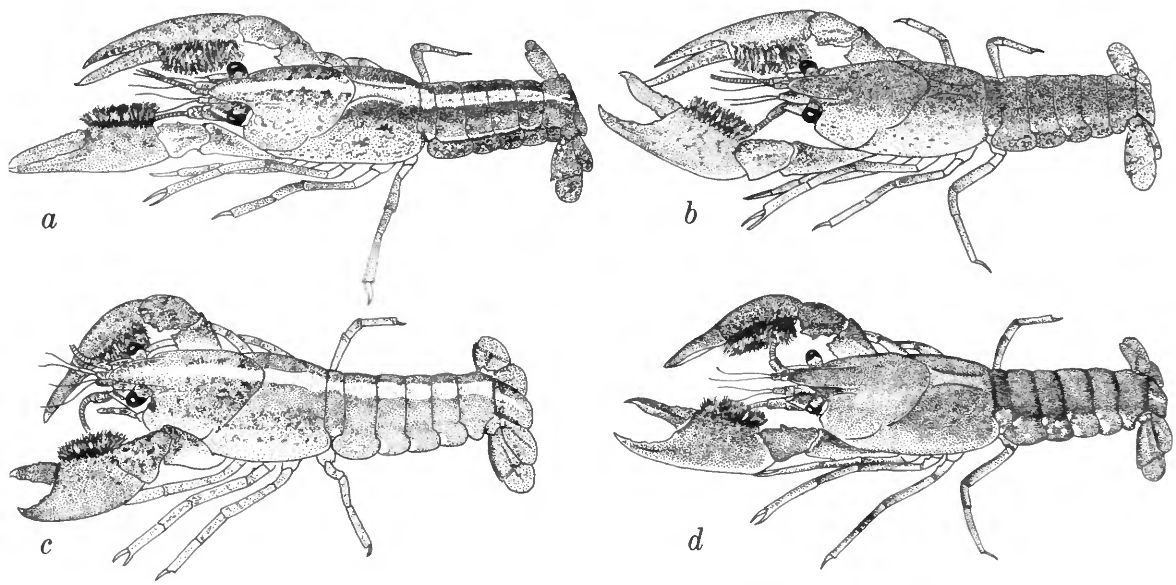


FIGURE 130.—Color patterns in members of subgenus *Leconticambarus*: *a*, *b*, *Procambarus (L.) barbatus* from 4.9 mi SE of Eulonia on St Rte 99, McIntosh Co; *c*, *P. (L.) pubischelae pubischelae* from 2.1 mi NW of St Rte 158 on Rte 82, Ware Co; *d*, *P. (L.) pubischelae pubischelae* from 4.8 mi E of Florida line on St Rte 94, Charlton Co.

river basins in Alabama and Florida eastward to the Coosawhatchie-Broad drainage system in South Carolina and southward throughout the panhandle and peninsular Florida. In Georgia, it occurs between the Suwannee and Savannah watersheds from the Tifton Upland and Vidalia Upland districts eastward to the Atlantic Ocean.

SPECIES OCCURRING IN GEORGIA.—Of the 14 species and subspecies assigned to this subgenus, *Procambarus (L.) barbatus*, *P. (L.) pubischelae deficiens*, and *P. (L.) pubischelae pubischelae* occur in Georgia.

HABITAT.—Like all except two members of the subgenus (*P. (L.) alleni* (Faxon, 1884:110) and *P. (L.) milleri* Hobbs), the three Georgia representatives are secondary burrowers, largely confined to temporary bodies of water, and thus spending much of their lives in simple burrows. Those individuals living on seepage slopes seldom leave their underground passageways. Occasional specimens have been found in sluggish lotic habitats, usually in dense submergent or emergent vegetation.

Key to Georgia Members of Subgenus *Leconticambarus*

1. Male with cephalodistal part of first pleopod sloping from base of central projection; female with cephalolateral parts of annulus ventralis produced in prominent, tuberculate, winglike projections, and decidedly broader anteriorly than posteriorly .... **barbatus**

   Male with cephalodistal part of first pleopod truncate to convex; female with annulus ventralis never produced in prominent projections, and never broader anteriorly than posteriorly 2

2. Male with hooks on ischia of third and fourth pereiopods and with prominent boss on coxa of fourth; female with annulus ventralis bearing tubercles laterally (or cephalolaterally) or with paired sublongitudinal ridges (Note: Intergrade populations may lack one or more of these characters.) .... ***pubischelae pubischelae***

   Male with hooks limited to ischium of third pereiopod and always lacking boss on coxa of fourth pereiopod; female with annulus ventralis lacking tubercles and sublongitudinal ridges .... ***pubischelae deficiens***

Procambarus (Leconticambarus) barbatus (Faxon)

FIGURES 18*b*, 130*a*, *b*, 131, 132, 240

Astacus penicillatus LeConte, 1856:401*.—Hagen, 1870:16.—Faxon, 1890:621; 1914:414*.—Hobbs, 1972a:2*; 1974b: 50 [not *Astacus penicillatus*, Olivier, 1791].

Cambarus penicillatus.—Hagen, 1870:31(?), 53, 54* [in part], 55 (?), 97* [in part], 107* [in part], pl I: figs. 93, 94 [not figs. 95, 96 = *P. (O.) ancylus* Hobbs, 1958b:164].—Faxon, 1884:138*[in part: not Mississippi and South Carolina]; 1885a:36-38* [in part], 158*, 167* [in part], 173* [in part], [not 168].—Underwood, 1886:371* [in part].—Ortmann, 1902:277.—Harris, 1903a:72, 118.—Hobbs, 1942b: 39, 40*; 1972a:2.

Cambarus barbatus Faxon, 1890:621 [in part: not specimens from Escambia River (= *P. (L.) escambiensis* Hobbs, 1942b:46)]; 1914:367, 370, 414*.—Hay, 1899b:959*, 964.—Harris, 1903a:58* [in part], 72* [in part], 118, 137 [in part], 138, 150 [in part], 152*, 154 (?).—Wolf, 1934: 104 [name only; probably error for *Cambarus (Erebicambarus) laevis* Faxon (1914:391) in Indiana and for *C. (E.) tenebrosus* Hay (1902b:232) in Kentucky].—Hobbs, 1940a: 389, 410, 414, 418; 1940b:3; 1942c: pl. II: figs. 2, 3; 1962: 273; 1972a:2; 1974b:50.

Cambarus (Cambarus) barbatus.—Ortmann, 1905a:102, 105*; 1906a:18.

Cambarus (Ortmannicus) barbatus.—Fowler, 1912:341 [by implication].

(?)*Astacus barbatus*.—Wolf, 1934:104 [name only].

Procambarus barbatus.—Hobbs, 1942a:340, figs. 6, 9; 1942b: 34*, 35-42*, 44*, 48, 54, 70, 108, 109, pl. II: figs. 1-5; 1943b:203; 1959:887*, fig. 31.28; 1962:273 [by implication]; 1966b:70; 1968b:K-8*, fig. 17a; 1974a:15.—Hoff, 1944:349, 356*—Pennak, 1953, fig. 288*c*.—Hart, 1959: 203.—Hart and Hart, 1974:21*, 28*, 63, 88*, 137.—Wharton, 1978:46*.

Procambarus (Leconticambarus) barbatus.—Hobbs, 1972a:8, figs. 1*m*, 2*f*, 9*a-g*; 1972b:53*, 150*, 154*, figs. 25b, 26f, 29c, 43h, 44f; 1974b:50,* fig. 204.—Hart and Hart, 1974:21*, 28*, 63, 88*, 137.—Hobbs III, Thorp, and Anderson, 1976:3, 5, 13, 32*-33, fig. 13.

The list of references cited above is believed to be a complete bibliography for the species.. Those citations noting the occurrence of this crayfish in Georgia are indicated by asterisks.

SUMMARY OF LITERATURE.—Perhaps the nomenclature of no other American crayfish has had as much confusion involved in its early history. Not realizing that the combination *Astacus penicillatus* had been used by Olivier in 1791 for a spiny lobster, LeConte (1856) applied it to a new crayfish from Georgia, the whereabouts of the types of which is unknown. In his monograph of the Astacidae, Hagen (1870:54), who did not have the opportunity to examine LeConte's types, applied the name *Cambarus penicillatus* to three lots of specimens that later were found to consist of representatives of three species: lot 250 from South Carolina contains members of *Procambarus (Ortmannicus) ancylus*; lot 254, representatives of *P. (Scapulicambarus) troglodytes*; and only lot 279 contains a specimen that is believed to be a member of LeConte's *A. penicillatus*. Faxon (1884: 138) pointed out the error in Hagen's identification of the specimens from South Carolina and questioned his determination of lot number 250. Further, he tentatively identified a second form male from eastern Mississippi as belonging to this species (the specimen is apparently lost but probably was a member of *Procambarus (O.) hybus* Hobbs and Walton, 1957:39). Faxon's (1885a) references to the species consist of an expanded discussion of the materials mentioned by him in 1884, comparing the specimen from eastern Mississippi with those from Georgia and South Carolina. In 1890, Faxon (p. 621) pointed out that LeConte's *Astacus penicillatus* must be rejected because of the priority established by Olivier, and he proposed the substitute name *Cambarus barbatus*. Unfortunately, he assigned 11 specimens from the "Escambia River at Flomaton," on the Alabama-Florida line, to the species, citing them in 1914 (p. 414) as paratypes of his *C. barbatus*. Some years later, Hobbs (1942b:48) referred Faxon's paratypes to a new species *Procambarus escambiensis* (Hobbs, 1942b:46). Thus the only extant specimen of the species was Faxon's "type" of *C. barbatus*, which was the "young" male mentioned by Hagen (MCZ 279). In order to establish the synonomy of Faxon's *Cambarus barbatus* with LeConte's *Astacus penicillatus*, Hobbs (1974b:50) designated this specimen as the neotype of LeConte's species. He (1974b:50) also restricted the rather vague type-locality implied by LeConte. The latter (1856:400) stated that of his new species "two of them [were] from the upper part of the State of Georgia, the rest from the low country." *Astacus spiculifer* and *A. latimanus* are noted as occurring in "Georgia superiore," thus the source of his specimens of the remaining species must be assumed to have been in "Georgia inferiore."

In his study of the genus *Cambarus*, Ortmann (1905a, 1906a) proposed several subgenera, introducing the combination *Cambarus (Cambarus) barbatus*. His error in assigning this species to the nominate subgenus was pointed out by Fowler (1912:341), and, in correcting Ortmann's mistake, implied that the name should be *Cambarus (Ortmannicus) barbatus*. No subsequent authors have used either combination, perhaps because Faxon (1914), in his checklist of the crayfishes of the family Astacidae, did not recognize Ortmann's subgenera. In the generic revision proposed by Hobbs (1942a), the combination *Procambarus barbatus* was introduced (p. 340) and was later modified by him (1972a:8) when he assigned the species to his subgenus *Leconticambarus*.

Until 1940, no reliable specific locality had been cited for the species; all previous references pertain to the specimens just discussed. In describing *Cambarus lunzi* (= *P. (O.) lunzi*), Hobbs (1940b:3) stated that *P. (L.) barbatus* had been dug from burrows in a roadside ditch 1.4 miles southeast of Early Branch on State Highway 28, Hampton County, South Carolina, nearby those of *C. lunzi*. Although no specific localities were cited, Hobbs (1942b) reported its occurrence in Bulloch, Effingham, Jenkins, Liberty, Long, and Screven counties, Georgia, and referred to the record from South Carolina given by him in 1940. Only two additional specific localities have been recorded, these by Hart and Hart (1974): one each in Liberty (pp. 21, 88) and McIntosh (p. 28) counties, where it served as host to *Ankylocythere ancyla* and *Entocythere dorsorotunda* Hoff (1944:332), and to *Ankylocythere hobbsi*, respectively.

Almost all references subsequent to 1940 have to do with relationships of this to other crayfishes or to its range. No data concerning aspects of its biology were recorded until Hobbs III, Thorp, and Anderson (1976:32–33) presented data that were extracted from the manuscript of this report. No adequate description of the species has been presented. LeConte's account (in Latin) is so general that virtually all of it may be applied to any one of a number of species. Had he not stated that "mas latere interiore chelarum pilositatem densam habet spongiam referente," it is doubtful that in the absence of the type it could be recognized. For this reason, a description of topotypes is offered here.

Diagnosis.—Rostrum without marginal spines or tubercles. Carapace lacking cervical spine, sometimes with small tubercle. Areola 4.0 to 9.1 times as long as broad and constituting 31.9 to 35.7 percent of entire length of carapace (38.6 to 45.0 percent of postorbital carapace length). Ventral surface of basis and ischium of third maxilliped densely bearded. First form male with palm of chela almost always bearded; hooks on ischia of third and fourth pereiopods, those on third frequently much smaller than those on fourth; coxa of fourth pereiopod with prominent caudomesial boss; first pleopods slightly asymmetrical, subcontiguous, bearing proximomesial spur and prominent proximomedian lobe, reaching coxae of third pereiopods, subapical setae present on cephalically sloping cephalodistal region; terminal elements consisting of (1) subspiculiform mesial process curved cephalodistally and somewhat laterally and far overreaching other terminal elements, (2) short, distally directed cephalic process arising from mesial surface of appendage and extending distally only slightly beyond tip of central projection, (3) caudal element comprising broad, subtruncate caudal knob, appearing broadly rounded distally in caudal aspect, and (4) small subtriangular cephalodistally inclined corneous central projection situated immediately cephalic to caudal knob. Female with annulus ventralis bearing very prominent, subconical, cephalolaterally projecting prominences, resulting in greatest width of annulus occurring distinctly cephalic to midlength; postannular sclerite not markedly smaller than annulus ventralis; first pleopod present.

Topotypic Male, Form I.—Body (Figure 131*a*, *i*) subovate, compressed laterally. Abdomen narrower than thorax (11.1 and 11.6 mm). Width of carapace less than height (11.6 and 12.4 mm) at caudodorsal margin of cervical groove. Areola 6.5 times as long as wide, with 2 punctations across narrowest part. Cephalic section of carapace almost 1.9 times as long as areola, latter occupying 35.0 percent of entire length of carapace and 42.7 percent of postorbital carapace length. Rostrum excavate dorsally with weakly thickened convergent margins, lacking marginal spines or tubercles, with usual submarginal row of setiferous punctations, and with moderately deep punctations in caudal part; acumen not delimited basally from remainder of rostrum. Subrostral ridge moderately strong and evident in dorsal aspect along basal third of rostrum. Postorbital ridge well developed, grooved dorsolaterally, and lacking spine or tubercle. Suborbital angle distinct. Branchiostegal spine clearly defined. Carapace punctate dorsally and granulate laterally, granules in hepatic and anteroventral branchiostegal region tuberculiform, those in area usually occupied by cervical spine no larger than others nearby. Abdomen longer than carapace (25.6 and 24.3 mm); pleura truncate ventrally. Cephalic section of telson with 2 spines in each caudolateral corner. Uropod with both lobes of proximal podomere bearing spine; mesial ramus with distolateral and median preapical spines, latter far removed from distal margin; lateral ramus with row of short spines immediately proximal to transverse suture, that immediately adjacent to lateralmost member rather long. Cephalic lobe of

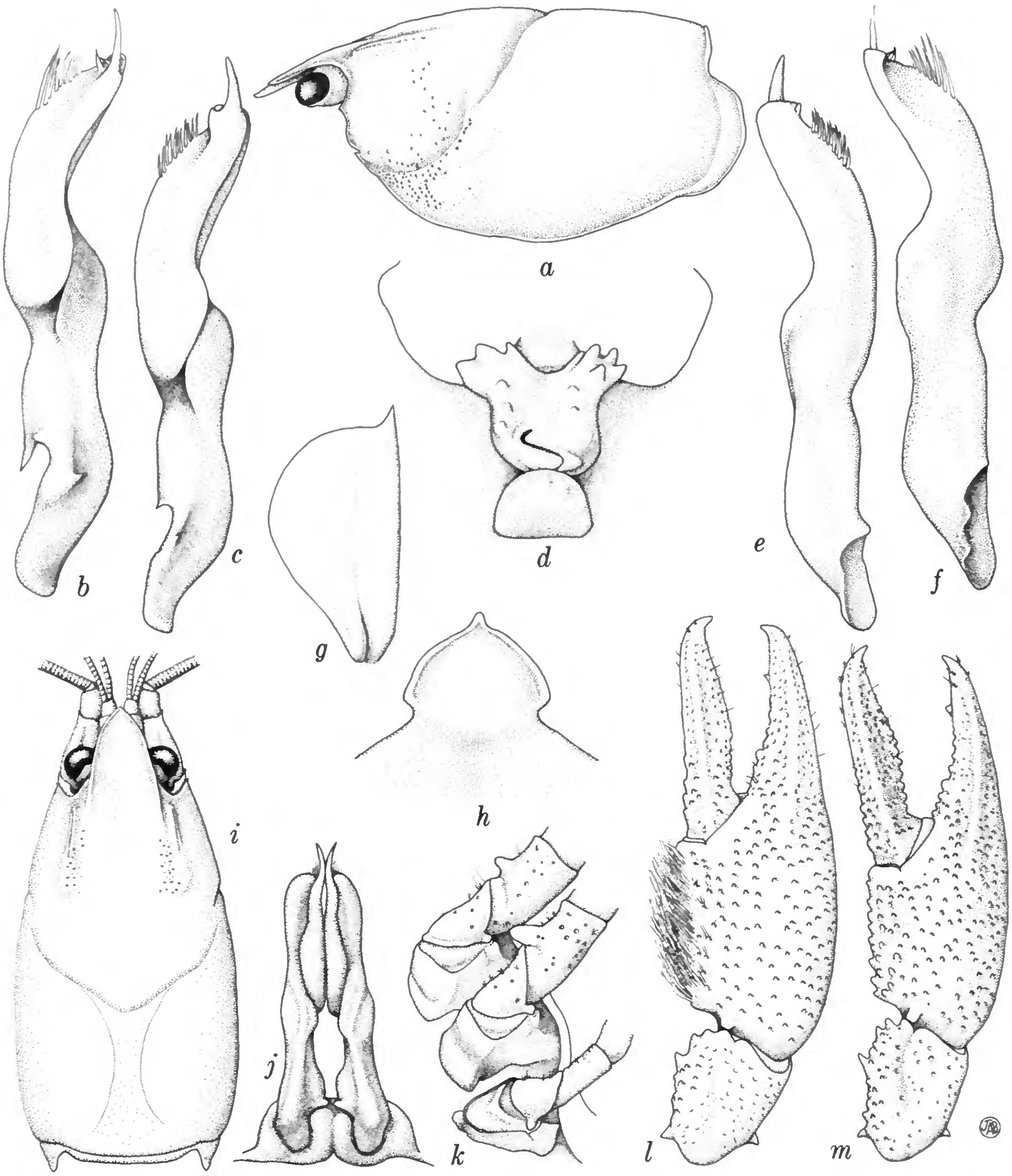


FIGURE 131.—*Procambarus (Leconticambarus) barbatus* (*c*, *e*, from second form male from 4.9 mi SE of Eulonia on St Rte 99, McIntosh Co; *d*, *m*, from female; all others from first form male from 2.5 mi W of Riceboro, Liberty Co): *a*, lateral view of carapace; *b*, *c*, mesial view of first pleopod; *d*, annulus ventralis; *e*, *f*, lateral view of first pleopod; *g*, antennal scale; *h*, epistome; *i*, dorsal view of carapace; *j*, caudal view of first pleopods; *k*, proximal podomeres of third, fourth, and fifth pereiopods; *l*, *m*, dorsal view of distal podomeres of cheliped.

epistome (Figure 131*h*) subovate and bearing small cephalomedian projection; posteromedian part of surface slightly elevated, margins not thickened, and fovea not clearly defined, area of usual occurrence shallowly excavate. Antennular peduncle with very small spine on midventral surface near midlength of basal podomere, mesial border of proximal podomere not strongly setose. Antennae extending caudally to third abdominal tergum, peduncle with small tubercle on basis and ischium. Antennal scale (Figure 131*g*) about twice as long as broad, greatest width distal to midlength, lamellar portion about 1.7 times as broad as thickened lateral portion, latter terminating in short spine. Third maxilliped with ventral surface of proximal podomeres through merus and peduncle of exopod conspicuously hirsute, bearing clusters of plumose setae.

Right chela (Figure 131*l*) moderately short, somewhat depressed, and subovate in cross section. Mesial surface of palm with prominent brushes of long plumose setae obscuring mesial rows of tubercles (mesialmost consisting of 8 or 9); lateral surface with row of squamous tubercles, and dorsal and ventral surfaces similarly tuberculate, tubercles extending onto basal parts of both fingers, ventral surface with prominent tubercle distolateral to articular condyle at base of dactyl. Fixed finger with rounded longitudinal ridge dorsally and ventrally, dorsal ridge flanked proximally by squamous tubercles replaced more distally by setiferous punctations, lateral surface weakly costate, and opposable margin with row of 6 tubercles along proximal three-fourths, second from base largest, and large tubercle projecting from lower level at base of distal fourth; clusters of minute denticles present along entire ventromesial margin except on corneous tip. Dactyl with dorsal and ventral surfaces similar to those of fixed finger; mesial surface bearing proximal subserrate row of 4 tubercles, decreasing in size distally, along proximal third of finger; opposable margin with row of 5 low, rounded tubercles along proximal third, and row of minute denticles between tubercles and continuing distally to corneous tip of finger.

Carpus of right cheliped longer than broad (7.0 and 5.1 mm), with mesial, dorsomesial, and ventromesial surfaces tuberculate, otherwise punctate; dorsal surface with shallow oblique depression; mesial surface with 1 tubercle larger than others; ventral surface with large tubercle at base of condyle on distolateral angle and row of 3 others mesially on distal margin.

Merus of right cheliped tuberculate dorsally and ventrally, those tubercles on dorsal surface increasing in size distally, with 2 preapical ones larger than others; mesial and lateral surfaces mostly punctate; ventral surface with mesial and lateral rows of 13 and 12 tubercles, respectively, distal members of lateral row forming arc bent distinctly mesially toward distalmost tubercle in mesial row. Ischium with 2 rows of tubercles, 6 ventromesially and 4 dorsolaterally.

Hook on ischium of third and fourth pereiopods (Figure 131*k*), that on third much smaller than that on fourth and not overreaching basioischial articulation, latter hook distinctly overreaching corresponding articulation. Coxa of fourth pereiopod with very prominent, often subacute, caudomesial boss; boss on fifth much less conspicuous but well developed, thin, and rounded distally.

Sternum between third, fourth, and fifth pereiopods deep and bearing prominent fringe of plumose setae on ventrolateral margins.

First pleopods (Figure 131*b,f,j*) as described in "Diagnosis."

Topotypic Female.—Differing from first form male, other than in secondary sexual characters, as follows: areola with 3 punctations across narrowest part; merus of third maxilliped devoid of plumose setae and those on ischium not so prominent; mesial surface of palm of chela (Figure 131*m*) without conspicuous brush of plumose setae obscuring irregular rows of tubercles, mesialmost row consisting of 8 or 9; opposable margins of fixed finger and dactyl with rows of 8 and 11 tubercles, respectively, and minute denticles arranged in single row interrupted by tubercles. (See "Measurements.")

Annulus ventralis (Figure 131*d*) moderately deeply embedded in sternum, comparatively small, its median length three-fifths maximum width, and, disregarding prominent cephalolateral projections, only slightly broader than postannular sclerite, taking projections into account about 1.5 times as broad; cephalic area studded with conical projections flanking broad, shallow median longitudinal trough; caudal part subplane and bearing tilted S-shaped sinus. Postannular sclerite, about two-thirds as wide as long, rather broadly rounded anteriorly, and with ventral surface bearing arc of small tubercles. First pleopod extending over posterior third of annulus when abdomen flexed.

MALE, FORM II (From McIntosh County, 4.9 miles SE of Eulonia).—Differing from first form male in following respects: rostrum slightly more acuminate; areola with 3 punctations across narrowest part; tubercle on ventral surface of ischium of antennular peduncle spiniform; opposable margins of fixed finger and dactyl of chela with rows of 8 and 10 tubercles, respectively; ventral surface of merus of cheliped with mesial and lateral rows consisting of 12 and 13, respectively; ischium of cheliped with 5 tubercles in both dorsolateral and ventromesial rows; hooks on ischia of third pereiopods reduced to small tubercles, neither overreaching basioischial articulation; boss on coxa of fourth pereiopod decidedly reduced, that on fifth not markedly so. (Also see "Measurements.")

First pleopod (Figure 131*c*,*e*) with subapical setae reduced in length; mesial process more robust and shorter but distinctly overreaching other terminal elements; caudal process not markedly smaller, but cephalic process and central projection rather poorly defined and neither protruding as in first form male.

COLOR NOTES.—Two color patterns have been observed in this crayfish: a "striped phase," characterized by a dorsomedian longitudinal light stripe, and a "speckled phase," in which small irregular dark spots are scattered over the carapace and dorsum of the abdomen. A random collection of 25 specimens collected 4.9 miles southeast of Eulonia on State Route 18 in McIntosh County consisted of 19 (8 males, 11 females) striped individuals and 6 (1 male, 5 females) speckled ones; in another collection of 31 specimens, there were 23 striped individuals and 8 that were speckled. In these the ratio of 3:1 (striped to speckled) approaches that reported by Volpe and Penn (1957) in the striped and spotted patterns in *Cambarellus shufeldtii* (Faxon, 1884). But in another sample of 86 specimens collected 1.9 miles east of State Route 80 on Route 119C in Bulloch County, only 26 (15 males and 11 females) were striped, and 60 (26 males and 34 females) were speckled.

The following is a description of the striped phase (Figure 130*a*): background color ranging from light olive to straw, or to pinkish to olive tan, or brown. Dorsum with dorsomedian longitudinal pale green to cream tan stripe extending almost from tip of rostrum to base of telson. In cephalic region, stripe subtended by irregular, often anastamosing dark brown to black splotches; dark pigment flanking stripe on branchiostegites and abdominal terga forming distinct bands of variable widths; smaller spots of same dark color interspersed with white ones, scattered over remainder of carapace, terga, pleura, telson, and uropods. Sometimes dark bands on abdomen very wide, almost reaching bases of pleura, where delimited by narrow pale stripe. Antennule and antenna dark olive to brown; antennal scale with pale longitudinal stripe on thickened lateral part. Cheliped dark brown dorsally from merus distally with almost black splotches and tubercles; dorsal surface of podomeres often nearly uniformly dark; ventral surface of podomeres much paler, with distal ones, particularly in first form males, orange, latter bleeding onto lateral surface of propodus. Brush on mesial side of palm of male pale gray in recently molted individuals, often becoming dark brown in those in late intermolt stages. Remaining pereiopods olive to brown (sometimes mottled) from dorsal surface of ischium distally; merus and carpus darker than other podomeres. Ventral part of cephalothorax pinkish to grayish cream or pale tan.

Speckled phase (Figure 130*b*) similar in color, but with dorsum darker than lateral regions and usually lacking any trace of stripes.

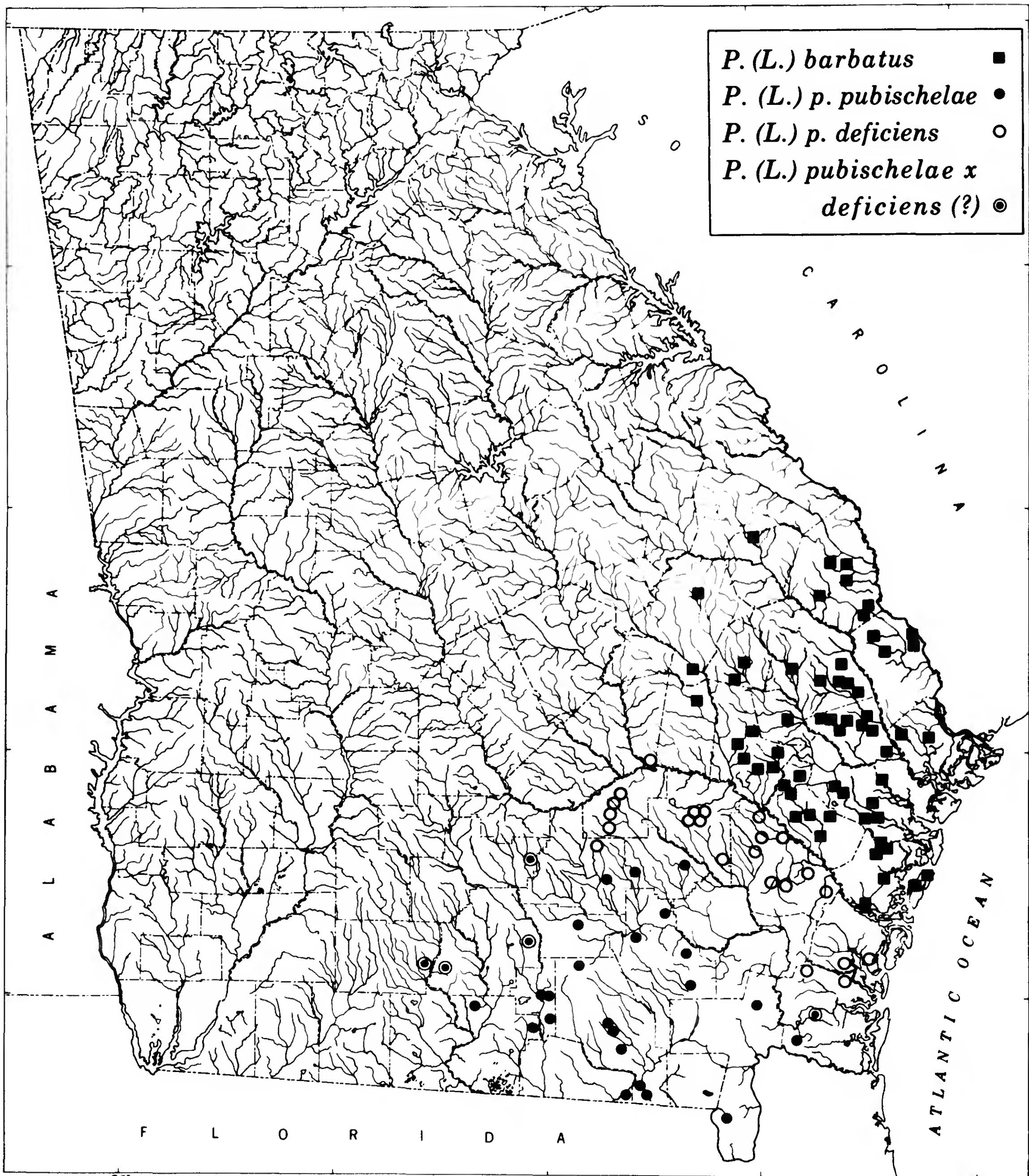


FIGURE 132.—Distribution of *Procambarus (L.) barbatus*, *P. (L.) pubischelae pubischelae*, and *P. (L.) pubischelae deficiens* in Georgia.

Measurements (mm)

	Topotypic male, form I	*Topotypic female*	*Male, form II*
Carapace			
Height	12.4	14.1	12.4
Width	11.6	13.0	12.0
Entire length	24.3	26.9	24.9
Postorbital length	19.9	22.7	20.4
Areola			
Width	1.3	1.5	1.4
Length	8.5	9.2	8.5
Rostrum			
Width	4.1	4.6	4.3
Length	5.3	5.6	5.9
Chela			
Length of mesial margin of palm	7.6	6.0	6.5
Width of palm	7.0	6.4	5.9
Length of lateral margin	19.5	17.5	17.8
Length of dactyl	9.9	10.1	10.1
Abdomen			
Width	11.1	12.1	10.9
Length	25.6	28.2	26.5

TYPE.—Neotype of *Astacus penicillatus* LeConte, MCZ 279 (♂I).

TYPE-LOCALITY.—"... the low country" of Georgia (LeConte, 1856:400); restricted by Hobbs (1974b:50) to 2.5 miles west of Riceboro, Liberty County, Georgia, in flatwoods.

RANGE.—Coastal Plain Province (in Georgia from the Vidalia Upland to the Barrier Island Sequence District) between the Edisto River, South Carolina, and the Altamaha River, Georgia.

GEORGIA SPECIMENS EXAMINED.—I have examined 459 specimens from 58 localities (Figure 132) in Bryan (9 localities), Bulloch (6), Candler (2), Chatham (2), Effingham (4), Emanuel (2), Evans (1), Jenkins (1), Liberty (5), Long (7), McIntosh (7), Screven (5), Tattnall (6), and Toombs (1) counties in the following drainage systems: Savannah, Ogeechee, Canochee, Ohoopee, and Altamaha.

VARIATIONS.—Among the most conspicuous variations is the relative width of the areola; while the narrowest ones occur in individuals found in the coastal portion of the range in Bryan and Liberty counties, and the broadest in Evans and Tattnall counties, the differences noted do not seem to be clinally oriented.

In almost all of the adult males, the mesial surface of the palm of the chela is bearded; however, in individuals in which the chela has been regenerated, the setal tufts are usually, if not always, absent. Generally, such regenerated chelae can be recognized by their slender, often distorted, contour. Two first form males are available that lack the bearded chelae, and the chelipeds are so nearly perfectly developed that they do not appear to have been replaced; nevertheless, the possibility that they were lost in one of the earlier instars cannot be excluded. Similarly, the matted setae on the ventral surface of the basis and ischium of the third maxilliped are much reduced in regenerated appendages.

Considerable variation exists in the degree of development and the disposition of the hook on the ischium of the third pereiopod. In some first form males, it is almost a replica of the well-developed hook on the ischium of the fourth pereiopod; in others it is less than half as large and directed almost perpendicular to the axis of the ischium; and, in a few individuals, it is so greatly reduced as to be almost tuberculiform.

Variations in color pattern are noted under "Color Notes."

SIZE.—The largest specimen available is a female with a carapace length of 31.3 (postorbital carapace length 25.3) mm. Corresponding lengths of the smallest and largest first form males are 18.0 (14.8) and 30.0 (25.6) mm, and of the smallest ovigerous female, 18.9 (15.2) mm.

LIFE HISTORY NOTES.—First form males have been collected from January to June, and in August, September, and December. Eight ovigerous females were taken from burrows in April, four in May, and one in June. The numbers of eggs carried by seven of them are as follows:

Carapace and postorbital carapace lengths (mm)	*Number of eggs*	*Diameter of eggs (mm)*
18.9 (15.2)	71	1.7–1.8
22.0 (18.2)	92	1.7–1.8
22.2 (18.2)	58	1.7–1.8
22.9 (19.3)	31	1.7–1.8
23.7 (19.5)	141	1.6–1.7
25.0 (21.1)	127	1.7–1.8
30.7 (25.4)	265	1.6–1.7

Seasonal Data

Sex/stage	*J*	*F*	*M*	*A**	*M*	*J*	*J*	*A*	*S*	*O*	*N*	*D*
♂I	3	8	5	12	13	4		2	1			9
♂II	3		2	17	13	4		2	4			8
♀	7	17	7	29	36	13	1	1	4			24
♂j	2			15	6				12			20
♀j	5			17	8				23			10
♀ ovig				8	4	1						

* 79 additional specimens examined for color pattern.

Ecological Notes.—*Procambarus (L.) barbatus* is a secondary burrower, usually occurring in temporary bodies of water and burrows. During the breeding season, or when the water table drops below the surface, this crayfish retreats into simple burrows that penetrate the ground to a depth of as much as one meter. The excavations usually consist of a single almost vertical or slightly sloping passage descending below the water table, where there is a slight enlargement. In some burrows, the passageway bifurcates; in many instances in which such burrows have been encountered, a first form male was in one branch and a female in the other. Not infrequently, a first form male and a female have been found together in a burrow consisting of a single passageway; however, in no instance have an ovigerous female and a male been taken from the same passageway. Usually, there is only a single opening to the surface, and never have I encountered more than two. If the burrow is newly constructed or recently "worked" it is marked by a low chimney that may be subcylindrical or very irregular. In most burrows inhabited by a pair of individuals, the chimney is plugged. The soils in which burrows have been found range from sandy clay to ones that are dark and rich in organic matter.

When the mouths of the burrows are flooded, the crayfish frequently leave their lairs and may be found in open water of pools or roadside ditches even during the daylight hours.

Crayfish Associates.—This crayfish has been collected in one or more localities with each of the following (the number of times they were found together is noted in parentheses): *Cambarus (D.) latimanus* (1), *Procambarus (H.) advena* (13), *P. (H.) pygmaeus* (7), *P. (H.) truculentus* (3), *P. (O.) a. acutus* (1), *P. (O.) enoplosternum* (2), *P. (O.) epicyrtus* (3), *P. (O.) litosternum* (6), *P. (O.) lunzi* (8), *P. (O.) pubescens* (1), *P. (O.) seminolae* (1), and *P. (S.) troglodytes* (10).

Procambarus (Leconticambarus) pubischelae pubischelae Hobbs, new combination

Figures 18*c*, 130*c*,*d*, 132–134, 242

Procambarus pubischelae Hobbs, 1942b:13, 15, 20, 21, 23, 29, 30, 34–38, 41–46* [in part], 48, 54, 59, 63, 69, 71, 78, 106, 113, 145, figs. 6–10, 216–225; 1959:887*; 1968b:K 10* [in part], fig. 17b.—Hart and Hart, 1974:21*, 86*, 90* [in part].—Burgess and Franz, 1978:167.

Procambarus pubischaelae.—Villalobos, 1955:38 [erroneous spelling].

Procambarus (Leconticambarus) pubischelae.—Hobbs, 1972a:8; 1972b:53* [in part], 151*, 154*, fig. 44a; 1974b:52* [in part], fig. 209.

The above citations are believed to comprise a complete bibliography of the subspecies. References to its occurrence in Georgia are indicated by an asterisk.

Summary of Literature Pertaining to Georgia.—In describing this crayfish, Hobbs (1942b) noted its occurrence in several counties in Georgia: Appling, Camden, Clinch, Colquitt, Cook, Lanier, Lowndes, Ware, and Wayne. In discussing variations, he pointed out several local variants: that from Appling County together with additional specimens from northern Camden, Coffee, Glynn, Jeff Davis, and from Montgomery and Wayne counties are assigned here to a separate subspecies.

All of the recorded data relating to the biology of this crayfish, except for three specific locality records in Georgia, are included with the original description. Hart and Hart (1974) reported its occurrence in Atkinson, Cook, and Lowndes counties, where it served as host to *Ankylocythere ancyla*, *Entocythere dentata* Crawford (1965:151), and *E. internotalus* in one or more of the three localities (these are noted under "Georgia Specimens Examined"). Other subsequent references include no data that are not presented with the original description.

DIAGNOSIS.—Rostrum without marginal spines or tubercles. Carapace lacking cervical spines. Areola 3.3 to 4.9 times as long as broad and constituting 29.2 to 32.8 percent of entire length of carapace (35.3 to 40.5 percent of postorbital carapace length). Ventral surface of basis and ischium of third maxilliped densely bearded. First form male with palm of chela almost always bearded; hooks on ischia of third and fourth pereiopods, and coxa of fourth pereiopod with strong caudomesial boss (see "Variations" for exceptions); first pleopods slightly asymmetrical, subcontiguous, bearing proximomesial spur, prominent proximomedian lobe, subapical setae situated cephalically on knoblike or subtruncate lobe; terminal elements consisting of (1) subspiculiform mesial process usually curved gently cephalodistally and distinctly overreaching other terminal elements, (2) short subdistally directed cephalic process reaching approximately same level as central projection, (3) caudal element consisting of stout lobe with or without U-shaped corneous ridge, rarely any part of which acute in caudal aspect, and (4) rounded to subtriangular, corneous central projection at cephalodistal extremity of caudal knob. Female with annulus ventralis bearing distinct ridge or tubercles laterally or cephalolaterally, sinus tilted and S-shaped; postannular sclerite almost as large as annulus and often conical; first pleopod present.

COLOR NOTES.—This crayfish occurs in two distinct color patterns: striped and speckled (Figure 130*c*,*d*). Both are actually speckled, but the former has a pale dorsomedian stripe extending from the rostrum to the sixth abdominal tergum, and the flecks, particularly on the abdomen, are not nearly so conspicuous as in those individuals lacking the median stripe. The striped pattern is described here.

Carapace olive to dark brown dorsally, fading ventrally, with darker brown to black flecks, latter often forming irregular reticulate patches. Paired small black spots on mesial mandibular adductor and antennal regions. Cephalic section with light tan median area extending from rostrum to cervical groove; areola similarly light tan. Abdomen with narrow median light tan stripe extending from base to cephalic fourth of sixth tergum. Stripe of first segment flanked by paired dark brown bands extending onto reduced pleura; succeeding four terga lighter brown except for paired bands caudally, bands decreasing in width posteriorly; anterolateral extremity of each tergum with 2 or 3 small cream spots, and pleura cream tan anteriorly. Sixth tergum mostly light brown but with very narrow dark line along caudal margin. Telson tan, with pair of oblique cream spots margined in deep brown anteriorly, and narrow median longitudinal cream stripe extending from between spots almost to caudal margin; cephalic section dark brown laterally and with similarly colored spines. Uropod uniformly brown except for darker keels, lateral margins, and distal margin of proximal section of lateral ramus. Antennular and antennal peduncles brown with darker mottlings; flagella deep brown, fading distally to olive. Chelipeds dark brown dorsally from distal two-thirds of merus to corneous tips of fingers; merus and carpus mottled in very dark brown to black, and all tubercles black; mesial surface of palm of chela of adult male with conspicuous brush of gray plumose setae; ventral surface of chela orange tan. Remaining pereiopods tan with olive brown suffusion dorsally from ischium through propodus. Ventral surface of body cream to pale tan.

TYPES.—Holotype, allotype, and morphotype, USNM 81284 (♂I, ♀, ♂II); paratypes, ANSP, MCZ, USNM.

TYPE-LOCALITY.—Cypress ponds and roadside ditch, 9.4 miles north of Lake City on U.S. Highway 441, Columbia County, Florida.

RANGE.—From the middle Satilla River drainage and Suwannee River basin in Georgia southward to Alachua and Flagler counties, Florida. In Georgia, this crayfish occurs in the Coastal Plain Province from the Tifton Upland across all of the districts to the east: Bacon Terraces, Okefenokee Basin, and Barrier Island Sequence.

GEORGIA SPECIMENS EXAMINED.—I have examined a total of 222 specimens from 38 localities as follows (unless otherwise indicated, all from burrows or shallow water in roadside ditches). *Atkinson County*: (1) N side of Pearson on US Hwy 441 (Hart and Hart, 1974:90), 1♀, 1j♂, 1j♀, 23 Apr

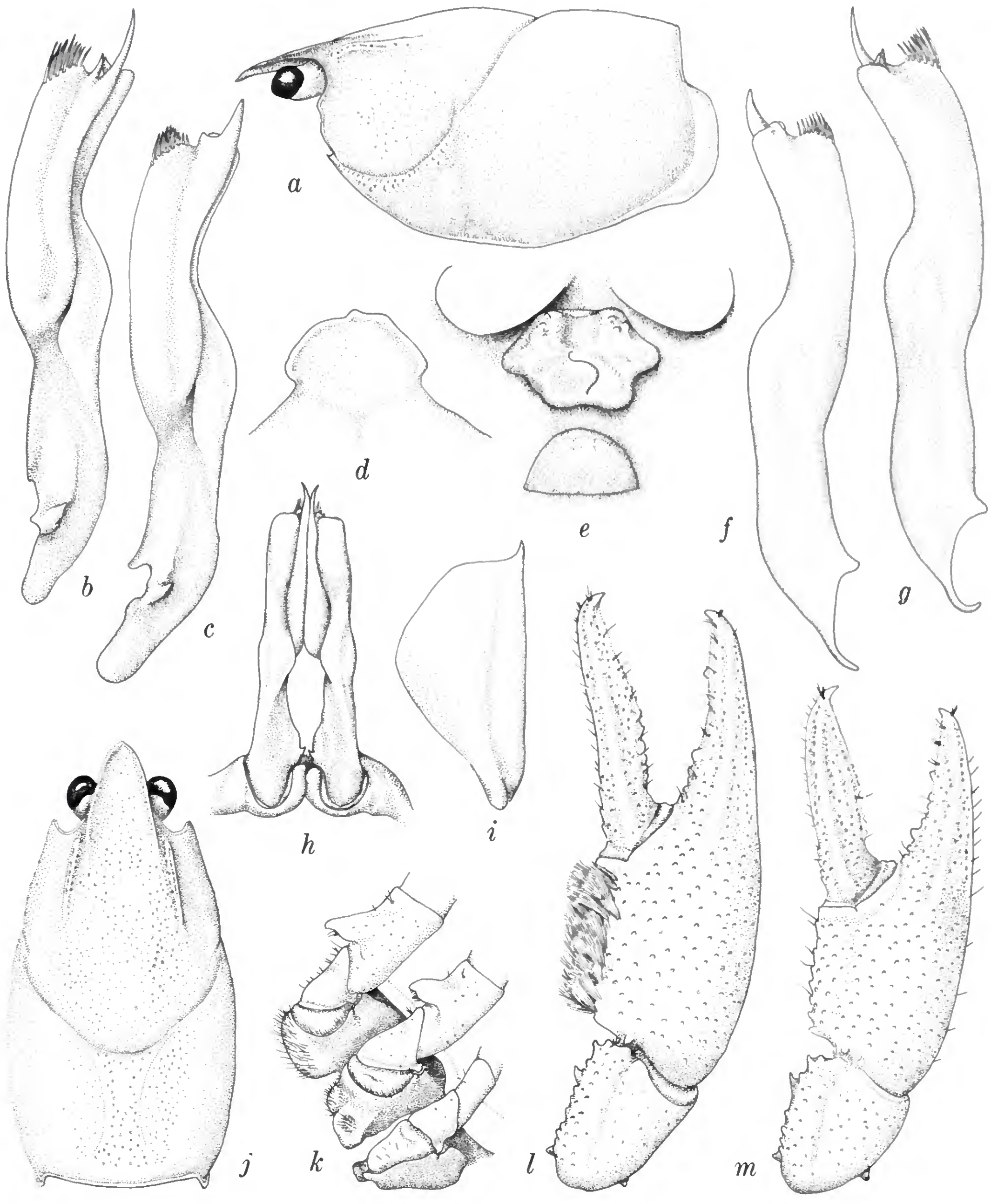


FIGURE 133.—*Procambarus (Leconticambarus) pubischelae pubischelae* (*c*, *f*, from second form male from Alapaha River 2.2 mi E of Lakeland on St Rte 37, Lanier Co; *e*, *m*, from female, and all others from first form male from 3.2 mi W of Clinch Co line on St Rte 37, Lanier Co): *a*, lateral view of carapace; *b*, *c*, mesial view of first pleopod; *d*, epistome; *e*, annulus ventralis; *f*, *g*, lateral view of first pleopod; *h*, caudal view of first pleopods; *i*, antennal scale; *j*, dorsal view of carapace; *k*, proximal podomeres of third, fourth, and fifth pereiopods; *l*, *m*, dorsal view of distal podomeres of cheliped.

1966, E. T. Hall, Jr., HHH, collectors; (2) 14.6 mi W of Waycross on US Hwy 82, 1♂I, 2♀, 5 Apr 1978, R. J. Dubois, D. J. Peters, J. E. Pugh, HHH; (3) 3.8 mi W of Ware Co line on US Hwy 82, 3♂I, 2♂II, 6♀, 1j♂, 5 Apr 1978, RJD, DJP, JEP, HHH; (4) 5.2 mi S of Pearson on US Hwy 221, 2j♂, 6 Apr 1978, RJD, DJP, JEP, HHH; (5) 0.2 mi SW of US Hwy 221 on St Rte 64, 2♂I, 2♂II, 9♀, 5j♀, 6 Apr 1978, RJD, DJP, JEP, HHH. *Bacon County*: (6) Alma, 1♂I, 2♂II, 4j♂, 5j♀, Sep 1949, C. Tuten; (7) 3.1 mi W of Appling Co line on St Rte 99, 1♂II, 2♀, 6 Oct 1977, T. A. English, Jr., HHH; (8) Bacon-Coffee Co line on St Rte 32, 1♂I, 1♂II, 3♀, 1♀ with young, 6 Oct 1977, TAE, HHH. *Berrien County*: (9) 2.5 mi W of St Rte 135 on Rte 76, 2♂I, 3♀, 1j♀, 23 Jun 1975, DJP, JEP, HHH; (10) 2.6 mi NW of Lanier Co line on St Rte 168, 1j♂, 6 Apr 1978, RJD, DJP, JEP, HHH; (11) 2.8 mi NW of Nashville on St Rte 125, 4♂I, 2♀, 1j♀, 6 Apr 1978, RJD, DJP, JEP, HHH. *Camden County*: (12) near Woodbine on US Hwy 17, 1♂I, 19 Dec 1939, HHH; (13) 2.2 mi NE of St Rte 40 on Rte 110, NE of Folkston, 1♀, 1♀ with young, 27 Sep 1972, ETH, W. D. Kennedy, HHH. *Charlton County*: (14) about 7.9 mi S of Brantley Co line on US Hwy 301, 1♂I, 1♂II, 4♀, 6j♂, 8j♀, 23 Aug 1965, J. E. Cooper, M. R. Cooper; (15) 4.3 mi E of Florida line on St Rte 94, 2♂I, 1♀, 30 Mar 1977, H. K. Wallace, HHH. *Clinch County*: (16) swamp stream 15.7 mi N of Fargo on US Hwy 441, 1♂II, 2♀, 27 Oct 1938, F. N. Young, Jr., HHH; (17) 6.7 mi S of Fargo on St Rte 94, 3♂I, 6♀, 3j♀, 30 Mar 1977, HKW, HHH; (18) 16.4 mi NW of Fargo on US Hwy 441, 2♂I, 2♀, 29 Mar 1977, HKW, HHH. *Coffee County*: (19) 7.0 mi W of Bacon Co line on St Rte 32, 2♂I, 1♂II, 2♀, 2 ovig ♀, 1♀ with young, 6 Oct 1977, TAE, HHH; (20) 6 mi E of Broxton on unnumbered road, 3♂I, 8♀, 1j♀, 4 Apr 1978, RJD, DJP, JEP, HHH. *Colquitt County*: (21) 10 mi W of Adel on St Rte 37, 1j♂, 28 Oct 1938, FNY, HHH. *Cook County*: (22) 1.5 mi W of Adel on St Rte 37, 1♂I, 1♂II, 3♀, 3♀ with young, 28 Oct 1938, FNY, HHH. *Echols County*: (23) 3.5 mi NE of Florida line on US Hwy 441, 1♀, 29 Mar 1977, HKW, HHH. *Irwin County*: (24) 1.7 mi W of Coffee Co line on St Rte 32, 1♂I, 24 Apr 1966, ETH, HHH. *Lanier County*: (25) 1.7 mi E of Stockton, 1♀, 2 ovig ♀, 28 Oct 1938, FNY, HHH; (26) Alapaha River 2.2 mi E of Lakeland on St Rte 37, 1♂II, 1♀, 24 Mar 1959, R. H. Gibbs; (27) 3.2 mi W of Clinch Co line on St Rte 37, 3♂I, 2 ovig ♀, 28 Sep 1972, ETH, WDK, HHH; (28) 0.8 mi W of Clinch Co line on St Rte 64, 1♂I, 3♀, 1j♀, 6 Apr 1978, RJD, DJP, JEP, HHH. *Lowndes County*: (29) 14.1 mi NE of Valdosta on US Hwy 84 (Hart and Hart, 1974:90), 1♂I, 3♀, 1j♂, 2 ovig ♀, 2♀ with young, 28 Oct 1938, FNY, HHH; (30) 2.1 mi N of Hahira on US Hwy 41, 1j♀, 28 Oct 1938, FNY, HHH. *Pierce County*: (31) 4.5 mi E of Rte S1918 on S598, 1♂I, 2♀, 5 Apr 1978, RJD, DJP, JEP, HHH. *Tift County*: (32) 1.4 mi NE of US Hwy 82 on Hwy 319, 1♂I, 3♂II, 3♀, 1j♀, 6 Apr 1978, RJD, DJP, JEP, HHH. *Ware County*: (33) 3.0 mi of Waycross, 2♂II, 22 Jul 1933, C. E. Burt; (34) 12 mi N of Waycross on US Hwy 1 (Hart and Hart, 1974:86), 6♂I, 5♀, 23 Aug 1937, HHH; (35) trib of Satilla River, 1♂II, 4♀, 18 Aug 1952, D. Schiefelbein; (36) 2.1 mi NW of St Rte 158 on US Hwy 82, 1♂I, 1♀, 1 ovig ♀, 26 Sep 1972, ETH, WDK, HHH; (37) 3.7 mi S of US Hwy 1 on St Rte 177, 1♂I, 27 Sep 1972, ETH, WDK, HHH; (38) 1.3 mi N of Rte S1493 on S2398, 2♂I, 1♂II, 8♀, 3j♂, 1j♀, 5 Apr 1978, RJD, DJP, JEP, HHH.

VARIATIONS.—There is considerable variation in this crayfish. In the northwestern and northeastern parts of its range there is evidence of intergradation between it and *P. (L.) pubischelae deficiens* (new subspecies). This seems rather obvious in specimens from Camden County in the east and in Berrien, Cook, Irwin, and Tift counties in the western part of the range, where populations exhibit an admixture of the characters of the two subspecies.

In the first form male from southern Camden County, both the hook on the ischium of the fourth pereiopod and the boss on the coxa are much reduced (Figure 134*o*), and the annulus ventralis of the young females is almost devoid of lateral tubercles. The first pleopod of the male is depicted in Figure 134*g,n*.

The males from Berrien County, while lacking a hook on the ischium of the fourth pereiopod, have a small boss on the coxa (Figure 134*p*), and in the females the annulus ventralis bears cephalolateral tubercles or a distinct cephalolateral elevated ridge. The first pleopod of the male is illustrated in Figure 134*b,i*. Those specimens from locality 11 are almost typical of *P. (L.) pubischelae deficiens*.

In Cook and Irwin counties, the males lack a hook on the ischium of the fourth pereiopod, but the boss on the coxa is rather well developed (Figure 134*q*), and in the females the annulus ventralis bears cephalolateral tubercles. The first pleopods of the males are illustrated in Figure 134*a,c,h,j*.

The male from Tift County is intermediate in all respects except for the long, strongly recurved mesial process of the first pleopod, which is distinctly like that of *P. (L.) p. deficiens*.

In first form males from Charlton and Ware counties, there are well-developed hooks on the ischia of the third and fourth pereiopods, and the boss on the coxa of the latter is very large (Figure 134*r*); the annuli ventrales, although lacking tu-

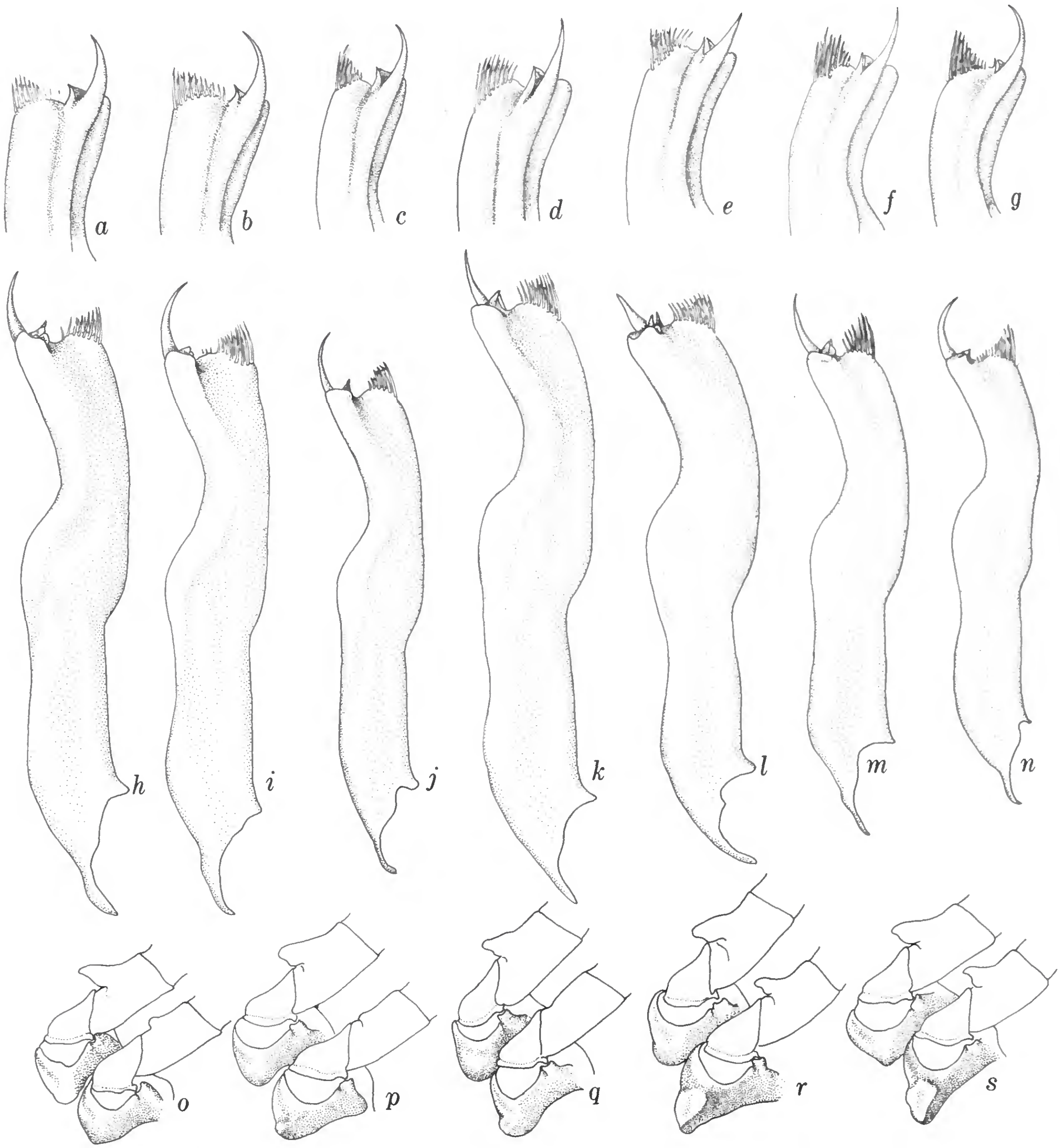


FIGURE 134.—*Procambarus (L.) pubischelae pubischelae*, variations (*a–g*, mesial view of terminal part of first pleopod of first form male; *h–n*, lateral view of first pleopod of first form male; *o–s*, basal podomeres of third and fourth pereiopods): *a*, *h*, Cook Co; *b*, *i*, *p*, Berrien Co; *c*, *j*, *q*, Irwin Co; *d*, *k*, Clinch Co; *e*, *l*, *r*, Ware Co; *f*, *m*, *s*, Charlton Co; *g*, *n*, *o*, Camden Co.

bercles, have comparatively high anterolateral ridges; the first pleopods are illustrated in Figure 134*e,f,l,m*. In males from Bacon County and from 12 miles north of Waycross, Ware County, the caudal knob is embellished with a distinct corneous ridge that is lacking or vestigial in specimens from other localities (Figure 134*l*).

SIZE.—The largest specimen available is a first form male with a carapace length of 29.2 (postorbital carapace length 24.1) mm. The smallest first form male has a corresponding length of 18.0 (14.5) mm, and the smallest female bearing eggs or young, 21.9 (17.8) mm.

LIFE HISTORY NOTES.—First form males have been collected in Georgia during March, April, June, August, September, and October; in addition, in Florida they have also been obtained during May, November, and December. Ovigerous females were found in Georgia during September and October, and in Florida they were collected in March, May, June and October. Females carrying young were obtained in Georgia in September and October, others were found in Florida during June and October. The number of eggs carried by six females from Georgia are as follows:

Carapace and postorbital carapace lengths (mm)	*Number of eggs*	*Diameter of eggs (mm)*
22.1 (18.0)	93	1.7–1.8
22.8 (18.1)	72	1.7–1.8
23.3 (19.3)	163	1.7–1.8
25.6 (21.4)	104	1.7–1.8
26.1 (21.3)	143	1.7–1.8
26.9 (21.4)	144	1.7–1.8

Seasonal Data

Sex/stage	*J*	*F*	*M*	*A*	*M*	*J*	*J*	*A*	*S*	*O*	*N*	*D*
♂I			7	19		2		7	6	5		1
♂II			1	8			2	2	2	5		
♀			11	44		3		13	2	16		
♂j				8				6	4	2		
♀j			3	11		1		8	5	1		
♀ ovig									3	6		
♀ with young									1	7		

ECOLOGICAL NOTES.—This species clearly vicariates for *P. (L.) barbatus* in the southern part of Georgia and in northern Florida. The two occupy similar habitats, and no differences in their habits have been noted.

In discussing this crayfish, Hobbs (1942b:45) wrote the following, which is applicable to the species in Georgia:

> I saw scores of open burrows scattered over the bottom of a shallow, temporary flatwoods pond west of Jacksonville shortly after a rainy season. Each burrow was about one and one-half feet deep and was marked by a small patch of yellow sandy clay around its opening. At the mouths of many of the burrows the crayfish could be seen with their chelae extended toward the opening, and, upon being disturbed, retreated into their holes. Occasionally, as I waded through the pond a crayfish would dart from a small clump of vegetation, scurry for a distance of one to four feet, and then disappear into one of the burrows. Some of these burrows had two openings, but all of them were otherwise very simple.

Apparently much of the life of this crayfish is spent in and about the mouth of the burrow, the crayfish leaving it only in search of food or a mate. During the day I have collected it (especially juveniles) from mats of aquatic plants or in open water of recently flooded ditches. At night, individuals are often found in open water several feet from a burrow.

Repeatedly pairs consisting of a male and female have been taken from burrows, and in each instance the male was in the first form. Generally there is at least an inch or two of water in the burrow; but I have dissected those that, although moist, contained no water, and the crayfish apparently were not affected by the lack of standing water. On all occasions when a male was found in a burrow with an ovigerous female or one carrying young, the passageway was forked, and the male was ensconced in one passage and the female in the other.

A few specimens have been collected in sluggish streams adjacent to low-lying flatwoods areas, and the young are commonly observed in flooded roadside ditches.

GEORGIA CRAYFISH ASSOCIATES—*Procambarus (L.) pubischelae pubischelae* has been collected with the following crayfishes (the number of times they have been found together are noted in parentheses): *P. (H.) pygmaeus* (5), *P. (H.) talpoides* (17), *P. (O.) seminolae* (25), and *P. (S.) paeninsulanus* (3).

Procambarus (Leconticambarus) pubischelae deficiens, new subspecies

FIGURES 18*d*, 132, 135, 241

Procambarus pubischelae Hobbs, 1942b:43 [in part]; 1966a:109; 1968b:K-10 [in part].—Hart and Hart, 1974:21 [in part], 90 [in part].

SUMMARY OF LITERATURE.—Hobbs (1942b:43) pointed out most of the distinctive features of this crayfish:

> One distinct variant occurs in the vicinity of Baxley, (Appling County) Georgia. The male is provided with hooks on the ischiopodites of only the third pair of pereiopods, but in one or two specimens there is a rudiment of a hook on the ischiopodite of the fourth. The areola is relatively broad with about three punctations in the narrowest part, and the rostrum is broader than in specimens from some of the other localities; the annulus ventralis bears no tubercles.

The specimens so characterized constitute a part of the type-series of this geographic race. In noting the range of the species (1966a, 1968b), he included that of *P. (L.) pubischelae deficiens*, which occurs principally immediately south of the Altamaha River. The only specific localities that have been cited for it are those of Hart and Hart (1974), who recorded it as a host of the ostracods *Ankylocythere ancyla* and *Entocythere internotalus*. (See "Specimens Examined.")

DIAGNOSIS.—Rostrum without marginal spines. Carapace lacking cervical spine or tubercle. Areola 3.3 to 5.0 times as long as broad and constituting 30.1 to 34.0 percent of entire length of carapace (36.7 to 41.0 percent of postorbital carapace length). Ventral surface of basis and ischium of third maxilliped densely bearded. Male with palm of chela bearded; hook on ischium of third pereiopod only; coxa of fourth pereiopod lacking caudomesial boss; first pleopods reaching coxae of third pereiopods when abdomen flexed, slightly asymmetrical, contiguous, bearing proximomesial spur, prominent proximomedian lobe, and subapical setae on cephalically situated knoblike or subtruncate lobe; terminal elements consisting of (1) subspiculiform mesial process curved cephalodistally and far overreaching other terminal elements, (2) short distally directed cephalic process arising from mesial surface of appendage and extending distally only slightly beyond tip of central projection, (3) caudal element comprising broad subtruncate caudal knob with caudomesial portion appearing subacute in caudal aspect, and (4) small triangular cephalodistally inclined corneous central projection situated immediately cephalic to caudal knob. Female with cephalolateral elevations of annulus ventralis, if present, low and lacking tubercles; greatest width of annulus near midlength, sinus tilted and S-shaped; postannular sclerite almost as large as annulus; first pleopod present.

HOLOTYPIC MALE, FORM I.—Body (Figure 135*a,j*) subovate, compressed laterally. Abdomen narrower than thorax (10.8 and 11.8 mm). Width of carapace less than height (11.8 and 12.5 mm) at caudodorsal margin of cervical groove. Areola 3.8 times as long as wide, with 3 or 4 punctations across narrowest part. Cephalic section of carapace 2.1 times as long as areola, length 31.8 percent of entire length of carapace (39.1 percent of postorbital carapace length). Rostrum excavate dorsally, with slightly thickened convergent margins, lacking marginal spines or tubercles, with usual submarginal row of setiferous punctations, and with moderately deep punctations in caudomedian portion; acumen not delimited basally from remainder of rostrum. Subrostral ridges moderately well developed and evident in dorsal aspect for only short distance beyond caudal margin of orbit. Postorbital ridge well developed, grooved dorsolaterally, and lacking spines or tubercles. Suborbital angle very weak. Branchiostegal spine small. Carapace punctate dorsally and granulate laterally; tubercles in area occupied by cervical spine in some other crayfishes scarcely larger than those immediately cephaloventral to them. Abdomen longer than carapace (27.1 and 23.6 mm); pleura truncate ventrally. Cephalic section of telson with 2 spines in each caudolateral corner, mesial pair movable. Uropod with 2 moderately well developed spines on basal podomere; mesial ramus with relatively strong distolateral spine and smaller premarginal distomedian one on median keel; lateral ramus with row of small

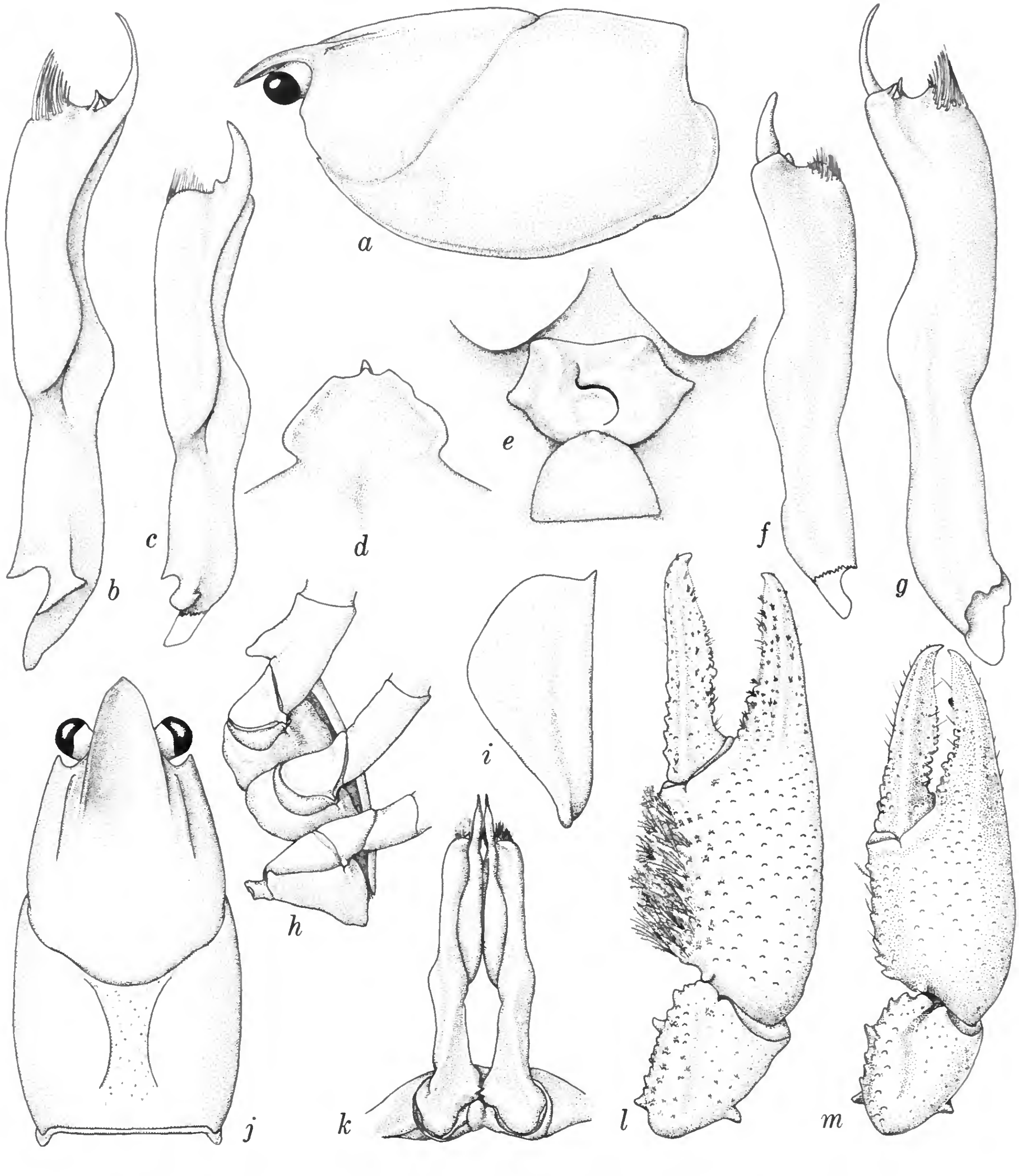


FIGURE 135.—*Procambarus (Leconticambarus) pubischelae deficiens* (all from holotype except *c*, *f*, from morphotype, and *e*, *m*, from allotype): *a*, lateral view of carapace; *b*, *c*, mesial view of first pleopod; *d*, epistome; *e*, annulus ventralis; *f*, *g*, lateral view of first pleopod; *h*, proximal podomeres of third, fourth, and fifth pereiopods; *i*, antennal scale; *j*, dorsal view of carapace; *k*, caudal view of first pleopods; *l*, *m*, dorsal view of distal podomeres of cheliped.

spines immediately proximal to transverse suture, largest immediately mesial to lateralmost member. Cephalic lobe of epistome (Figure 135*d*) subtriangular, with cephalic prominence somewhat truncate but with small cephalomedian projection; surface concave, margins not thickened, and fovea represented by relatively shallow depression. Antennular peduncle with small spine on ventral surface near midlength of basal podomere, mesial border of entire peduncle with plumose setae, not conspicuously developed on ultimate podomere. Antennal peduncle with ischium bearing spiniform tubercle; flagellum extending caudally only slightly beyond caudodorsal margin of carapace. Antennal scale (Figure 135*i*) about 2.1 times as long as broad, greatest width distal to midlength, lamellar portion about twice as wide as thickened lateral part, latter terminating in short spine.

Third maxilliped with ventral surface of proximal podomeres through basal half of merus, and also peduncle of exopod, conspicuously hirsute.

Right chela (Figure 135*l*) moderately short, somewhat depressed, and subovate in cross section. Mesial surface of palm with conspicuous brush of long plumose setae obscuring several rows of tubercles (mesialmost consisting of approximately 12); lateral surface with row of squamous tubercles, and dorsal and ventral surfaces with many similar but more prominent ones, although all becoming more depressed proximolaterally and at base of fixed finger; ventral surface with prominent tubercle distolateral to articular condyle at base of dactyl. Fixed finger with broadly rounded longitudinal ridge dorsally and ventrally, dorsal ridge flanked proximally by squamous tubercles giving way more distally to setiferous punctations; lateral surface very weakly costate, and opposable margin with row of 8 low tubercles along proximal three-fourths, third from base largest, and large tubercle projecting from lower level at base of distal fourth; clusters of minute denticles present between tubercles in row and forming comparatively broad band extending distally from sixth tubercle to base of corneous tip of finger. Dactyl with dorsal and ventral surfaces similar to those of fixed finger, and mesial surface bearing subserrate row of 5 tubercles, decreasing in size distally, along proximal half; opposable margin with row of 10 low, rounded tubercles along proximal three-fourths, and minute denticles as on fixed finger.

Carpus of right cheliped longer than broad (7.0 and 4.6 mm), with mesial, dorsomesial, and ventromesial surfaces tuberculate, otherwise punctate; dorsal surface with shallow oblique depression; mesial surface with 1 tubercle larger than others; ventral surface with moderately large tubercle at base of condyle on distolateral angle and 2 others mesially on distal margin.

Merus of right cheliped tuberculate dorsally and ventrally, dorsal tubercles generally progressively larger distally, with 2 preapical ones distinctly larger than others; mesial and lateral surfaces mostly punctate; ventral surface with mesial and lateral rows of 13 tubercles each, distal members of lateral one forming arc bent distinctly mesially toward large spikelike tubercle on distomesial angle. Ischium with row of 5 (left with 4) tubercles mesially, proximalmost deflected somewhat ventrally, larger and more squamous than others; dorsal margin with row of 3.

Hook on ischium of third pereiopod only (Figure 135*h*); hook simple and slightly overreaching distal extremities of corresponding basis. Coxa of fourth pereiopod without caudomesial boss; that on fifth prominent, subacute, and obliquely flattened.

Sternum between third, fourth, and fifth pereiopods rather deep and bearing heavy fringe of plumose setae on ventrolateral margins.

First pleopods (Figure 135*b,g,k*) as described in "Diagnosis."

Allotypic Female.—Differing from holotype, other than in secondary sexual characters, as follows: areola more densely punctate but with only 3 punctations across narrowest part; cephalic lobe of epistome with cephalomedian projection much reduced (third maxilliped and antennular peduncle as in holotype); chela with mesial surface of palm less conspicuously hirsute (Figure 135*m*) and bearing only 7 tubercles in mesialmost row; opposable margin of fixed finger of chela with row of 6 tubercles, and minute denticles arranged in single broken row rather than occurring in clusters and distal band; opposable margin of dactyl with row of 8 tubercles; distoventral margin of carpus with row of 4 or 5. (See "Measurements.")

Annulus ventralis (Figure 135*e*) moderately deeply embedded in sternum, rather small, and less than 1.5 times as broad as large postannular sclerite; cephalic area shallowly excavate, lacking tubercles or ridges, and caudal half somewhat depressed; sinus dextrally tilted and S-shaped. Postannular plate with small subacute cephaloventral projection extending ventrally, obscuring caudomedian portion of annulus. First pleopod reaching midlength of annulus ventralis.

MORPHOTYPIC MALE, FORM II.—Differing from holotype in following respects: cephalic extremity of rostrum rounded with no indication of acumen; areola with 5 punctations across narrowest part; mesial margin of antennular peduncle less hirsute than in either holotype or allotype; epistome with concave cephalic margin and very weak median projection; chela regenerated, mesial surface of palm with 7 tubercles in mesialmost row and lacking plumose brush of setae; rudiment of hook present on ischium of fourth pereiopod, that on third much smaller than corresponding one in holotype. (See "Measurements.")

First pleopod (Figure 135*c,f*) reaching caudal portion of coxa of second pereiopod with abdomen flexed; mesial process heavier but similar to and disposed as that in holotype; cephalic process also heavier but less conspicuous; caudal knob more rounded and with adnate central projection caudally; cephalodistal setiferous area as in holotype.

COLOR NOTES.—The color does not differ in any major aspect from that of either the striped or speckled phase of the nominate subspecies of *P. (L.) pubischelae* or *P. (L.) barbatus*.

TYPES.—The holotypic male, form I, allotypic female, and morphotypic male, form II (numbers 133315, 133316, 133317, respectively), are deposited in the National Museum of Natural History, Smithsonian Institution, as are the paratypes, consisting of 5♂I, 23♂II, 38♀, 13j♂, 41j♀, and 4 ovigerous ♀.

Measurements (mm)

	Holotype	*Allotype*	*Morphotype*
Carapace			
Height	12.5	12.1	12.8
Width	11.8	11.7	12.9
Entire length	23.6	22.9	24.3
Postorbital length	19.2	18.7	20.5
Areola			
Width	2.0	1.9	2.1
Length	7.5	7.5	7.8
Rostrum			
Width	4.3	4.0	4.5
Length	5.3	5.2	5.2
Chela			
Length of mesial margin of palm	7.0	5.2	7.6
Width of palm	6.3	5.3	5.9
Length of lateral margin	17.4	13.4	20.2
Length of dactyl	9.9	7.0	10.9
Abdomen			
Width	10.8	11.2	11.1
Length	27.1	26.0	28.3

TYPE-LOCALITY.—Roadside ditch, 3 miles south of Baxley, Appling County, Georgia, on U.S. Highway 1.

RANGE.—Restricted to the Coastal Plain Province of Georgia (in the Vidalia Upland, Bacon Terraces, and the Barrier Island Sequence districts) between the Ocmulgee-Altamaha and Satilla rivers (one locality situated immediately north of the Altamaha in Montgomery County).

GEORGIA SPECIMENS EXAMINED.—I have examined a total of 186 specimens from 24 localities as follows (those lots comprising the type series are marked with an asterisk). *Appling County*: *(1) type-locality, 2♂I, 1♂II, 5♀, 23 Aug 1937, HHH, collector; *(2) 1.5 mi S of Baxley on US Hwy 1, 3♂II, 2♀, 2 Jan 1938, HHH; *(3) 2 mi S of Baxley, 1♀, 7 Sep 1929, E. P. Creaser; *(4) 2.0 mi NE of Baxley on St Rte 144, 1♂I, 2♀, 3j♂, 5j♀, 5 Oct 1977, T. A. English, Jr., HHH; *(5) 1.1 mi W of Wayne Co line on St Rte 99, 2♀, 3 ovig ♀, 6 Oct 1977, TAE, HHH. *Camden County*: (6) about 12 mi S of Brunswick on US Hwy 18, 2♀, 19 Dec 1939, HHH; (7) 1.2 mi N of Rte S1850 on Rte S110, 1♂I, 1♀ with young, 27 Sep 1972, E. T. Hall, Jr., W. D. Kennedy, HHH. *Coffee County*:

(8) 0.4 mi SW of Jeff Davis Co line on US Hwy 221 (Hart and Hart, 1974:21), 1♂II, 1♀, 10j♂, 7j♀, 23 Apr 1966, ETH, HHH. *Glynn County*: (9) 11.3 mi S of Brunswick on US Hwy 17, 1♂I, 3♀, 27 Feb 1945, HHH; (10) 6 mi N of Brunswick on US Hwy 17 (Hart and Hart, 1974:90), 2♂II, 1♀, 27 Feb 1945, N. T. Blount, HHH. *Jeff Davis County*: *(11) 1.3 mi SW of Hazelhurst on US Hwy 221, 1♂I, 1♀, 2j♂, 1j♀, 23 Apr 1966, ETH, HHH; *(12) 3.6 mi SW of Hazelhurst on US Hwy 221 (Hart and Hart, 1974:21), 1♂I, 15♂II, 8♀, 7j♀, 23 Apr 1966, ETH, HHH; (13) 6.1 mi S of Denton on US Hwy 221, 4j♂, 1j♀, 23 Jun 1975, D. J. Peters, J. E. Pugh, HHH; (14) 4 mi S of US Hwy 341 on Hwy 221, 1♂I, 2♂II, 5♀, 23 Jun 1975, DJP, JEP, HHH; (15) 1 mi S of US Hwy 341 on Hwy 221, 1♀, 23 Jun 1975, DJP, JEP, HHH. *Montgomery County*: (16) 1.4 mi N of Jeff Davis Co line on US Hwy 221, 1♂II, 2♀, 23 Jun 1975, DJP, JEP, HHH; 1♂II, 1j♂, 20 Apr 1977, C. E. Carter, JEP, HHH. *Wayne County*: *(17) about 0.5 mi N of Jesup on St Rte 3, 1♂I, 8♀, 8j♂, 17j♀, 31 Dec 1938, HHH; 5♂II, 10♀, 11j♀, 1 ovig ♀, 27 Mar 1939, H. H. Wallace, HHH; (18) 13.6 mi NW of Jesup on St Rte 169, 1♂I, 1♂II, 5♀, 3♀ with young, 5 Oct 1977, TAE, HHH; 1♂I, 2♂II, 1♀, 4j♂, 2j♀, 3♀ with young, 27 May 1979, G. B. Hobbs, HHH; (19) just E of town limit of Odum on St Rte 27, 1♀, 26 May 1979, GBH, HHH; (20) 0.7 mi E of Rte S605 on Rte S1491, 2♂I, 3♂II, 6♀, 27 May 1979, GBH, HHH; (21) 5.6 mi E of Screven on Rte S1920, 1 ovig ♀, 25 May 1979, GBH, HHH; (22) 0.5 mi N of Rte S1920W on US Hwy 301, 1♀, 25 May 1979, GBH, HHH; (23) 1.0 mi SE of Gardi on US Hwy 341, 1♂I, 1♂II, 7♀, 28 May 1979, GBH, HHH; (24) 0.4 mi NE of US Hwy 341 at Akin on unnumbered road to Union Church, 3♂I, 1j♂, 1 ovig ♀, 28 May 1979, GBH, HHH.

VARIATIONS.—This subspecies is remarkably uniform throughout its range, and only in the extreme southeastern and western parts has evidence of its continuity with the typical subspecies been observed: in southern Camden, Berrien, Cook, Irwin, and Tift counties. (See "Variations" under the nominate subspecies.) One of the three males from the southeasternmost locality in Wayne County (locality 24 above) has small hooks on the fourth pereiopods but lacks bosses on the coxae.

SIZE.—The largest specimen available is a second form male with a carapace length of 27.2 (postorbital carapace length 22.4) mm. The smallest and largest first form males have corresponding lengths of 19.7 (16.0) mm and 23.9 (19.8) mm, respectively, and those of the smallest female bearing eggs or young, 20.9 (16.5) mm.

LIFE HISTORY NOTES.—First form males have been collected in February, April, May, June, August, September, October, and December. Ovigerous females were found in March (1), May (2), and October (3), and females with young in September (1) and October (3). (See "Seasonal Data.")

A tabulation of the number of eggs or young carried by six females follows. An asterisk indicates rostrum broken.

Carapace and postorbital carapace lengths (mm)	*Number of eggs/young*	*Diameter of eggs (mm)*
20.9 (16.5)	122e	1.5–1.7
* (18.3)	123e	1.8
22.8 (18.7)	100e	1.8–1.9
23.5 (19.0)	96e	1.7–1.8
23.5 (18.4)	112y	
23.8 (18.7)	98y	
24.3 (20.1)	128y	

Seasonal Data

Sex/stage	*J*	*F*	*M*	*A*	*M*	*J*	*J*	*A*	*S*	*O*	*N*	*D*
♂I		1		3	7	1		2	1	2		1
♂II	3	2	5	16	6	3		1		1		
♀	2	4	10	10	16	8		5	1	9		10
♂j				13	5	4				3		8
♀j			11	15	2	1				5		17
♀ ovig			1		2					3		
♀ with young					6				1	3		

ECOLOGICAL NOTES.—This subspecies occupies habitats that differ in no obvious way from those frequented by the nominate subspecies and *P. (L.) barbatus*.

RELATIONSHIPS.—There seems to be no reason to doubt that this crayfish has its closest relationship with *P. (L.) pubischelae pubischelae* and differs from it most conspicuously in that the males lack a hook on the ischium of the fourth pereiopod and a boss on the coxa of the same appendage, and possesses a more strongly recurved mesial process on the first pleopod; the females exhibit an annulus ventralis lacking tubercles or sublongitudinal ridges laterally.

CRAYFISH ASSOCIATES.—*Procambarus (L.) pubischelae deficiens* has been collected with the following crayfishes (the number of times they have been found together are noted in parentheses): *Procambarus (H.) caritus* (6), *P. (H.) talpoides* (5), and *P. (O.) seminolae* (12).

ETYMOLOGY.—From the Latin *deficiens* (to be wanting), so named because of the absence of a hook on the ischium of the fourth pereiopod, a boss on the coxa of the same appendage of the male, and tubercles or sublongitudinal ridges on the annulus ventralis.

Subgenus *Ortmannicus*

Subgenus *Cambarus*.—Ortmann, 1905a:97 [in part; not Erichson, 1846:97].

Subgenus *Ortmannicus* Fowler, 1912:341 [in part].—Hobbs, 1972a:9 [type-species: *Astacus Blandingii* Harlan, 1830: 464].

Subgenus *Ortmanmanicus*.—Hobbs, 1942a:342 [in part; erroneous spelling].

DIAGNOSIS.—Body pigmented or albinistic, eyes with or without pigment. Rostrum with or without marginal spines, tubercles, and median carina. Carapace with or without 1 cervical spine. Areola obliterated or as wide as 2.9 times as long as broad and constituting 25 to 43 percent of entire length of carapace. Third maxilliped never with more than proximal half of ventral surface of ischium obscured by plumose setae. Chela without beard or cristiform row of tubercles on mesial surface of palm. First 3 pairs of pereiopods without conspicuous brush of setae extending from basis to merus. Simple hooks on ischia of third pereiopods and simple or bituberculate ones on fourth. Coxa of fourth pereiopod with bulbous or subangular caudomesial boss. First pleopods of Georgia representatives reaching coxae of third pereiopods, asymmetrical, overlapping basally, with or without proximomedian lobe and lacking proximomesial spur; although hump on cephalic surface often present, shoulder usually absent, if present, that on right pleopod never folded caudally against mesial surface of pleopod; subapical setae present. Terminal elements of first pleopod consisting of lanceolate to subspiculiform mesial process directed caudodistally and frequently somewhat laterally; spiculiform to hood- or bladelike cephalic process situated cephalic or cephalomesial to central projection and directed caudodistally to caudally; caudal process (sometimes flanked mesially by ridgelike adventitious process) and/or caudal knob usually present (former bladelike to dentiform and situated caudal or caudomesial to central projection; caudal knob variable in size and form and situated between caudal and cephalolateral surface of distal part of appendage); and central projection massive to small, beaklike or bladelike to dentiform, and directed caudally, caudodistally, or distally. Mesial ramus of uropod with distomedian spine often reduced and never extending beyond margin of ramus. (Modified from Hobbs, 1972a).

RANGE.—From New England and the southern Great Lakes region southward and southwestward to Florida and northern Veracruz, Mexico. In Georgia it is largely confined to the Coastal Plain Province; two crayfishes (*P. (O.) a. acutus* and *P. (O.) pubescens*) have invaded the Piedmont Province, and one (*P. (O.) lophotus*), the Ridge and Valley Province.

GEORGIA SPECIES.—Of the 49 species and subspecies assigned to the subgenus, 11 (probably 12), representing three species groups, occur in Georgia. The *blandingii* Group: *Procambarus (Ortmannicus) acutissimus*, *P. (O.) a. acutus*, and *P. (O.) lophotus*; the *pictus* Group: *P. (O.) angustatus*, *P. (O.) enoplosternum*, *P. (O.) epicyrtus*, *P. (O.) litosternum*, and *P. (O.) pubescens*; and the *seminolae* Group: *P. (O.) fallax*, *P. (O.) leonensis* (?), *P. (O.) lunzi*, and *P. (O.) seminolae*.

HABITAT.—Virtually all members of the *pictus* Group frequent lotic habitats and rarely have individuals of any of the species comprising it been found more than a few meters from a body of flowing water. There is evidence that most of the females retreat to burrows prior to ovulation and remain there until the young have become independent. The members of the *blandingii* and *seminolae* groups have a far broader ecological tolerance, living in streams, ponds, lakes, temporary bodies of water in borrow pits, and roadside ditches. All are able burrowers, constructing a

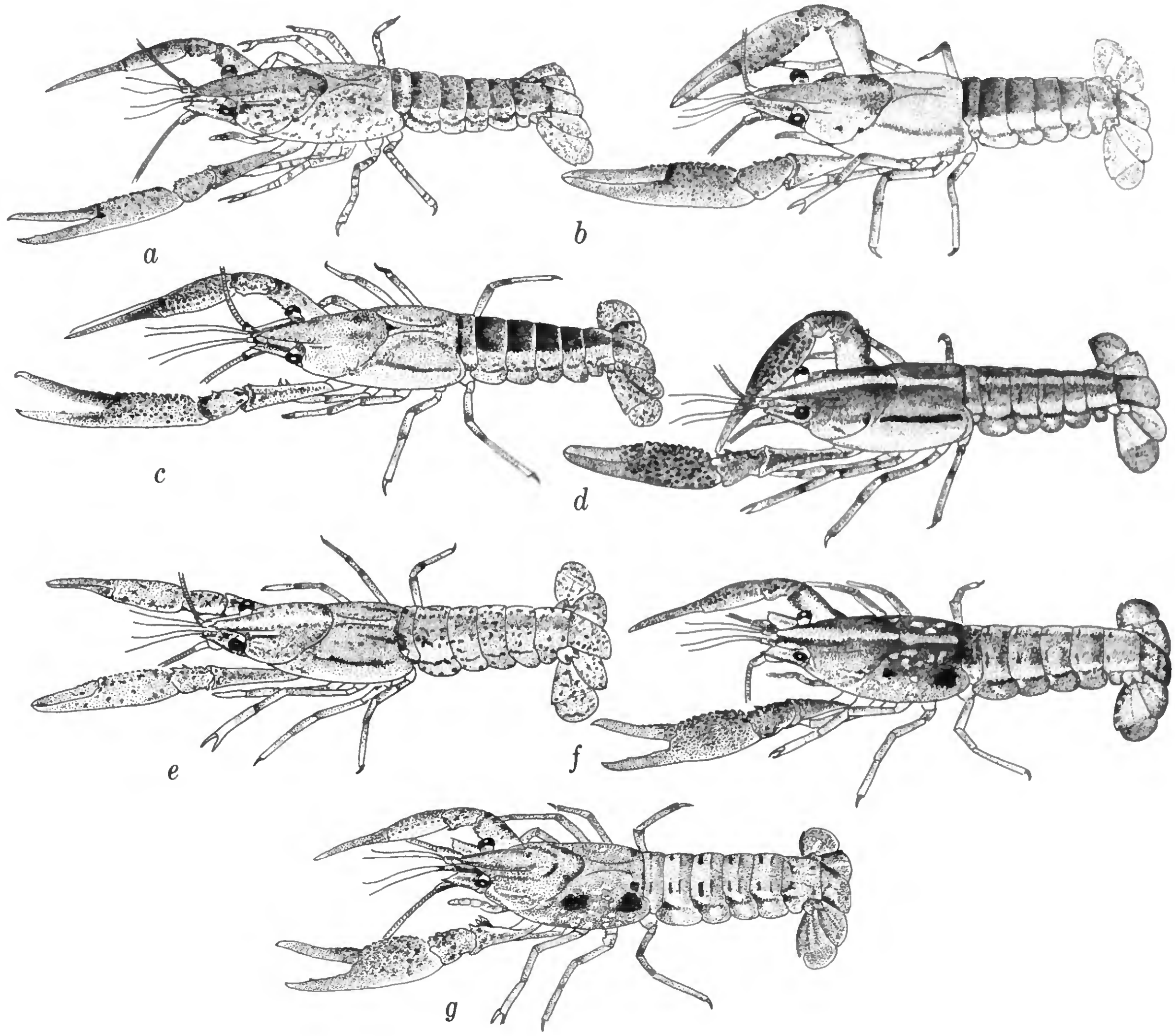


FIGURE 136.—Color patterns in members of subgenus *Ortmannicus*: *a*, *Procambarus (O.) acutissimus* from 4.2 mi W of Randolph Co line on US Hwy 82, Quitman Co; *b*, *P. (O.) acutus acutus* from 3.0 mi S of St Rte 80 on Rte 23, Burke Co; *c*, *P. (O.) lophotus* from creek on Jay's Mill Rd in Chickamauga Battlefield Park, Catoosa Co; *d*, *P. (O.) lunzi* from 2.3 mi S of US Hwy 280 on St Rte 119, Bryan Co; *e*, *P. (O.) fallax* from 0.4 mi N of Florida line on US Hwy 441, Echols Co; *f*, *P. (O.) seminolae* from 1.1 mi W of Wayne Co line on St Rte 99, Appling Co; *g*, *P. (O.) leonensis* from Lake Bradford slough, Leon Co, Florida.

single vertical to slightly sloping (occasionally inverted Y-shaped) passageway that may or may not reach the water table.

REMARKS.—The species comprising the *blandingii* Group, at least in Georgia, seem to be allopatric, but the total range of *P. (O.) acutissimus* is almost completely surrounded and partly overlapped by that of *P. (O.) a. acutus*. The range of *P. (O.) lophotus*, which in Georgia is isolated from those of *P. (O.) acutissimus* and *P. (O.) a. acutus*, overlaps that of both in Alabama. In the *seminolae* Group, *P. (O.) fallax*, *P. (O.) leonensis*, and *P. (O.) lunzi* are allopatric, but the northeastern part of the range of *P. (O.) seminolae* is shared with *P. (O.) lunzi*, and more than half of the southern part of its range encompasses the northern segment of that of *P. (O.) fallax*.

In Georgia, the *pictus* Group is confined to a narrow belt of the coastal plain and lower piedmont between the Savannah and Altamaha river basins, where there is a surprising amount of overlap in the ranges of such closely allied species. Almost certainly much of this is due to introductions resulting from the activities of fishermen. Excluding *P. (O.) angustatus*, the distribution of which is unknown, the range of each of the other four members of the group overlaps that of the other three—in some instances, to be sure, by "outlier" populations.

Identification of the male members of this group (particularly those in the first form) is comparatively easy, but occasionally the females offer considerable difficulty. One must depend almost exclusively on the secondary sexual characteristics to be certain of the identity of any of them.

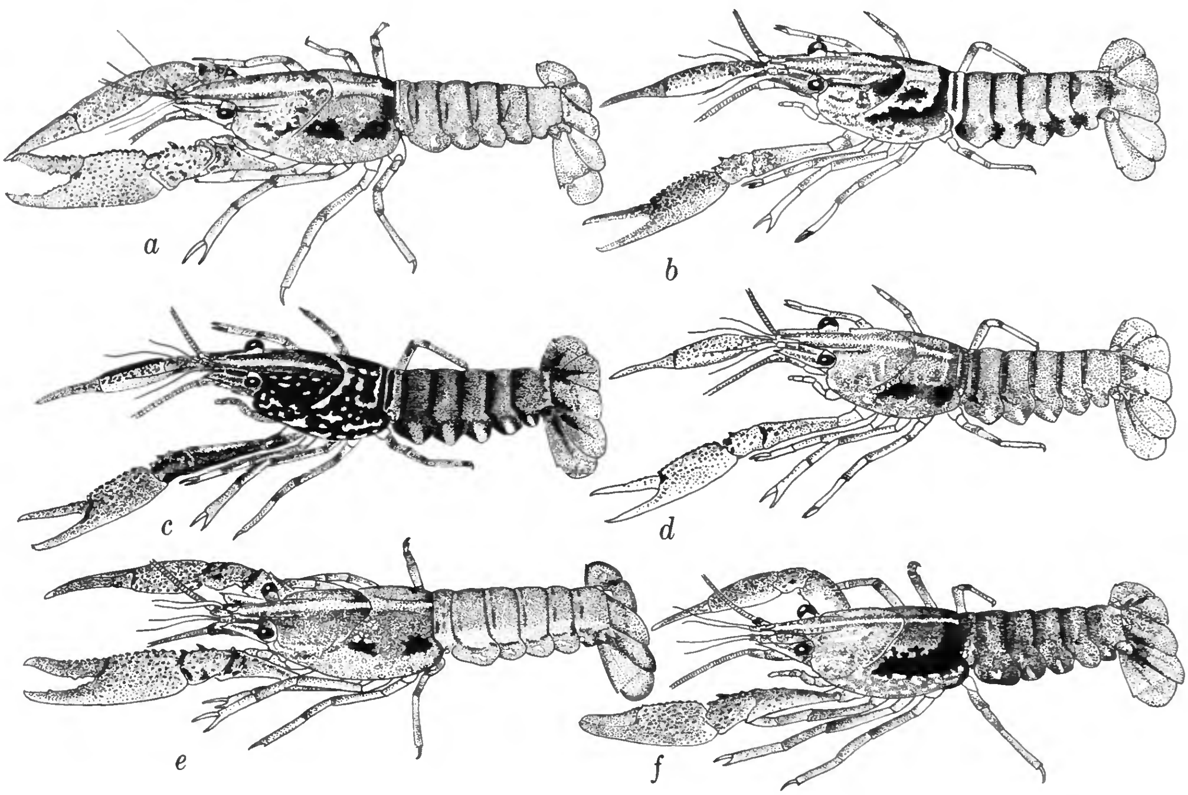


FIGURE 137.—Color patterns in members of subgenus *Ortmannicus*: *a*, *Procambarus (O.) epicyrtus* from South Ford of Ogeechee Creek at US Hwy 301, Screven Co; *b*, *P. (O.) enoplosternum* from Butler Creek in Augusta, Richmond Co; *c*, same from Rocky Creek 5.0 mi S of Burke Co line on Rte S1321, Screven Co; *d*, same from 2.9 mi SW of Wrightsville on St Rte 57, Johnson Co; *e*, *P. (O.) litosternum* from Sam's Creek at St Rte 46, Candler Co; *f*, *P. (O.) pubescens* from McBean Creek at Burke–Richmond Co line on St Rte 56.

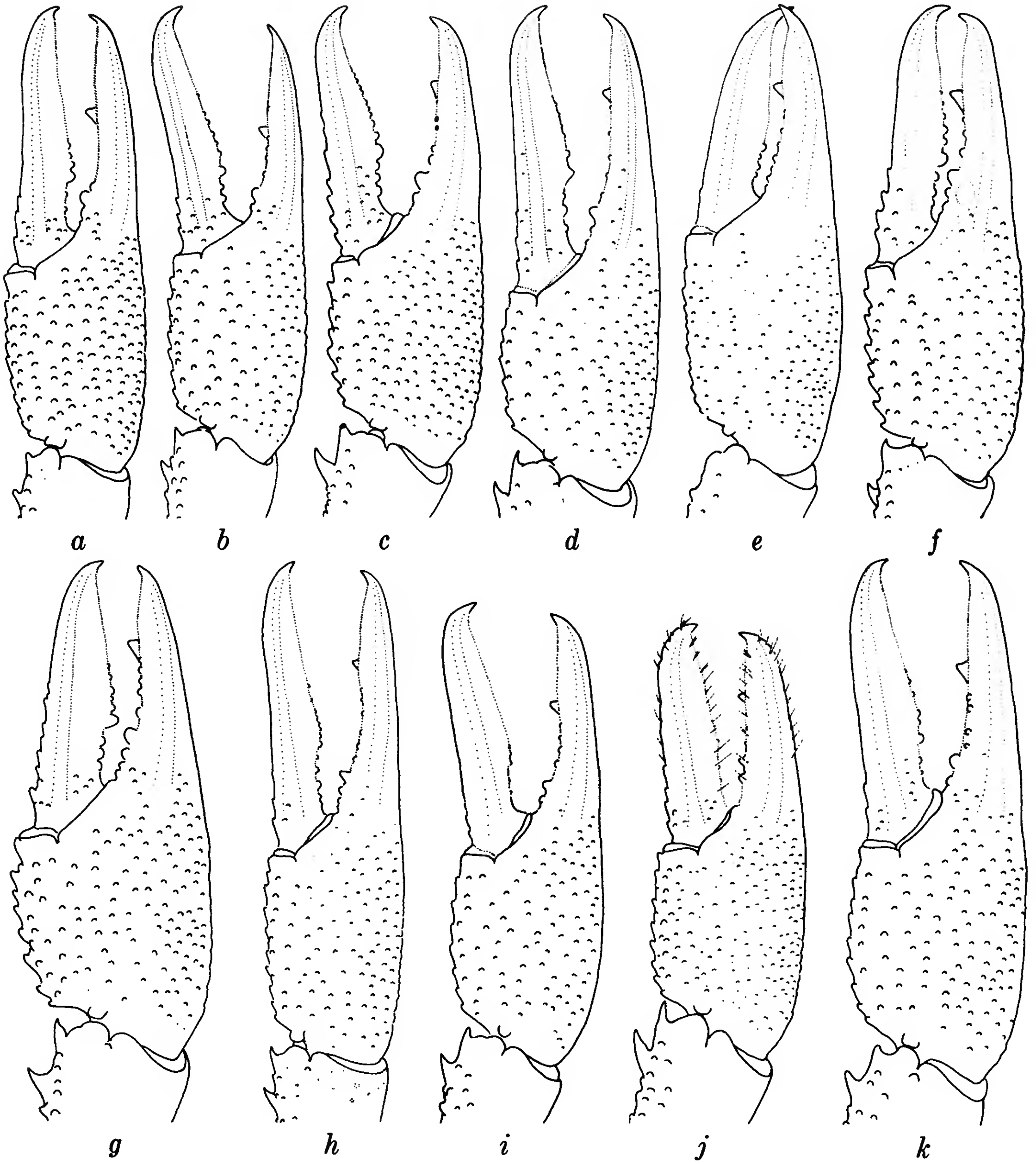


FIGURE 138.—Dorsal view of distal podomeres of chelipeds of female members of subgenus *Ortmannicus*: *a*, *Procambarus (O.) acutissimus* from Quitman Co; *b*, *P. (O.) acutus acutus* from Burke Co; *c*, *P. (O.) enoplosternum* from type-locality, Toombs Co; *d*, *P. (O.) epicyrtus* from type-locality, Screven Co; *e*, *P. (O.) fallax* from Clinch Co; *f*, *P. (O.) leonensis* from Leon Co, Florida; *g*, *P. (O.) litosternum* from type-locality, Emanuel Co; *h*, *P. (O.) lophotus* from Catoosa Co; *i*, *P. (O.) lunzi* from Bryan Co; *j*, *P. (O.) pubescens* from type-locality, Burke-Richmond Co line; *k*, *P. (O.) seminolae* from Jeff Davis Co.

Key to Georgia Members of Subgenus *Ortmannicus*
(Based on first form male)

1. Caudal knob of first pleopod well developed and situated lateral or cephalolateral to central projection (the *blandingii* Group) 2
   Caudal knob, if present, situated caudal or caudolateral to central projection 4
2. Distal extremity of caudal knob situated lateral to cephalic base of cephalic process; caudal process twisted and obscuring tip of central projection in lateral aspect .... ***acutus acutus***
   Distal extremity of caudal knob situated lateral to base of central projection; caudal process straight and never obscuring tip of central projection in lateral aspect 3
3. Distal fourth of appendage inclined caudally; caudal knob directed caudodistally; distinct gap present between central projection and caudal process .... ***lophotus***
   Distal fourth of appendage tapering cephalically but not inclined; caudal knob directed distally; base of caudal process overlapping part of central projection .... ***acutissimus***
4. Areola rarely less than 5 times as long as wide, if so, central projection of first pleopod either long and scythelike or reduced to very small toothlike projection; caudal knob never forming tumescent bulge on caudolateral end of shaft (the *seminolae* Group) 5
   Areola rarely more than 5 times as long as wide, if so, caudal knob forming tumescent bulge on caudolateral end of shaft of first pleopod; central projection never scythe- or toothlike (the *pictus* Group) 8
5. First pleopod with cephalic process directed distally and not hooding long, scythelike central projection .... ***seminolae***
   First pleopod with cephalic process directed caudodistally and usually partly hooding bladelike or dentiform central projection 6
6. First pleopod with central projection dentiform, never bladelike .... ***leonensis***
   First pleopod with central projection bladelike 7
7. First pleopod with mesial process flattened and lanceolate; apex of central projection never reaching level of caudal margin of distal expanded part of pleopod .... ***fallax***
   First pleopod with mesial process not flattened, tapering from base; apex of central projection at least reaching level of caudal margin of distal expanded part of pleopod .... ***lunzi***
8. First pleopod with both caudal knob and cephalic process very small, former reduced to small tumescent knob .... ***angustatus***
   First pleopod with either or both caudal knob and cephalic process well developed 9
9. First pleopod with caudal knob bulbous 10
   First pleopod with caudal knob subtruncate 11
10. Distal part of first pleopod strongly deflected caudally; caudal process

frequently almost as conspicuous as central projection ...... ***epicyrtus***
Distal part of first pleopod not strongly deflected caudally; caudal process not nearly so conspicuous as central projection .... ***enoplosternum***

11. First pleopod with cephalic process straight and far overreaching central projection distally; caudal knob not partly surrounding caudal base of central projection and not delimited laterally by longitudinal groove .... ***pubescens***
First pleopod with cephalic process short and hooding basal part of central projection; caudal knob ending in curved ridge along caudal side of central projection and delimited laterally by conspicuous longitudinal groove .... ***litosternum***

The *blandingii* Group

Procambarus (Ortmannicus) acutissimus (Girard)

FIGURES 15*c*, 136*b*, 138*a*, 139–142, 243

Cambarus acutissimus Girard, 1852:91.—Hagen, 1870:7, 9, 37.—Faxon, 1885a:11.—Fleming, 1939:299.—Hobbs, 1967a:124, 130; 1972a:2.
Cambarus acutus [in part].—Hagen, 1870:9.—Some authors prior to 1942.
Cambarus Blandingii var. *acuta* [in part].—Faxon, 1884:136; 1885a:20, 22.—Underwood, 1886:368.
Cambarus blandingii acutus [in part].—Faxon, 1914:413, followed by many authors prior to 1942.
Procambarus blandingii acutus [in part].—Hobbs, 1942b:94, and most authors from 1942 to 1955.
Procambarus acutissimus.—Hobbs, 1955a:98; 1959:890; 1962: 286, 288, fig. 51; 1967a:130, 131; 1968b:K-8, fig. 23e.—Hobbs and Walton, 1959:41; 1960b:123, 128.—Fitzpatrick and Payne, 1968:20.—Hobbs III, 1969:21, 30, 41, tab. 3.—Hobbs and Hall, 1974:199.—Hart and Hart, 1974:30, 87, 88, 90, 134.
Procambarus (Ortmannicus) acutissimus.—Hobbs, 1972a:9; 1972b:56, 150, 154, 155, figs. 21d, 46d; 1974b:53, fig. 246.—Bouchard, 1976c:14.
Procambarus acutissumus.—Hart and Hart, 1974:31 [erroneous spelling].

The references cited here constitute as near a complete bibliography of the species as I have been able to assemble. The lack of understanding of the species from 1870 to 1955, during which time there were no new records, misled authors during that period to follow Hagen's error in uniting Girard's *Cambarus acutissimus* and *Cambarus acutus* under the latter name.

SUMMARY OF LITERATURE.—The following brief description of this crayfish was offered by Girard, 1852: "Rostrum much more elongated than in any of the species of the same group; very much tapering and very acute, with slight indications of the lateral spines which are so well developed in *C. Blandingii.* The anterior abdominal pair of legs is terminated by a slender and recurved tip." The specimens on which this description was based were taken "from an affluent of Mobile river in Kemper Co., Miss.," and were received from D. C. Loyd, Esq. There is no statement as to how many specimens Girard had, and only two second form males that had been deposited in the Academy of Natural Sciences of Philadelphia were available to Hagen (1870). The latter erred on page 7 in transcribing Missouri for Mississippi in repeating Girard's locality, and on page 9 stated that "*C. acutissimus* is the second form of the male of *C. acutus.*" Referring to the "two young dry males" in the Academy of Natural Sciences, Hagen emphasized this opinion concerning their identity as follows: "There is no doubt that these males are the young of the species above described [*Cambarus acutus*], and I think also the veritable *C. acutissimus* Gir. . . ."

Faxon (1884, 1885a), considering Girard's *Cambarus acutus* to be a varietal form of *Cambarus Blandingii* (Harlan, 1830), and following Hagen's treatment of *C. acutissimus,* placed the latter in synonymy with his *Cambarus Blandingii* var. *acuta.* Faxon, in turn, was followed by Underwood (1886). In his checklist of the crayfishes, Faxon (1914) elevated his variety to subspecific rank, using the combination *Cambarus blandingii acutus* and continued to consider *C. acutissimus* a junior synonym of it.

Hobbs (1955a:98) resurrected Girard's *acutissimus*, assigning it to the genus *Procambarus*, without comment and recorded the first specific locality for the species, "11.3 miles south of Macon on Route 45, Noxubee County, Mississippi." Even though Hobbs (1962) illustrated the first pleopod of the species and noted that the range encompassed the Tombigbee, Alabama, and Choctawhatchee drainages in Alabama and Mississippi, he did not present a reason for separating his *P. acutissimus* from *P. blandingii acutus* until he (1967a: 130) stated:

> The 'paratypes' [of Girard's *C. acutissimus*], however, which are still extant, and located in the Academy of Natural Sciences of Philadelphia, clearly indicate the necessity for recognizing *C. acutissimus* as a distinct species. It has subsequently been collected from a number of localities in eastern Mississippi and western Alabama. . . .

The second specific locality cited for the species was that of Hobbs and Walton (1959): 18.8 miles east of Montgomery on Route 80, Macon County, Alabama, and Fitzpatrick and Payne (1968) noted that it had been found in the Sand Creek watershed in Oktibbeha County, Mississippi.

Hobbs III (1969) and Hart and Hart (1974) reported its occurrence in several localities in Alabama and Mississippi, where it served as host to some five species of entocytherid ostracods. Hobbs (1972b; 1974b) presented additional illustrations and defined its range. Hobbs and Hall (1974), in discussing siltation, reported that "tremendous populations occur in roadside ditches in which the water is so laden with finely divided particulate matter (principally clay particles) that a Secchi disk disappears at a depth of less than 5 cm below the surface." Those references not mentioned add nothing to our knowledge of the species except in terms of opinions of its affinities with other crayfishes.

This species is first recorded from Georgia herein.

Diagnosis.—Rostrum with or without marginal spines, tubercles, or angles at base of acumen, and lacking median carina. Carapace with or without 1 pair of cervical spines or tubercles. Areola 6.3 to 16.0 times as long as broad and constituting 29.7 to 35.4 percent of entire length of carapace (40.0 to 44.9 percent of postorbital carapace length). Antennal peduncle with well-developed spine, sometimes reduced to tubercle, on ischium. Ventral surface of basis and usually at least proximal half of ischium of third maxilliped with long plumose setae among simple stiff ones. Basis of cheliped without mesial spine. Mesial surface of palm of chela of male with row of 8 to 12 tubercles. Male with simple hooks on ischia of third and fourth pereiopods, both overreaching basioischial articulation, and that on fourth opposed by prominent tubercle on basis. First pleopods strongly asymmetrical and reaching coxae of third pereiopods; cephalic surface of neither member of pair with shoulder; subapical setae restricted to distal part of caudal knob; mesial process slender, often subspiculiform, and directed caudally to caudodistally and somewhat laterally; cephalic process corneous, acute, curved caudally almost at right angle to shaft of appendage, and somewhat hooding basal part of central projection; latter terminal element corneous, beaklike, situated between cephalic and caudal processes, and also directed caudally almost at right angle to shaft of appendage; caudal element consisting of caudal knob and caudal process; former subacute, located at cephalolateral base of central projection, its distal border studded with subapical setae, and basally continuous with lateral ridge on pleopod extending proximally for from one-fifth to half length of appendage; caudal process, situated on caudomedian extremity of shaft of appendage, mostly corneous, tapering to acute tip distally, not quite reaching apex of central projection; adventitious process lacking. Female with sternum anterior to annulus conspicuously multituberculate; annulus ventralis subspindle shaped, highly variable both in surface contour and in configuration of sinus, latter varying from single simple curve to S-shaped; first pleopod present.

Color Notes (Figure 136*b*).—Carapace brown dorsally, becoming suffused with red dorsolat-

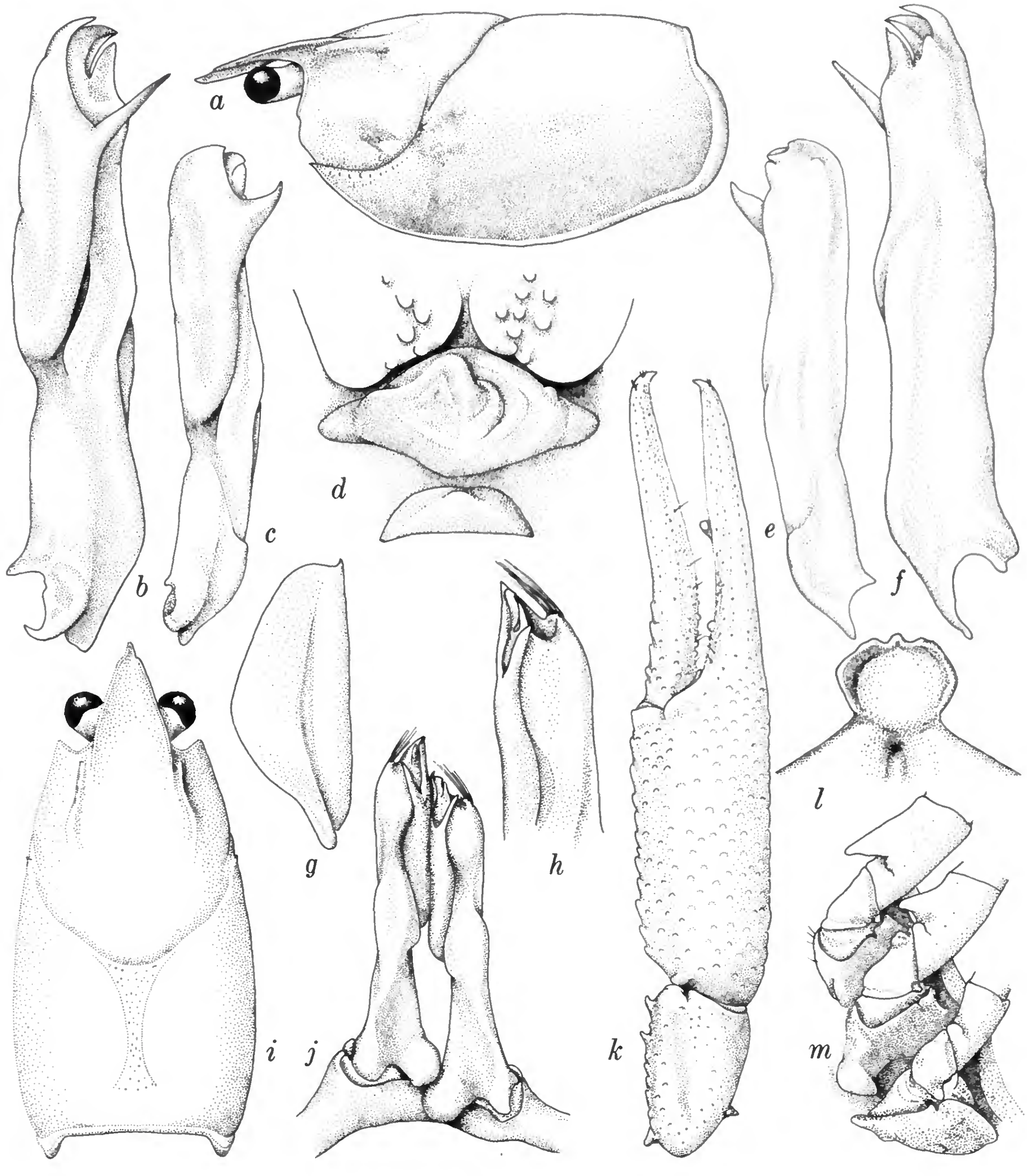


FIGURE 139.—*Procambarus (Ortmannicus) acutissimus* from 4.2 mi W of Randolph Co line on US Hwy 82, Quitman Co (all from first form male except *c*, *e*, from second form male, and *d*, from female): *a*, lateral view of carapace; *b*, *c*, mesial view of first pleopod; *d*, annulus ventralis; *e*, *f*, lateral view of first pleopod; *g*, antennal scale; *h*, caudal view of distal part of first left pleopod; *i*, dorsal view of carapace; *j*, caudal view of first pleopods; *k*, dorsal view of distal podomeres of cheliped; *l*, epistome; *m*, proximal podomeres of third, fourth, and fifth pereiopods.

erally, and fading to pinkish tan or gray ventrally. Symmetrically arranged black spots occurring dorsally, 1 pair in hepatic region, and another at lateral junction of rami of cervical groove; branchiostegite with rather narrow longitudinal black stripe; posterior extremity of stripe joining submarginal one and coursing caudally from at least midlength of branchiostegite to and along anterior margin of caudal flange; pale pinkish gray to cream spots intermingled with dark tan ones scattered over most of lateral surface of carapace. Abdomen with broad dorsomedian, almost black stripe gently tapering caudally from first to sixth abdominal tergum; median stripe flanked by paired, narrower pink ones, and they, in turn, by yet narrower scalloped brownish to black stripe extending along bases of pleura; ventral parts of pleura mottled with tan and brown spots on pinkish background; telson and uropods also mottled with tan and brown on olive tan. Antennular and antennal peduncles and flagella olive brown, peduncles with black markings. Dorsal surface of distal 4 podomeres of third maxilliped olive tan. Cheliped tan to brown dorsally from distal part of ischium to yellowish apex of fingers; all podomeres with black tubercles and/or spines; lateral part of chela suffused with orange, and ventral surface more orange than tan. Remaining pereiopods olive brown dorsally from ischium distally, merus and carpus darker than other podomeres, and those of chela of second pereiopod paler than distal podomeres of other pereiopods.

TYPES.—ANSP 309 (2♂II).

TYPE-LOCALITY.—Affluent of Mobile River, Kemper County, Mississippi.

RANGE.—This crayfish is largely confined to the lower Piedmont and upper Coastal Plain provinces of Alabama and eastern Mississippi; a single locality for it occurs in the Fall Line Hills District of the Coastal Plain Province in Quitman County, Georgia. In Alabama, it is known from the following counties: Autauga, Bullock, Calhoun, Coffee, Dallas, Greene, Hale, Jefferson, Lowndes, Macon, Marengo, Montgomery, Perry, Pike, Shelby, Sumter, and Wilcox; in Mississippi, it has been collected in Clay, Kemper, Lauderdale, Noxubee, and Oktibbeha counties.

SPECIMENS EXAMINED.—*Quitman County:* pools and burrows along roadside adjacent to Pataula Creek, 4.2 mi W of Randolph Co line on US Hwy 82, 1♂I, 2♀, 3j♂, 4j♀, 17 Apr 1974, D. J. Peters, HHH, collectors. In addition, I have examined 634 specimens from Alabama and Mississippi collected in a number of localities in the counties listed under "Range."

VARIATIONS.—With so few specimens available from Georgia, no conclusion can be drawn concerning the consistency of differences noted in the juveniles and adults, but the areola appears to be comparatively broader and shorter in the young. Over its entire range, this crayfish exhibits a rather striking array of variations, not only in features of the carapace but also in the secondary sexual characters. Although the name "*acutissimus*" was derived from the strongly acute rostrum of the specimens from Kemper County, Mississippi, that were available to Girard, the range of variability in the form of the rostrum in material from the Tombigbee-Mobile Basin in the county is rather striking (Figure 141*c*,*d*). In specimens from farther upstream in Oktibbeha County (Figure 141*e*,*f*), well-developed marginal spines are present. Postorbital and cervical spines are absent in most adult members from Kemper County, and those on the basis and ischium of the antennal peduncle are rudimentary at best; in contrast, all of these spines are well developed in representatives from Oktibbeha County. In their reduced spination, the Georgia specimens (Figure 141*a*,*b*) more nearly resemble those from Kemper County. The first pleopods of those from the two Mississippi areas are much more similar to one another than is either to the pleopod of the Georgia male. The major differences lie in the disposition of the caudal process—which in specimens from Mississippi (Tombigbee Basin) are more elongate, extending much farther proximally than in crayfish from elsewhere in the range—and in the lateral surface of the pleopod. In males from the Tombigbee watershed (Figure 142*f*,*l*), there is a strong, comparatively sharp, straight ridge extending proximally from the caudal knob; in the material from the Choctawhatchee and Chattahoochee basins (Figure 142*a*,*b*,*g*,*h*), the ridge is not so well defined and is

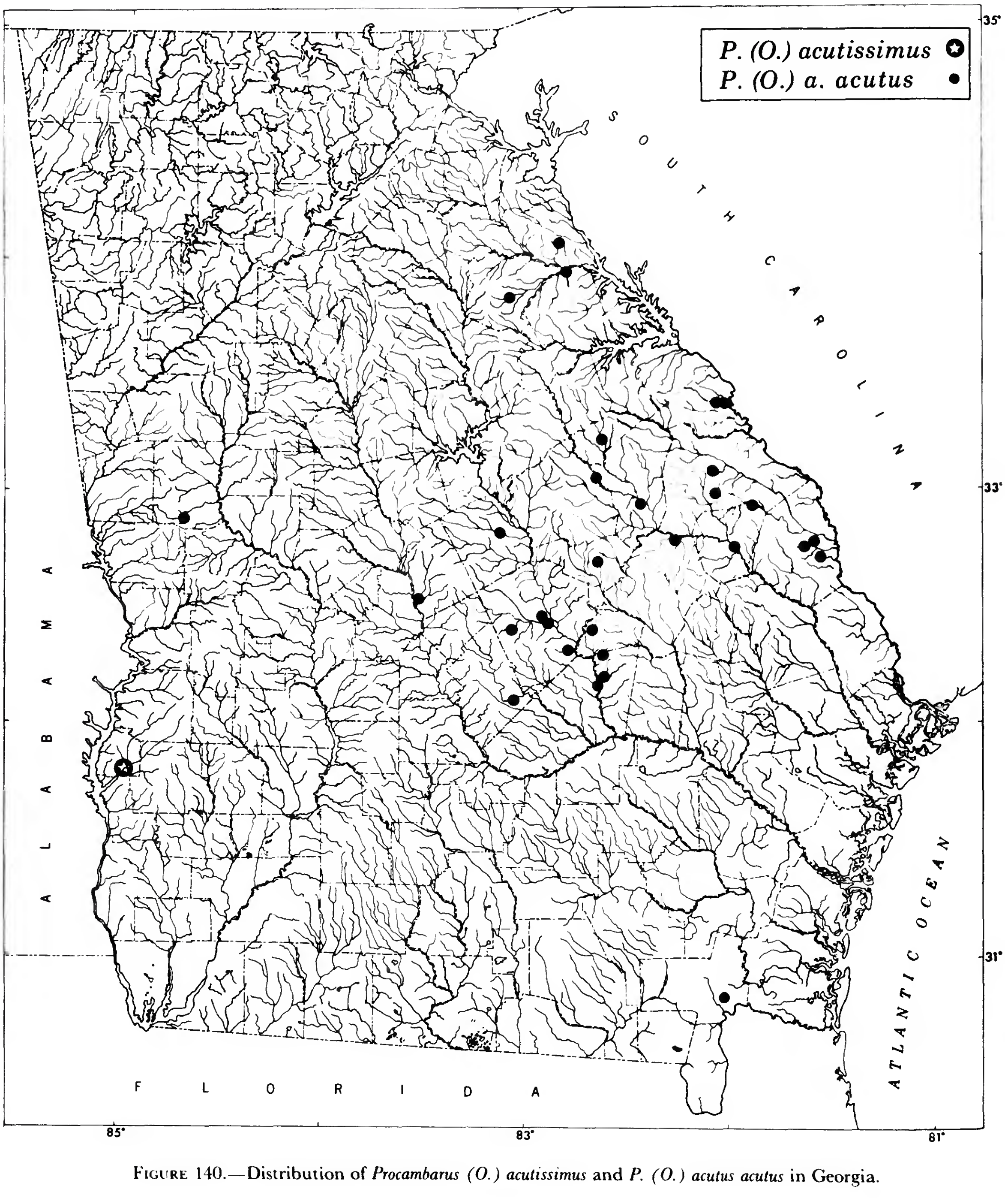


FIGURE 140.—Distribution of *Procambarus (O.) acutissimus* and *P. (O.) acutus acutus* in Georgia.

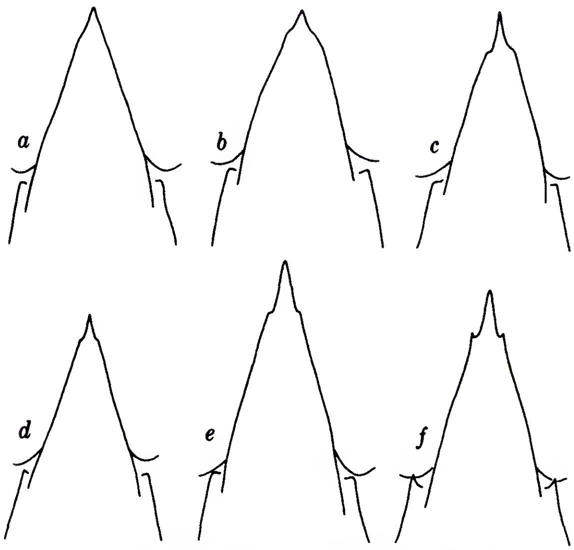


FIGURE 141.—*Procambarus (O.) acutissimus*, variation in rostrum: *a, b*, Pataula Creek, Quitman Co, Georgia; *c, d*, tributary of Noxubee River, Kemper Co, Mississippi; *e, f*, tributary of Sand Creek, Oktibbeha Co, Mississippi.

arched cephalically. The mesial process of the pleopod in the specimen from Georgia is directed less strongly laterally (Figure 142*g*) than it is in those from other parts of the range and is deflected most in representatives of the Tombigbee populations (Figure 142*k,l*). As pointed out elsewhere, the annulus ventralis is highly variable, but those of the two females from Georgia resemble the annuli of specimens from the type-locality more closely than those of members of the species I have examined from elsewhere. The most conspicuous difference that seems to exist is in the surface contour of the annulus, which ranges from comparatively smooth with a ventromedian elevation to one that is irregular and equally as sculptured as that illustrated (Figure 139*d*). The shape of the sinus varies from a simple arc to consisting of two hairpin curves situated along the median line near midlength of the annulus.

SIZE.—Only three adult specimens have been collected in Georgia. The first form male has a

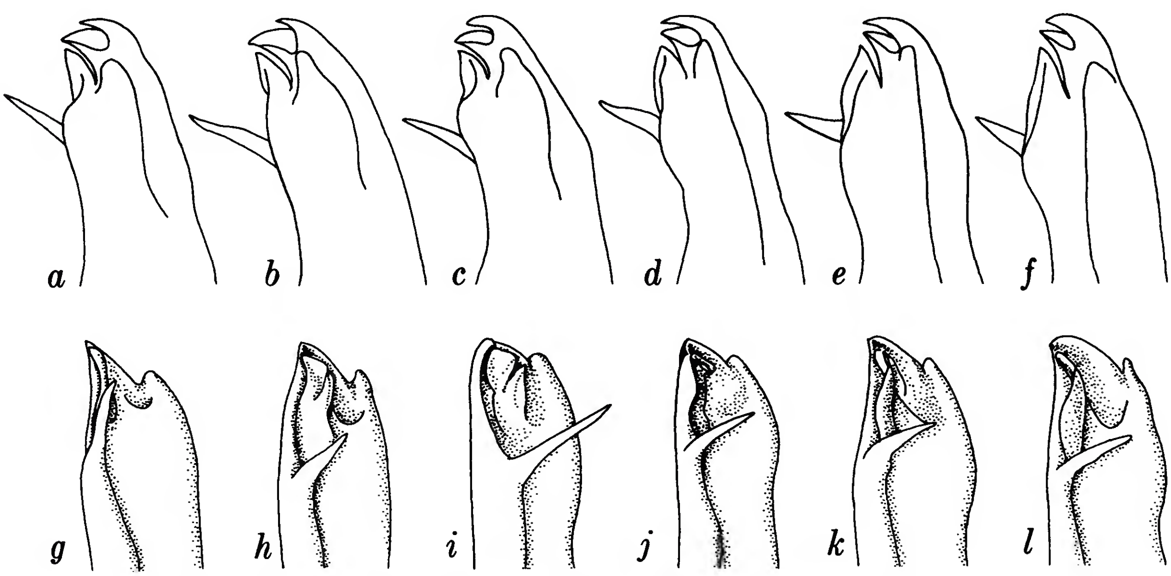


FIGURE 142.—*Procambarus (O.) acutissimus*, variations in first pleopod of first form male (*a–f*, lateral view; *g–l*, caudal view): *a, g*, Chattahoochee Basin, Quitman Co, Georgia; *b, h*, Choctawhatchee Basin, Coffee Co, Alabama; *c, i*, Alabama Basin, Montgomery Co, Alabama; *d, j*, Tombigbee Basin, Sumter Co, Alabama; *e, k*, Noxubee-Tombigbee Basin, Kemper Co, Mississippi; *f, l*, Tombigbee Basin, Oktibbeha Co, Mississippi.

carapace length of 32.3 (postorbital carapace length 25.6) mm; corresponding lengths of the two females are 34.8 (27.2) mm and 34.1 (26.8) mm.

LIFE HISTORY NOTES.—Throughout its range, first form males have been collected in March, April, June to September, and in December. It therefore seems likely that such males may be found during every month of the year. The fact that no ovigerous females or ones carrying young occur among the 130 adult females that have been examined by me strongly suggests that they retreat to burrows prior to egg laying, remaining in them until the young become independent; unfortunately there are no data, in the absence of a knowledge of growth rate, that suggest a season of ovulation.

Seasonal Data (Alabama, Georgia, and Mississippi)

Sex/stage	*J*	*F*	*M*	*A*	*M*	*J*	*J*	*A*	*S*	*O*	*N*	*D*	*?*
♂I			8	32		4	4	3	1			1	3
♂II		2	6	48	3	11	2	2	1	2			1
♀		1	10	84	4	13	8	4	1			1	4
♂j		1	3	156		5			1	2			
♀j		1	10	190		9			1		1		

ECOLOGICAL NOTES.—This crayfish, like most members of the *blandingii* Group of the subgenus *Ortmannicus*, indeed like many members of the genus *Procambarus*, frequents habitats ranging from temporary fluctuating pools or ponds to permanent lotic habitats, some even with a moderately swift current. It also constructs simple burrows that are occupied during dry seasons, and, as pointed out above, probably by females prior to ovulation. Specimens have been collected in roadside pools that are choked with emergent and submergent plants and in others in which there is no trace of macroscopic plants. In the latter pools, I have found population sizes that were almost unbelievably large, and the water so roiled, presumably due to the activity of the crayfish, that the suspended particles made the bed of the pool obscure, even at the edge where the water was hardly more than one centimeter deep.

In the Georgia locality, one of the females was taken from a pool and was feeding on a juvenile of the same species. The first form male and the other female were obtained from a single, simple burrow topped by a plugged chimney some seven centimeters tall.

GEORGIA CRAYFISH ASSOCIATES.—Collected with *P. (O.) acutissimus* in the pool and adjacent burrows along Pataula Creek were *Cambarus (D.) striatus* and *C. (L.) d. diogenes*.

Procambarus (Ortmannicus) acutus acutus (Girard)

FIGURES 15*b*, 136*a*, 138*b*, 140, 143–145, 244

Cambarus acutus Girard, 1852:91.
Astacus Blandingii [in part].—LeConte, 1856:400*.
Cambarus acutus var. A.—Hagen, 1870:36.
Cambarus acutus var. B.—Hagen, 1870:36.
Cambarus blandingii [in part].—Many authors from 1870 to 1962.
Cambarus stygius Bundy, 1876:3. [Type not extant. Type-locality, Lake Michigan at Racine, Racine County, Wisconsin].
Cambarus Blandingii, var. *acuta*.—Faxon, 1884:113; 1885a:20, pl. 7: figs. 2, 2′, 2″, 2*a*, 2*a*′.
Cambarus Stygius.—Underwood, 1886:373 [*lapsus calami*].
Cambarus blandingii acutus.—Faxon, 1890:619.
Cambarus blandingii blandingii [in part].—Many authors from 1890 to 1962.
Camborus blandingii acutus.—Williamson, 1899:47 [erroneous spelling].
Cambarus blandingi acutus.—Ortmann, 1905a:105.
Cambarus (Cambarus) blandingi acutus.—Ortmann, 1905a:126 [by implication].—Fleming, 1938:301.
Cambarus (Ortmannicus) blandingii acutus.—Fowler, 1912:341 [by implication].—Fleming, 1938:303.
Procambarus blandingii acutus.—Hobbs, 1942a:343 [by implication].
Procambarus blandingii blandingii [in part].—Many authors from 1942 to 1962.—Villalobos, 1959:316 [in part].
Ortmannicus blandingi acutus.—Rhoades, 1942:1.
Cambarus blandingi acutis.—Roberts, 1944:364 [erroneous spelling].
Procambarus acutus acutus.—Hobbs, 1968b:K-8*, figs. 21o, 23d; 1967a:130.—Reimer, 1969:56*.—Hart and Hart, 1974: 21*-24, 26, 30*-33, 59, 60, 64, 71, 73, 85, 87-89, 90*, 91, 93, 109, 119, 129*, 134.—Wharton, 1978:220*.
Procambarus (Ortmannicus) acutus acutus.—Hobbs, 1972a:9; 1972b:57*, 150*, 154-156*, figs. 5f, 27d, 47a; 1974b:53*, fig. 240.—Hobbs III, Thorp, and Anderson, 1976:3, 11, 33-35*, figs. 14, 23.

Procambarus (Ortmannicus) actus actus.—Payne and Riley, 1974: 127 [erroneous spelling].
Procambarus actus.—Comeaux, 1976:614 [erroneous spelling].
Procambarus (Ortmanicus) acutus acutus.—Hobbs III, Thorp, and Anderson, 1976:58 [erroneous spelling].
Procambasrus acutus acutus.—Huner, 1977:10 [color photograph; erroneous spelling].

The above list of references by no means constitutes a complete bibliography of the species; insofar as I am aware, it is a complete synonomy except for possible misidentifications; it also includes a number of citations to illustrations and all references to the occurrence of the species in Georgia (noted by asterisks) that I have encountered.

SUMMARY OF LITERATURE.—This crayfish is perhaps the least understood of any member of the genus *Procambarus*. Considering the fact that the name *acutus* as applied to this crayfish appears in the literature in various combinations almost as frequently as do those used for *Procambarus (S.) clarkii*, it is surprising that not even the range of the species can be clearly defined. The confusion surrounding its identity began with Hagen (1870), who believed that Girard's (1852) *Cambarus acutus* and *Cambarus acutissimus* were synonymous, and he was very uncertain as to the range in variation in Harlan's *Astacus Blandingii*. Matters were not helped when Bundy (1876) described *Cambarus stygius*, a name that remained a "species inquirendum" (suspected of being synonymous with Girard's *C. acutus* as early as 1885 by Faxon) until Creaser (1932:335) declared it a synonym of *Cambarus blandingii acutus* (= Girard's *C. acutus*). Faxon (1884, 1885a) treated Girard's species as a variety "*acuta*" of *Cambarus Blandingii*, and in 1890 he introduced the combination *Cambarus blandingii acutus*. Nevertheless, there was still a question as to the distinction between it and the nominate subspecies. As nearly as I can determine, the assignment of members of the species to the two subspecies rested almost solely on the source of the specimens: those in the Atlantic drainage were assigned to *Procambarus blandingii blandingii* and those in the Gulf watershed to *P. b. acutus*. This distinction persisted until 1962, when Hobbs, after examining the cotypes of *Procambarus acutissimus* and obtaining topotypes of it, as well as of *P. acutus* and *P. blandingii*, illustrated the diagnostic features of the three but indirectly admitted that he could not define the ranges of the latter two, to which he applied the subspecific ranks proposed by Faxon: *Procambarus blandingii blandingii* and *P. b. acutus*. In 1967, Hobbs became convinced that the range of the latter almost completely surrounded that of the former, and, in failing to find any evidence of a gene exchange in areas where their ranges were contiguous, he proposed recognizing *P. acutus* as distinct from *P. blandingii*. He recognized two geographic subspecies, *P. a. acutus*, and *P. a. cuevachicae* (Hobbs, 1941a:1), and in 1972 (b: p. 57) he stated that the nominate subspecies inhabited "sluggish to moderately flowing streams and lentic habitats in the coastal plain and piedmont from Maine to Georgia, from Minnesota to Ohio, and from the Florida panhandle to Texas; intergrades with *P. a. cuevachicae* in Texas and northern Mexico." There are several "variants" of *P. a. acutus*, a few of which appear to be regionally restricted, and indeed one or more should perhaps be accorded specific or subspecific rank. Until a comprehensive study of the species throughout its range can be undertaken, considerable doubt will attend the assignment of specimens to either of the currently recognized subspecies. Furthermore, all ecological and life history data that have been recorded for the species will have to be reevaluated should the ranges of the two have to be redefined.

Until Hart and Hart (1974) cited four precise records for *P. a. acutus* in Georgia (see "Georgia Specimens Examined" below), there were no reported localities for the species in the state. In treating "*Astacus Blandingii*," LeConte (1856:400) gave the range as "Habitat in Georgiae et Carolinae regionibus intermediis." Inasmuch as this crayfish is not known to occur within the state, it is probable that the specimens he had observed in Georgia were members of *P. a. acutus*. Hagen (1870:45) questioned LeConte's record for Georgia and did not include either *C. acutus* or *C.*

blandingii in his list of crayfishes from the state (1870:100). No further reference to the occurrence of the species in Georgia appeared until Villalobos (1959:316), in discussing "*Procambarus b. blandingii*," concluded from published records that this crayfish occurs in Georgia but cited no authority. On the basis of personal communication from Hobbs, Reimer (1969:56) defined the range of the species in almost the same terms as that quoted above from Hobbs (1972b). Georgia was again mentioned in statements concerning the range by Hobbs (1968a, 1974b) and Hobbs III, Thorp, and Anderson (1976).

DIAGNOSIS.—Rostrum usually with marginal spines, tubercles, or at least distinct angles at base of acumen, rarely with margins tapering from base to apex of acumen; median carina absent. Carapace with 1 pair of cervical spines or tubercles. Areola 5.4 to 19.7 (average 11.5) times as long as broad and constituting 27.8 to 35.9 (average 32.5) percent of entire length of carapace (40.7 to 47.3, average 44.1, percent of postorbital carapace length). Antennal peduncle with spine or subacute tubercle on ischium. Lateral half of ventral surface of ischium of third maxilliped sometimes with long plumose setae on proximal half, always absent on distal half. Basis of cheliped without mesial spine. Mesial surface of palm of chela of male with mesialmost row of tubercles consisting of 7 to 9. Male with simple hooks on ischia of third and fourth pereiopods, both overreaching corresponding basioischial articulation but neither opposed by tubercle on corresponding basis. First pleopods asymmetrical and reaching coxae of third pereiopods; proximomesial extremity of both strongly angular; distal half of shaft gently inclined caudally; cephalomesial surface with rudimentary shoulder; subapical setae studding caudal knob and forming row around cephalic side of appendage to caudomesial base of cephalic process and largely obscuring cephalic process and much of central projection; mesial process rather slender, elongate, subcylindrical or somewhat flattened, and directed caudodistally and laterally; cephalic process hooding base of central projection, becoming compressed, and forming narrow corneous bladelike element extending caudodistally subparallel to, but not reaching so far as, central projection; latter most conspicuous of terminal elements, strongly sclerotized, tapering, somewhat twisted toward apex, and directed caudodistally; caudal process also strongly sclerotized, flattened, tapering distally, and contiguous to caudolateral base of central projection; caudal knob, studded with long, simple setae, situated at lateral base of cephalic process; adventitious process lacking. Female with sternum cephalic to annulus ventralis sometimes lacking projections or tubercles, but more frequently with at least 1 pair of small tubercles and with caudal margin produced (rarely in distinct lobes), overhanging (ventrally) cephaloventral part of annulus; latter subovate, with prominent dextral elevation near midlength, under which tongue from sinistral side disappearing; sinus S-shaped although skewed; postannular sclerite at least two-thirds as broad as annulus; first pleopod present.

COLOR NOTES (Figure 136*a*).—Carapace tan dorsally, fading laterally to pale mauve with cream to white markings. Dark brown to almost black flecks and paler brown splotches present over entire carapace; dark brown stripe flanking ventral side of postorbital ridges, and caudalmost part of gastric region also brown. Abdomen with broad, dorsomedian, longitudinal, brown stripe, dark anteriorly and fading posteriorly; each tergum darker anteriorly than elsewhere, and caudal margin very pale cream tan, sometimes suffused with pink; paired, pale pinkish stripes flanking median dark one, and these in turn bounded ventrolaterally by scalloped dark stripe extending along bases of pleura; remainder of latter pale pink. Telson with pair of reddish brown spots anterolaterally, otherwise it and uropods pinkish tan, with brown flecks and irregular dark tan splotches; entire dorsum of abdomen with brown to black flecks. Antennular and antennal peduncles pinkish tan with dark brown markings, flagella very pale tan, antennular flagella banded with brown; antennal scale pinkish cream, with brown splotches on lateral border and lamellar

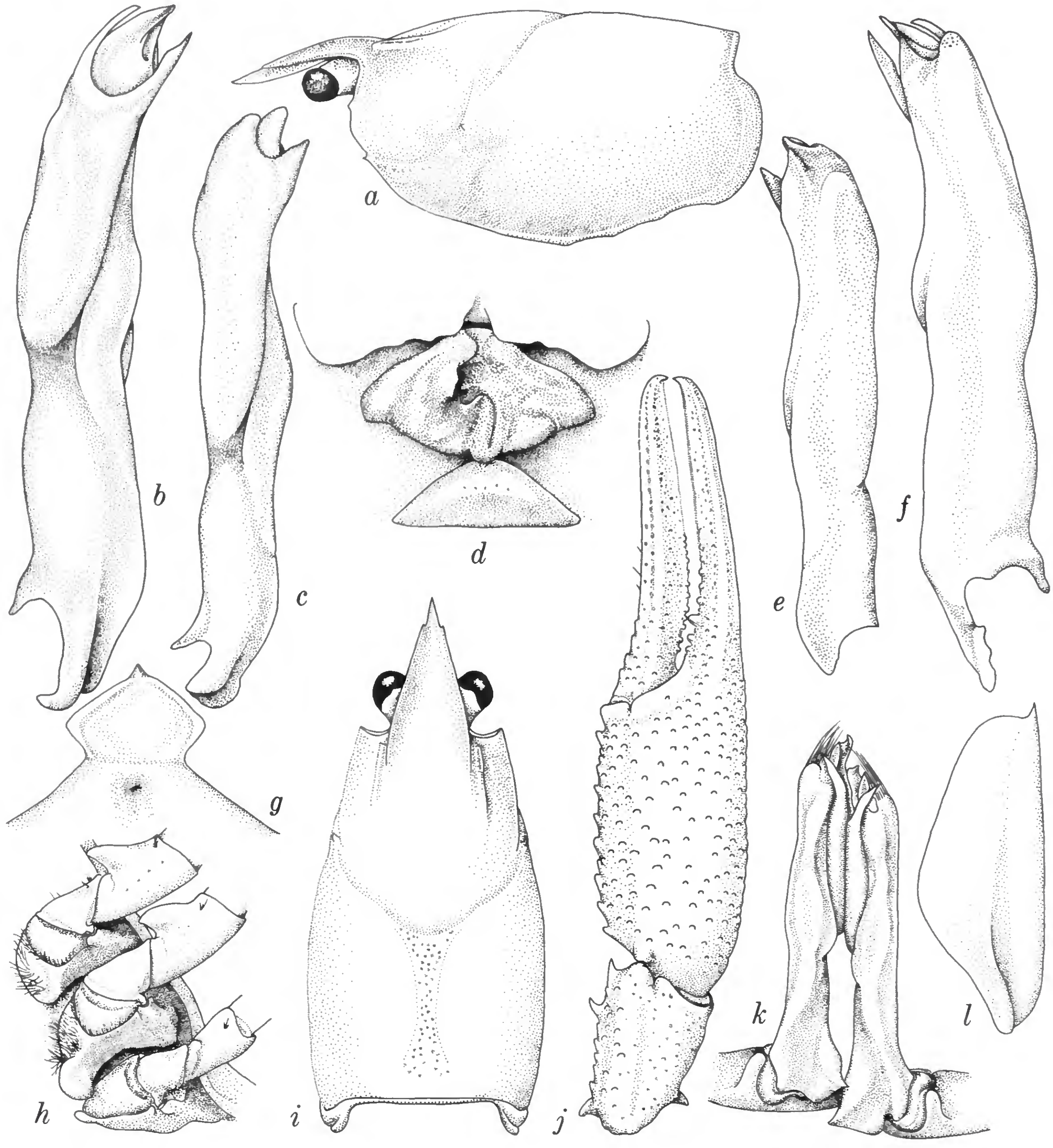


FIGURE 143.—*Procambarus (Ortmannicus) acutus acutus* (*c*, *e*, from second form male from Buck Creek at Rte S1321, 3.8 mi E of Sylvania, Screven Co; *d*, from female, and all others from first form male from Walnut Branch 3 mi SW of Waynesboro, Burke Co): *a*, lateral view of carapace; *b*, *c*, mesial view of first pleopod; *d*, annulus ventralis; *e*, *f*, lateral view of first pleopod; *g*, epistome; *h*, proximal podomeres of third, fourth, and fifth pereiopods; *i*, dorsal view of carapace; *j*, dorsal view of distal podomeres of cheliped; *k*, caudal view of first pleopods; *l*, antennal scale.

area pink. Third maxilliped with dorsal surface of ischium pinkish cream distally and splotched with tan. Dorsal surface of cheliped from distal part of basis to pale tips of fingers pinkish tan, with irregular light brown to almost black markings, most tubercles on palm of chela and carpus very dark. Remaining pereiopods also pinkish tan with irregular darker bands and splotches. Sternal area of cephalothorax cream to pinkish cream.

TYPES.—Not extant.

TYPE-LOCALITY.—An affluent of Mobile River in Kemper County, Mississippi.

RANGE.—"Coastal plain and piedmont from Maine to Georgia, from Florida panhandle to Texas, and from Minnesota to Ohio; intergrades with *cuevachicae* in southwestern Texas and northern Mexico" (Hobbs, 1974b:53). In Georgia it has been found in only three localities in the Piedmont Province: in Elbert, Meriwether, and Wilkes counties, and it was introduced in the Meriwether County locality (fide J. H. Chandler, Jr.) from Louisiana. All except one of the many localities in the Coastal Plain Province lie in the Fall Line Hills and Vidalia Upland districts. A single specimen was found in a roadside park in Charlton County, the only known locality for the species in Georgia that is situated south of the Altamaha River. I strongly suspect that its presence there resulted from an introduction, probably by fishermen. Additional collections should be made in the Folkston area to determine whether or not a population of the species has become established there.

GEORGIA SPECIMENS EXAMINED.—I have examined 207 specimens from the following localities. *Burke County:* (1) Walnut Branch, 3 mi SW of Waynesboro (Hart and Hart, 1974:21), 5♂I, 4♀, 1938, H. M. Blount, collector; (2) Brinson's Mill, 8 mi SW of Waynesboro, 2j♂, 14 Apr 1944, HHH; 3j♂, 3j♀, 15 Aug 1944, HHH. *Charlton County:* (3) creek, 2 mi N of Folkston on US Hwy 1, 1♂I, 1938, H. E. Hale. *Dodge County:* (4) Little Ocmulgee River at Jay Bird Springs on St Rte 165, 2j♀, 22 Apr 1966, E. T. Hall, Jr., HHH. *Elbert County:* (5) trib to Broad River 6 mi SE of Elberton on St Rte 17, 3♂II, 3♀, 14 Jun 1972, D. J. Peters, J. E. Pugh, HHH. *Emanuel County:* (6) backwaters of Ogeechee River at St Rte 56, 1♀, 7 Aug 1939, G. B. Hobbs, HHH. *Glascock County:* (7) Rocky Comfort Creek E of Gibson on St Rte 80, 4♂II, 2♀, 4j♂, 1j♀, 27 Apr 1966, ETH, HHH. *Jefferson County:* (8) 8 mi N of Wadley on US Hwy 1, 1♂I, 2♂II, 4♀, 23 Aug 1937, HHH. *Jenkins County:* (9) flood plain of Ogeechee River at St Rte 25, 3j♂, 2j♀, 27 Mar 1939, H. H. Wallace, HHH; (10) Beaverdam Creek at Burke Co line on St Rte 23, 1♀, 16 Aug 1939, G. Sadler. *Johnson County:* (11) trib to Ohoopee River 5 mi E of Wrightsville on St Rte 57, 1j♀, 27 May 1950, W. J. Houck. *Laurens County:* (12) 5 mi S of Dublin on St Rte 19, 1♀, 20 Jun 1975, DJP, JEP, HHH; (13) 7 mi S of Dublin on St Rte 19, 1♂II, 1♀, 20 Jun 1975, DJP, JEP, HHH; (14) 20.6 mi S of Dublin on St Rte 19, 1♂II, 1♀, 20 Jun 1975, DJP, JEP, HHH; (15) Stitchihatchee Creek at St Rte 338 (Dexter city limit), 1♂II, 3♀, 1j♂, 2j♀, 21 Apr 1977, C. E. Carter, JEP, HHH. *Meriwether County:* (16) National Fish Hatchery at Warm Springs, 1♂I, 1♂II, 1♀, 22 Apr 1977, J. H. Chandler, Jr., CEC, JEP, HHH. *Montgomery County:* (17) Flat Creek 1.3 mi S of Treutlen Co line on US Hwy 221 (Hart and Hart, 1974:21, 90), 1♂II, 3j♀, 22 Apr 1966, ETH, HHH; (18) roadside ditch 8.3 mi S of Treutlen Co line on US Hwy 221, 3♂I, 1♂II, 2♀, 22 Apr 1966, ETH, HHH. *Oglethorpe County:* (19) Long Creek 3.1 mi SE of Lexington on US Hwy 78, 1♂I, 3♂II, 4♀, 3j♂, 2 Apr 1978, R. J. Dubois, DJP, JEP, HHH. *Richmond County:* (20) locality unknown, 2♀, 1j♀, 19 Nov 1883, C. C. Jones, Jr.; (21) Butler Creek off US Hwy 25 in Augusta, 1j♀, 16 Apr 1977, CEC, C. W. Hart, Jr., JEP, HHH; (22) Butler Creek on St Rte 56, S of Augusta, 2♂II, 1♀, 17 Apr 1977, CEC, CWH, JEP, HHH. *Screven County:* (23) 1.5 mi E of Bascom, 5j♂, 3j♀, 26 Nov 1972, G. K. Williamson; (24) Buck Creek at Rte S1321, 3.8 mi E of Sylvania, 3♂II, 3♀, 2j♂, 1j♀, 18 Apr 1977, CEC, CWH, JEP, HHH; (25) 1.6 mi SE of Rte S1431 on St Rte 24, 1♂II, 2j♂, 2j♀, 18 Apr 1977, CEC, CWH, JEP, HHH; (26) trib to Jackson Branch on Rte S9720, 6 mi SE of Buck Creek Church, 1j♂, 5j♀, 18 Apr 1977, CEC, CWH, JEP, HHH. *Treutlen County:* (27) 16 mi SE of Dublin on St Rte 29 (Hart and Hart, 1974:21, 90), 1♀, 2j♂, 4j♀, 22 Apr 1966, ETH, HHH. *Twiggs County:* (28) 0.5 mi E of Houston Co line on St Rte 96 (Hart and Hart, 1974:30, 129), 30j♂, 27j♀, 21 Apr 1966, ETH, HHH. *Washington County:* (29) Ogeechee swamp at Jefferson Co line on St Rte 88, 1♂II, 1♀, 1j♂, 1j♀, 15 Jun 1972, DJP, JEP, HHH. *Wilkes County:* (30) flood plain of Broad River at St Rte 17, 1j♂, 16 Apr 1977, CEC, CWH, JEP, HHH; 8j♂, 5j♀, 2 Apr 1978, RJD, DJP, JEP, HHH. *Wilkinson County:* (31) creek 0.9 mi E of St Rte 112 on Rte 57, 1♂II, 1♀, 19 Jun 1975, DJP, JEP, HHH.

VARIATIONS.—As in many members of the genus that exhibit a broad ecological tolerance, one of the most conspicuous variations observed is that existing in the rostrum (Figure 144). Particularly in those populations frequenting temporary lentic habitats, the margins of the rostrum are often strongly convergent from base to apex, with only the faintest suggestion as to the position occupied by marginal spines in younger instars.

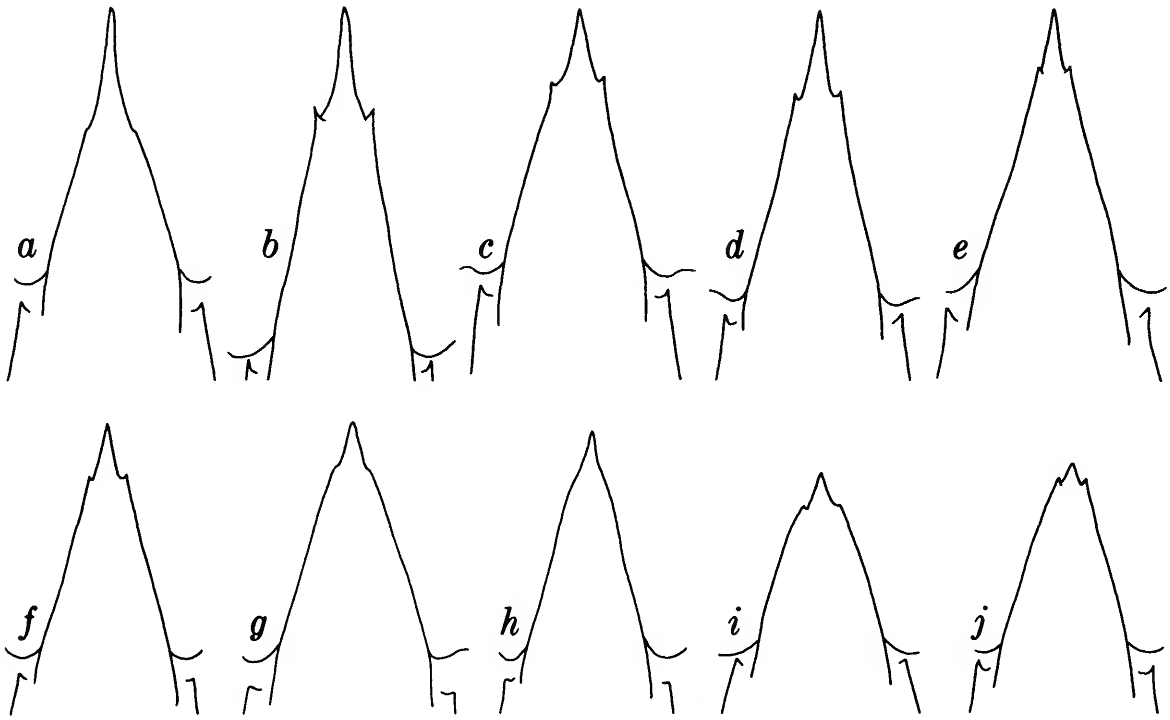


FIGURE 144.—*Procambarus (O.) acutus acutus,* variations in rostrum in Georgia: *a–c,* Laurens Co; *d,* Glascock Co; *e,* Treutlen Co; *f–h,* Jefferson Co; *i,* Charlton Co; *j,* Meriwether Co.

Also there are considerable differences in the development of the spines as well as in the relative length of the acumen. The width of the areola is also highly variable, even in specimens from a single locality. The antennal scale seems in some degree to reflect the length of the rostrum, frequently being proportionately shorter in specimens having a short rostrum. There are too few adult males to be able to interpret whether or not the variations in the pleopods are individual ones or whether certain of them are typical of individuals occurring in different parts of the range in Georgia.

The specimens from Meriwether County represent a population that was recently introduced into ponds of the Fish Hatchery at Warm Springs from Louisiana. The first pleopod of the first form male collected there is rather strikingly different from that of first form males from other localities in the state (Figure 145). Particularly noticeable are the longer mesial and longer, less acute cephalic processes and the more mesially deflected central projection in the specimen from Meriwether County. Differences among the pleopods of the remaining first form males from Georgia are much less obvious.

The annulus ventralis also exhibits rather striking variations, chief among which is the degree of elevation of the dextral part near midlength. Both in juveniles and in some adults the dextral elevation is little higher than the sinistral surface, so that the recognition of the dextrally directed "tongue" disappearing beneath the elevation is hardly discernible. In other adults (Figure 143*d*) the elevation is very high, with a well-defined tongue passing dorsally beneath its mesial margin. Originally I had supposed that the annuli with little elevation were typical of juvenile females and that those with strong dextral prominences were characteristic of the adult female;

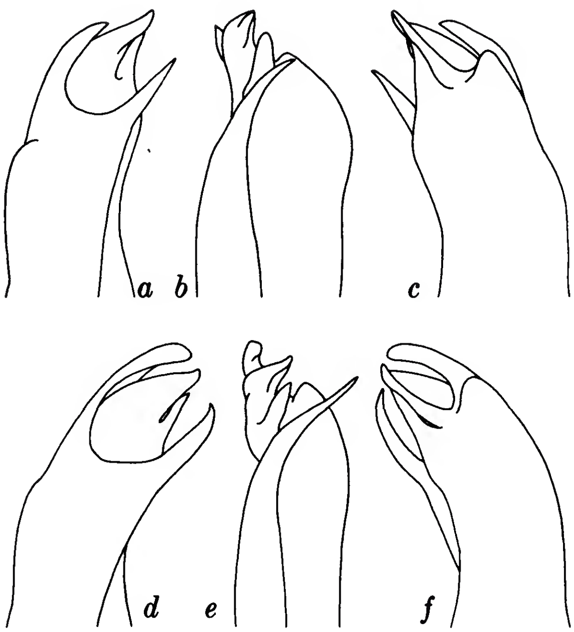


FIGURE 145.—*Procambarus (O.) acutus acutus,* distal part of first pleopods (male, form I) of native (*a–c*) and introduced (*d–f*) populations (*a*, *d*, mesial view; *b*, *e*, caudal view; *c*, *f*, lateral view): *a–c*, 8.3 mi S of Treutlen Co line on US Hwy 221, Montgomery Co; *d–f*, National Fish Hatchery at Warm Springs, Meriwether Co.

however, some of the largest females possess annuli that I had assumed to be the juvenile type. Similar observations have been made in other species of the genus *Procambarus*. These observations suggest the possibility that a tendency exists in the females of these crayfishes to exhibit a cyclic dimorphism in the annulus ventralis that parallels that in the first pleopod of the male.

The greatest difference in the annulus of the female from Meriwether County, and in specimens from elsewhere, is in the strongly depressed tongue that lies in a concavity, thus making an even greater differential in the elevations of the left and right sides of the annulus.

SIZE.—The largest specimen available is a second form male, having a carapace length of 58.9 (postorbital carapace length 43.2) mm. Corresponding lengths of the smallest and largest first form males are 36.4 (27.9) mm and 56.8 (42.5) mm, respectively. No females carrying eggs or young have been found in Georgia.

LIFE HISTORY NOTES.—Virtually nothing is known of the life history of this crayfish in the southeastern part of its range, and only in Texas has a careful study been conducted on one of the variants (Albaugh, 1975). In Georgia, first form males have been collected in April, August, and in "the fall." Neither ovigerous females nor ones carrying young have been found in the state. In Alabama first form males were collected in March, April, June, July, and September; in Florida during April and May, and in South Carolina during every month of the year except May. Among the hundreds of specimens available from the four southeasternmost states, there are no ovigerous females and only one carrying young, that taken in Alabama in September.

Seasonal Data

Sex/stage	*J*	*F*	*M*	*A*	*M*	*J*	*J*	*A*	*S*	*O*	*N*	*D*	*?*
♂I				5				1					6
♂II				17		8		2			2		
♀				17		7		6					4
♂j			3	59		1					5		
♀j			2	56	1	1					4		

ECOLOGICAL NOTES.—This crayfish certainly is not so rare in Georgia as the few records included here suggest. Nevertheless, I cannot explain why I have failed to find it more frequently, unless within its range in the state I devoted more effort to collecting in clear streams and in burrows than in pools and sluggish deep creeks. Although *P. (O.) a. acutus* has been found in clear, moderately flowing streams, it seems to occur in larger numbers in lentic habitats or in very sluggish streams that are often choked with vegetation. Among the lentic habitats in which it has been found are backwaters of large streams, borrow pits, pools in roadside ditches, and in impounded farm ponds.

There is no question that those members dwelling in fluctuating bodies of water burrow during dry seasons, and there is evidence that at least the adults burrow with the onset of cold weather during the late fall or early winter. During the spring and summer, I have found them singly and in pairs in simple subvertical burrows in roadside ditches. That even those females dwelling in streams probably retreat to burrows prior to laying their eggs is highly likely in view of the fact that no ovigerous females are present among the hundreds of specimens available from Alabama, Florida, Georgia, and South Carolina. The comparatively rare occurrence of the species in any part of its known range in Georgia and its apparent absence (except for the introduction noted above) in the Flint-Chattahoochee segment of the Piedmont Province and Fall Line Hills District of the Coastal Plain Province are puzzling, for it is a common species in Alabama and occurs abundantly in South Carolina. Such is even less understandable in view of the ability of the species to maintain populations in such diverse habitats as those in which it has been found in Georgia. The only species that appears likely to be vicariating for this crayfish in the southwestern part of the state is *Procambarus (S.) paeninsulanus*, the only Georgia representative of the subgenus *Scapulicambarus* with which it has not been found associated.

GEORGIA CRAYFISH ASSOCIATES.—The following species have been found with *P. (O.) a. acutus* in Georgia (the number of localities shared by them is noted in parentheses): *Cambarus (D.) harti* (1), *C. (D.) latimanus* (6), *C. (D.) reflexus* (1), *C. (D.) striatus* (1), *Faxonella clypeata* (4), *Procambarus (D.) devexus* (2), *P. (H.) caritus* (1), *P. (L.) barbatus* (1), *P. (O.) enoplosternum* (8), *P. (O.) epicyrtus* (1), *P. (O.) pubescens* (2), *P. (O.) seminolae* (1), *P. (S.) howellae* (3), and *P. (S.) troglodytes* (2).

Procambarus (Ortmannicus) lophotus Hobbs and Walton

FIGURES 2, 15*d*, 136*c*, 138*h*, 146, 147, 251

Procambarus lophotus Hobbs and Walton, 1960b:123–129, figs. 1–11.—Hobbs, 1962:286, 288, fig. 46; 1968b:K-10, fig. 23b.—Hobbs III, 1969:21, tab. 3—Bouchard, 1972:32, 43, 53, 58, 68, 84, 108; 1976a:563, 576, 577.—Hobbs and Hall, 1974:203–204*.—Hart and Hart, 1974:30, 63*, 126.

Procambarus a. acutus.—Anonymous, 1970c:39*.

Procambarus (Ortmannicus) lophotus.—Hobbs, 1972a:9; 1972b: 57*, 151, 154*, fig. 46g; 1974b:58, fig. 245.—Bouchard, 1972:86; 1976a:577; 1976c:14.—Fitzpatrick, 1976:57.—Hobbs and Walton, 1977:609.

Procambarus (Ortmannicus) sp.—Hart and Hart, 1974:134*.

These citations are believed to constitute a complete bibliography of the species. References to its occurrence in Georgia are identified by asterisks.

SUMMARY OF LITERATURE.—Following the description of this crayfish from central Alabama, Hobbs (1962) endeavored to point out its affinities to other members of the *blandingii* Section of the genus *Procambarus*, and he included it in his key (1968b) to the crayfishes of the southeastern part of the United States. Hobbs III (1969) cited it as one of the hosts of the entocytherid ostracod *Ankylocythere sinuosa* (Rioja, 1942:203). Anonymous (1970c), on the basis of my identification, recorded the occurrence of *P. a. acutus* in Rock Creek at State Route 193, 0.5 mile north of Flintstone, Walker County, Georgia. In recognizing several subgenera of the genus *Procambarus*, Hobbs (1972a) assigned it to the subgenus *Ortmannicus* and included it in his key (1972b) to the North and Middle American crayfishes, citing its distribution as follows: "Lentic and lotic habitats in tributaries of the Alabama River from Clarke County, Alabama, to Gordon and Catoosa counties, Georgia, and in the Tennessee drainage in Polk County, Tennessee, and northwestern Georgia" (1972b:57). In treating the occurrence of the species in Tennessee, Bouchard (1972:86) stated the range in that state to include "Ridge and Valley province from the Hiwassee River system to Walden Gorge," and noted that first form males had been found in April and November and that ovigerous females occupy burrows. His ecological note stated: "Predominately in small to medium size streams; more common in vegetation, leaf litter, etc., secondary burrower." Hobbs and Hall (1974:203–204) cited the second locality record in Georgia, "Nance Spring Creek, a tributary to the Conasauga River in Whitfield County . . . ," stating that this crayfish lived in a segment of the stream in which the oxygen concentration ranged from 4.6 to 7.6 mg/l, but downstream where the concentration was reduced to 0.4 to 0.7 mg/l the crayfish was absent. No new data were included in Hobbs' (1974b) checklist. Hart and Hart (1974:63, 134), in addition to citing records of the occurrence of the species in Alabama, pointed out that in the Chickamauga National Park in Walker County, Georgia, this crayfish serves as host to *Dactylocythere mecoscapha* (Hobbs and Walton 1960a) and *Uncinocythere simondsi*. The host of the latter ostracod was identified as *P. (Ortmannicus)* sp. In his summary of the crayfishes of the Cumberland Plateau, Bouchard (1976a:577) gave the range of *P. (O.) lophotus* as

> tributaries of Tennessee River east of Walden Gorge to Hiwassee River basin and Coosa River system . . . where it is most common in pools of springs and small to medium sized streams primarily in leaf litter and dense concentrations of aquatic vascular plants such as *Nasturtium*. Tertiary burrower. Uncommon. . . . This species is much more abundant below the Fall Line especially in lentic environments, although it does not hesitate to enter lotic environs. It is collected wherever there is adequate cover (e.g., dense concentrations of aquatic vascular plants and leaf litter).

Fitzpatrick (1976) and Bouchard (1976c) presented no previously unpublished data and Hobbs and Walton (1977) described a new ostracod from Tennessee that infests this species.

DIAGNOSIS.—Rostrum with or without marginal spines or tubercles, if without, margins angulate at base of acumen, median carina absent. Carapace with 1 pair of small cervical spines or tubercles. Areola 8.8 to 15.8 (average 11.6) times as long as broad and constituting 28.8 to 35.3 (average 32.0) percent of entire length of carapace (40.5 to 46.2, average 41.6 percent of postorbital carapace length). Antennal peduncle with spine or tubercle on ischium. Lateral half of ventral surface of ischium of third maxilliped lacking conspicuous mat of long plumose setae. Basis of cheliped without mesial spine. Mesial surface of palm of chela of male not bearded but with mesialmost row of tubercles consisting of 9 to 11. Male with simple hooks on ischia of third and fourth pereiopods, that on third and sometimes that on fourth overreaching corresponding basioischial articulation, and that on fourth opposed by submarginal tubercle on basis. First pleopods asymmetrical and reaching coxae of third pereiopods; distal part of appendage gently inclined caudally and with weak hump cephalically proximal to base of cephalic process; subapical setae partly obscuring cephalic process and central projection mesially and laterally; mesial process subspiculiform and directed caudodistally and somewhat laterally; cephalic process short, with acute apex and hooding base of central projection; caudal element consisting of leaflike caudal process at caudolateral base of central projection and small, rounded caudal knob at cephalolateral base of cephalic process; central projection short, subtriangular, acute and directed caudodistally; cephalic and caudal processes and central projection corneous. Female with sternum cephalic to annulus ventralis marked by narrow, deep submedian cleft, flanked by tubercles, frequently projecting slightly over cephalic part of annulus ventralis; latter subovate to subrectangular with greatest diameter in transverse plane, ventral surface subplane, rather weakly sculptured, and bearing distinct caudomedian protuberance; sinus forming sigmoid curve, originating almost on median line in cephalic fourth and ending on caudomedian protuberance; tongue directed dextrally or sinistrally. Postannular sclerite slightly less than two-thirds as wide as annulus and convex ventrally; first pleopod present.

COLOR NOTES (Figure 136*c*).—Carapace largely tan with pinkish lavender suffusion and fading ventrally to pinkish cream. Cephalic section with single pair of small black spots abutting cervical groove on level with paired charcoal stripes marking lateral surface of branchiostegites. Pinkish cream stripe extending from ventral part of orbit posteroventrally to cervical groove; cephalic border of mandibular and ventral branchiostegal regions cream to white. Areola slightly darker than adjacent areas. Caudal ridge charcoal; flange bluish cream. Abdomen with broad, median, longitudinal, charcoal to black band extending from first tergum posteriorly to fifth or sixth (pattern on latter variable), progressively

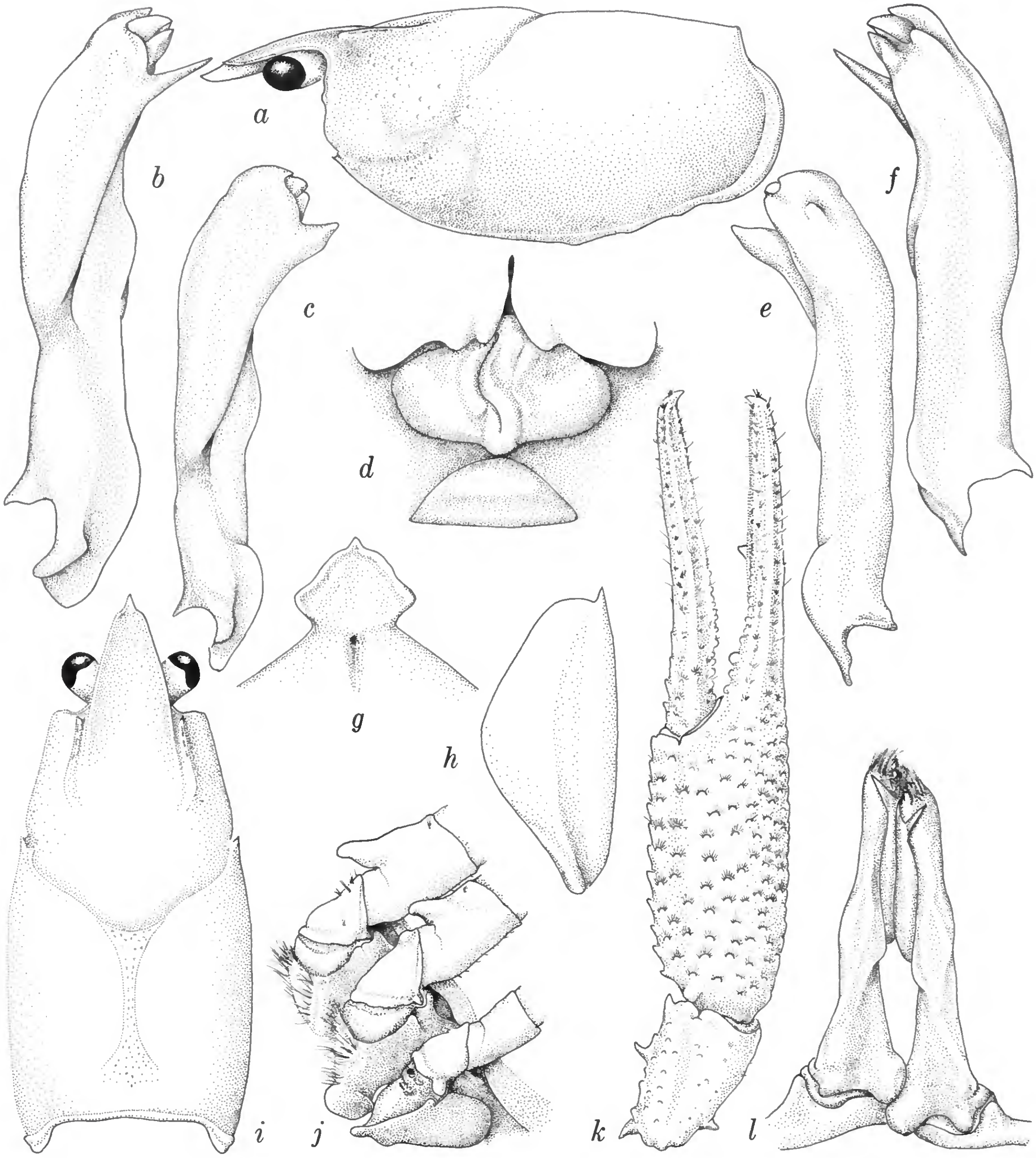


FIGURE 146.—*Procambarus (Ortmannicus) lophotus* from tributary to Peavine Creek 2 mi upstream from St Rte 2, Catoosa Co (all from first form male except *c*, *e*, from second form male, and *d*, from female): *a*, lateral view of carapace; *b*, *c*, mesial view of first pleopod; *d*, annulus ventralis; *e*, *f*, lateral view of first pleopod; *g*, epistome; *h*, antennal scale; *i*, dorsal view of carapace; *j*, proximal podomeres of third, fourth, and fifth pereiopods; *k*, dorsal view of distal podomeres of cheliped; *l*, caudal view of first pleopods.

narrowing posteriorly. Dark band flanked laterally by narrower pink bands bearing paired cream spots on each tergum; pink band, in turn, flanked ventrolaterally by greenish tan bands along bases of pleura, remainder of pleura surfaces pink with pale cream mottlings. Telson and uropods pinkish tan with reddish brown flecks and spots; paired lateral spots at base, keels, and lateral margins dark brown. Antennular and antennal peduncles pinkish cream with olive brown margins and flecks; flagella pale to bright green, fading distally to cream tan. Antennal scale pinkish cream, margined in olive brown, and with reddish brown splotch on lamella abutting thickened lateral part. Cheliped olive tan to orange tan from merus distally, tubercles olive brown to charcoal, major ones on merus and carpus white to cream tipped. Fingers nearly always olive, with charcoal tubercles; ventral surface of chela pink. Remaining pereiopods olive to pinkish olive, with distal parts of podomeres slightly darker than more proximal ones. Ventral surface of body cream to pinkish cream.

TYPES.—Holotype, allotype, and morphotype, USNM 104404, 104405, 104406, (♂I, ♀, ♂II); paratypes, TU, USNM.

TYPE-LOCALITY.—Roadside ditch, 3.4 miles northeast of Haynesville on State Route 111, Lowndes County, Alabama.

RANGE.—Alabama drainage system from Clarke County, Alabama, to Gordon, Walker, and Whitfield counties, Georgia, and in the Tennessee River basin in Walker and Whitfield counties, Georgia, and Polk County, Tennessee. In Georgia it has been found only in the Ridge and Valley Province, where it occurs in the Chattooga and Oostanaula-Conasauga river systems and in the basins of Chattanooga and South Chickamauga creeks. It has not been found in any of the habitats examined in Floyd County nor in any part of the Etowah Basin where no other crayfish seems to be vicariating for it. Whether or not the apparent gap in its range in the Coosa between Saint Clair County, Alabama, and Chattooga and Gordon counties, Georgia, is real or not remains to be determined.

SPECIMENS EXAMINED.—I have examined a total of 419 specimens, of which 336 were collected in Alabama, 1 in Tennessee, and 82 from the following localities in Georgia. *Catoosa County:* (1) Hurricane Creek off St Rte 151, 4.3 mi N of Ringgold, 1j♂, 24 Apr 1968, E. T. Hall, Jr., HHH, collectors; (2) West Chickamauga Creek at St Rte 146 near Tennessee St line, 1♀, 15 Sep 1970, M. W. Walker, B. A. Caldwell; (3) trib to Peavine Creek about 2 mi upstream from St Rte 2, 1♂I, 2♂II, 5♀, 1j♂, 25 Apr 1977, J. E. Pugh, HHH; (4) creek at Museum in Chickamauga National Military Park, 2♂II, 1♀, 1j♀, 25 Apr 1977, JEP, HHH; (5) creek at Jay's Mill Rd in Chickamauga National Military Park, 2♂I, 1♀, 25 Apr 1977, JEP, HHH. *Chattooga County:* (6) Chattooga River above confluence with Spring Creek, NE of Lookout Hall Church, 1♂II, 1j♂, 5 Sep 1974, G. L. Peterson, BAC; (7) Chattooga River below confluence with Spring Creek, 1♂II, 12 Sep 1974, GLP, BAC; (8) Chattooga River approximately 100 m downstream from Chappel Creek, 1♀, 12 Sep 1974, GLP, BAC; (9) Chattooga River 0.5 mi N of Tate Rd, 2j♂, 28 Aug 1974, GLP, BAC; (10) Chattooga River at St Rte 100, 2♂II, 1♀, 25 Sep 1974, GLP, BAC. *Gordon County:* (11) Conasauga River at Rte S1800 NE of Resaca, 2j♂, 1j♀, 11 Oct 1969, ETH, HHH; (12) stream about 2 mi N of Calhoun on US Hwy 41, 1♂I, 2♂II, 8♀, 6j♂, 6j♀, 12 Apr 1958, T. L. Johnson, HHH; (13) trib to Oostanaula River, 3.2 airmi WNW of Plainville on Rd 232, 1♀, 2 Jul 1974, McCaleb and Johnson. *Walker County:* (14) Rock Creek at St Rte 193 about 1.5 mi N of Eagle Cliff, 2j♂, 2j♀, 29 Aug 1969, ETH, MWW, 1j♂, 1j♀, 3 Nov 1976, ETH, W. D. Kennedy; (15) City Creek 50 m above confluence with Town Creek in Linwood, 2j♂, 2j♀, 5 Sep 1974, GLP, BAC; (16) Chattanooga Creek at Eagle Cliff, 1j♂, 3 Nov 1976, ETH, WDK; (17) stream in Chickamauga National Military Park, 3♂II, 1♀, 1j♂, 1j♀, 19 Apr 1954, JEP, S. R. Telford, HHH; (18) trib to South Chickamauga Creek 9.8 mi E of Dade Co line on St Rte 143, 1♀, 2 May 1967, T. Unestam, HHH. *Whitfield County:* (19) Nance Spring Creek at US Hwy 41 N of Resaca, 1♂II, 1♀, 1j♂, 9 Jun 1971, ETH, BAC; (20) Swamp Creek off US Hwy 41, 1j♀, 29 Oct 1975, G. Q. Tuggle, MWW; (21) Swamp Creek at River Bend Church Rd, about 0.5 mi from confluence with Conasauga River, 1♂II, 2j♂, 2j♀, 29 Oct 1975, GQT, MWW; (22) Swamp Creek between Interstate Hwy 75 and US Hwy 41, 1j♀, 12 Oct 1976, MWW, K. W. Martin.

VARIATIONS.—The only conspicuous variation observed among the limited number of specimens from Georgia is in the rostrum: the length, the angle of convergence of the margins, and the ornamentation at the base of the acumen. As in many tertiary burrowers, the rostrum of most of the larger individuals is proportionately shorter than in the smaller (younger) ones, the angle

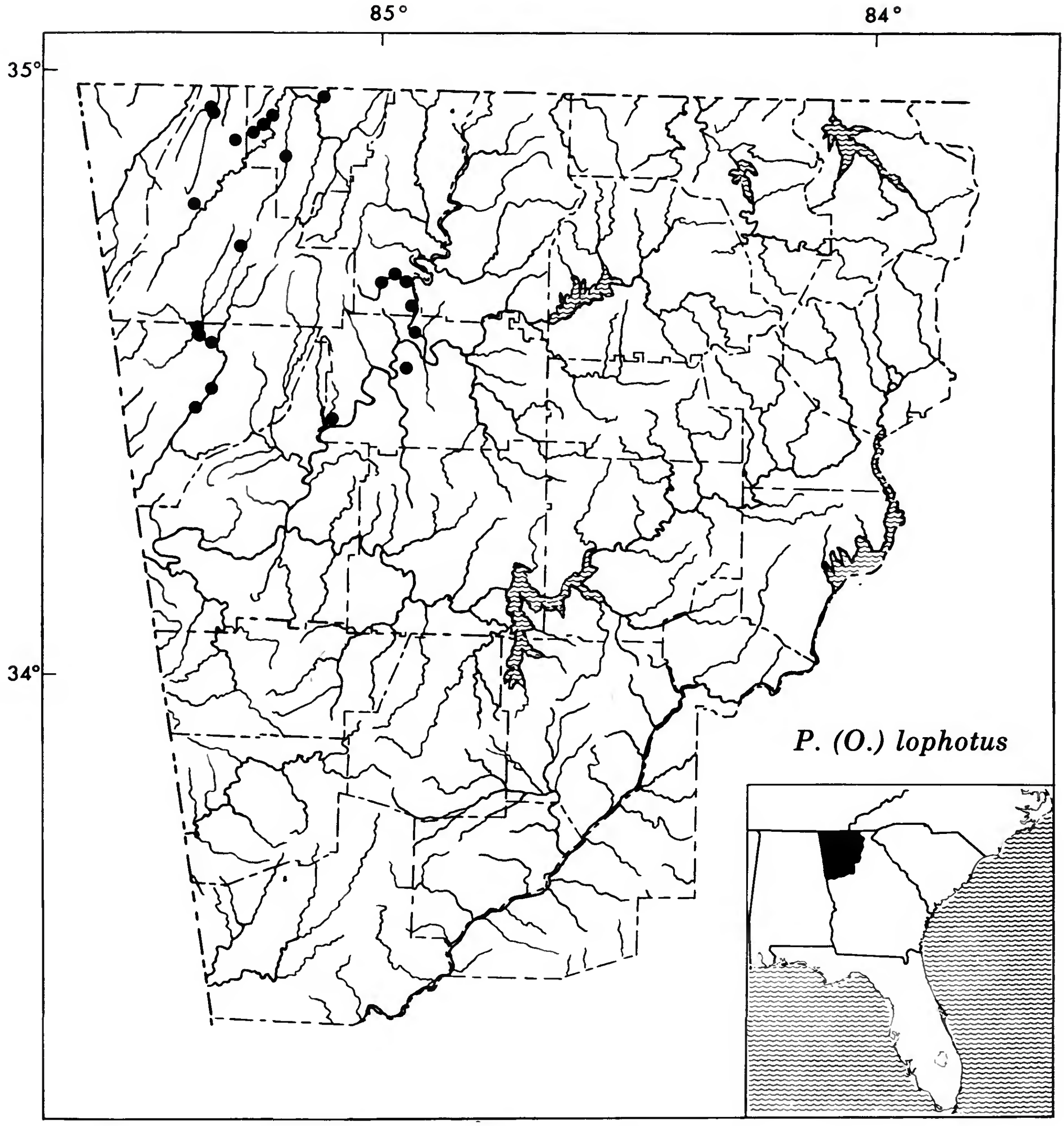


FIGURE 147.—Distribution of *Procambarus (O.) lophotus* in Georgia.

formed by the converging margins is generally greater in the larger crayfish, and the size of the marginal spines seems to diminish with an increase in carapace length; these spines are often represented by rudimentary tubercles or weak, angular interruptions of the margins at the base of the acumen. It should be emphasized that some of the larger specimens exhibit one or more of the rostral characteristics usually associated with the juveniles. The cervical and postorbital spines are usually more conspicuous in the juveniles than in the adults, and in many of the latter the cervical spine is reduced to a tubercle and the postorbital spines become obsolete. While in the female the sternum anterior to the annulus ventralis is always narrowly and deeply cleft, the number of tubercles borne on it varies from a single pair of moderately large ones to a number of smaller ones. There is no evidence that any of these variations are locally or regionally restricted within the range of the species. In describing this crayfish, Hobbs and Walton (1960b:128) noted almost the same rostral variations recorded here and they also stated that "the areola is proportionately broader in immature animals, occasionally being only seven times longer than broad."

Size.—The largest specimen collected in Georgia is a second form male, possessing a carapace length of 50.4 (postorbital carapace length 37.7) mm. The smallest and largest first form males have corresponding lengths of 31.5 (23.7) mm and 47.1 (36.3) mm, respectively. Females bearing eggs or young have not been examined by me.

Life History Notes.—First form males have been collected only in April in Georgia but also in June in Alabama. To my knowledge, ovigerous females or ones carrying young have not been reported although Bouchard (1972:86) stated that females "occupy burrows while carrying eggs." Inasmuch as 67 adult females have been obtained during the month of April and none was ovigerous, I suspect that egg laying occurs in the late summer and/or early fall. (See "Seasonal Data.")

Seasonal Data (Alabama, Georgia, and Tennessee)

Sex/stage	*J*	*F*	*M*	*A*	*M*	*J*	*J*	*A*	*S*	*O*	*N*	*D*
♂I				48		2						
♂II		4		63		1			4	1	2	
♀		1		83	1	3	1		3	1		
♂j		14		80		1		4	3	6	2	
♀j		10		68				2	2	7	2	

Ecological Notes—The largest series of this species from Georgia was collected from a small stream tributary to the Oostanaula River, two miles north of Calhoun, Gordon County. There the creek was some 1.5 to 2 m wide and 0.5 m deep, and the cloudy (yellowish) water was flowing with a moderate current over a silt-covered sand and rocky bottom. Sharing the creek with *P. (O.) lophotus* was *C. (D.) striatus.* In a sluggish, clay-bottomed stream that joined Peavine Creek in Catoosa County, specimens were seined from a pool of water supporting a dense, grayish particulate matter. The bottom consisted of water-soaked clay, in which the collector sank to his knees. The only plants observed in the pool were clumps of an emergent sedge. In the Chickamauga National Military Park, this crayfish was found in shallow, crystal clear streams, flowing with a moderate current over a sand and silt bottom, with scattered rock litter. Most of the crayfish were concealed under rocks but a few were found among debris. When disturbed, several individuals swam as much as three to seven meters before coming to rest. (See quotation from Bouchard (1976a) in "Summary of Literature.")

Although none of the specimens from Georgia were collected from burrows, I am reasonably certain that they construct simple ones as they do in roadside ditches in Alabama (Hobbs and Walton, 1960b:127), and as reported by Bouchard (1972:86).

Georgia Crayfish Associates.—*Procambarus (O.) lophotus* has been collected with the following species (the numbers of times they have been taken together are included in parentheses): *Cambarus (D.) striatus* (8), *C. (H.) girardianus* (3), *C. (J.) unestami* (1), *C. (L.) acanthura* (3), *C. (P.) coosae* (2), *C. (P.) extraneus* (3), *C. (P.) scotti* (3), *Orconectes erichsonianus* (7), *O. spinosus* (3), and *Procambarus (Pe.) spiculifer* (1).

The *pictus* Group

Procambarus (Ortmannicus) angustatus (LeConte)

Figures 13*c*, 148, 149, 245

Astacus angustatus LeConte, 1856:401-402.—Hagen, 1870:9, 10.—Hobbs, 1972a:2.

Cambarus angustatus.—Hagen, 1870:34, 48, 50, 52, 97, 100, 107, pl I: figs. 65-67, pl. III: fig. 146.—Faxon, 1884:110, 137; 1885a:30-33, 158, 173; 1914:413.—Underwood, 1886:366.—Hay, 1899b:959, 963.—Ortmann, 1902: 277.—Harris, 1903a:58, 71, 150, 152.

Cambarus (Cambarus) angustatus.—Ortmann, 1905a:102, 128.

Cambarus (Ortmannicus) angustatus.—Fowler, 1912:341 [by implication].

Procambarus angustatus.—Hobbs, 1958a:78-79, 86, fig. 19; 1958b:160; 1959:889; 1962:273, 284, fig. 34; 1968b:K-8, fig. 25j; 1972a:2.

Procambarus (Ortmannicus) angustatus.—Hobbs, 1972a:9; 1972b:62, 150, 154, fig. 49d; 1974b:54, fig. 226.

The above references are believed to constitute a complete bibliography of the species. Inasmuch as all of the citations are based upon LeConte's original description and his type from a single vague locality, lower Georgia, all citations are applicable to the occurrence of the species in the state.

SUMMARY OF LITERATURE.—LeConte's type of this crayfish, which is no longer extant, is the only specimen that, to my knowledge, has ever been collected. The brief description (in Latin) offered by him is, as might be anticipated, inadequate to distinguish this crayfish from its relatives.

Hagen (1870:50) added a few additional observations on the external features of this specimen and included illustrations of the first pleopod. These figures are difficult to interpret, and figure 66 more closely resembles the pleopod of *P. (Pe.) spiculifer* than that of the type of *P. (O.) angustatus*, and figure 67 resembles neither. (Perhaps these illustrations were drawn from the other specimen mentioned by Hagen, "... I have only two single specimens....") Also depicted were the antennal scale, the cephalic lobe of the epistome, and the lateral spine on the basis of the antennal peduncle. In discussing the species, even though he was not thoroughly convinced that it should be recognized as distinct from LeConte's *Astacus spiculifer*, he pointed out the more obvious differences between the two.

Faxon (1884) added no new information concerning *P. (O.) angustatus* but contrasted it with his *Cambarus pubescens*. In his "Revision of the Astacidae," Faxon (1885a:30-31) quoted LeConte's description and presented additional descriptive notes (see "Holotypic Male, Form I" below). He also noted (p. 30) that "this species is known only through a dry type specimen in the Museum of the Academy of Natural Sciences of Philadelphia," not mentioning the second specimen reported by Hagen (which, to my knowledge, has not been referred to subsequently). On pages 32 and 33, he contrasted it with *P. (O.) pubescens* and *P. (Pe.) spiculifer*.

Prior to my examining the type specimen and the publication of my study of the *pictus* Group (1958a), insofar as I have been able to determine, all other authors based their remarks concerning the species on the contributions of LeConte, Hagen, and Faxon. In my discussion of the evolution of this group, I attempted to show in what respects this crayfish resembles its relatives and included a lateral view of the distal part of the first pleopod. Additional illustrations were included in Hobbs (1974b). Except for nomenclatural changes, and the inclusion of the taxon in keys, nothing else of import appears in the literature.

DIAGNOSIS.—Rostrum with marginal spines, lacking median carina. Carapace with 1 pair of cervical spines. According to Faxon's measurements, areola about twice as long as broad and constituting 27.3 percent of entire length of carapace; on basis of Figures 148*a* and 245*a*, considerably greater than twice as long as broad, constituting 28.3 percent of entire length of carapace (41.0 percent of postorbital carapace length). Antennal peduncle with spine on ischium. Lateral half of ventral surface of ischium of third maxilliped lacking conspicuous mat of long plumose setae. Basis of cheliped without mesial spine. Mesial surface of palm of chela of male not bearded but with mesialmost row of tubercles consisting of 12. Male with simple hooks on ischia of third and fourth pereiopods, in first form male that on both overreaching corresponding basioischial articulation and that on fourth opposed by prominent protuberance on cephalodistal end of basis. First pleopods reaching coxae of third pereiopods and almost certainly asymmetrical (only dextral member present when I examined the specimen); distal fourth of shaft very weakly inclined caudodistally and cephalic surface devoid of hump; subapical setae present; mesial process slender, tapering (distal part broken), and directed caudodistally; cephalic process, small and triangular, situated at cephalic base of central projection; latter corneous, beaklike, and directed caudodistally; caudal element represented by rather small, tumescent caudal knob on distal caudolateral extremity of shaft of appendage; caudal and adventitious processes absent.

HOLOTYPIC MALE, FORM I.—Some years ago, I examined the type of this crayfish and made sketches and the photographs that are included herein (Figures 148, 149). Several years later, I returned to the Academy of Natural Sciences of Philadelphia, hoping to prepare a full description and to make additional drawings of the specimen. Unfortunately, it could not be located, and a further search for it a few months ago also proved futile. Thus it must be assumed to be lost.

Following a free translation of LeConte's description and a quotation from Faxon (1885a) are additional observations based on my notes, photographs, and sketches made during the early 1950s.

Rostrum concave, strongly acuminate, also strongly and acutely unidenticulate toward apex. Antennal scale equal in length to antennal peduncle. Cephalothorax punctate, more sparsely toward side with hardly any punctations, *linea ordinaria* [= cervical groove] armed with pointed spine. Thorax entirely punctate, few toward side, lacking tubercles or granules. Areola broad. Dorsum as in aforementioned [i.e., smooth with series of transverse punctations]. Chela small, narrow, subcylindrical, punctate, without tubercles or granules, except on interior margin which is provided with few

FIGURE 148.—*Procambarus* (*Ortmannicus*) *angustatus* (holotype): *a*, dorsal view of cephalothoracic region; *b*, lateral view of same; *c*, dorsal view of distal podomeres of cheliped.

inconspicuous denticles, fingers straight, punctate, and carinate. Carpus smooth and tri- or quadripunctate. Merus smooth, small spines on upper surface; lower surface with two rows of spines of which anterior [distal] two larger and longer. Telson trispinose on both sides. (Free translation of LeConte, 1856:401–402.)

Faxon (1885a:31) stated:

The Philadelphia type agrees well with LeConte's description. The chela, however, under close inspection, is seen to be covered with obsolescent, ciliate, squamous tubercles, and the areola is moderate rather than wide [thus contrasting with a calculation based on his measurements]. The fingers are ciliated along their inner margins. There is a single lateral spine on each side of the thorax, three spines on the right side of the telson, four on the left side. Carpus with two prominent spines on the inside, and one below, near the exterior articulation of the hand. The sides of the rostrum converge but little from the base to the lateral spines. The acumen is long. The sexual appendages are figured by Hagen. ... It resembles *C. Lecontei* in general appearance, the shape of hand, and number of lateral thoracic and telson spines. The first pair of abdominal legs are different, resembling those of *C. spiculifer*, but different from either. The sides of the rostrum are more nearly parallel than in *C. Lecontei*, in this respect resembling *C. versutus*. It seems to be a very much smaller species than its near allies.

Body subovate (Figure 148*a*,*b*); width less than depth at caudodorsal margin of cervical groove. Rostrum excavate dorsally, with gently convergent margins not swollen, slightly elevated, and with spines at base of acumen; latter reaching distal end of antennular peduncle. Postorbital ridge prominent, grooved dorsolaterally, and ending cephalically in spine; suborbital angle small and obtuse. Cervical and branchiostegal spines strong. Cephalic section of telson with 3 spines in dextral and 4 in sinistral corners. Antenna broken; antennal scale (Figure 149c) broadest proximal to midlength; antennule with strong spine on ventral surface of proximal podomere. Right chela (Figure 148*c*) subovate in cross section, slender; palm tuberculate; fingers with weak, median, longitudinal ridges, and if opposable margins bearing tubercles, latter obscured by broad band of minute denticles. Carpus with dorsal, shallow, oblique trough, flanked mesially by subsquamous tubercles and laterally by punctations; mesial surface with 2 prominent spiniform tubercles in distal half (more distal one on distomesial

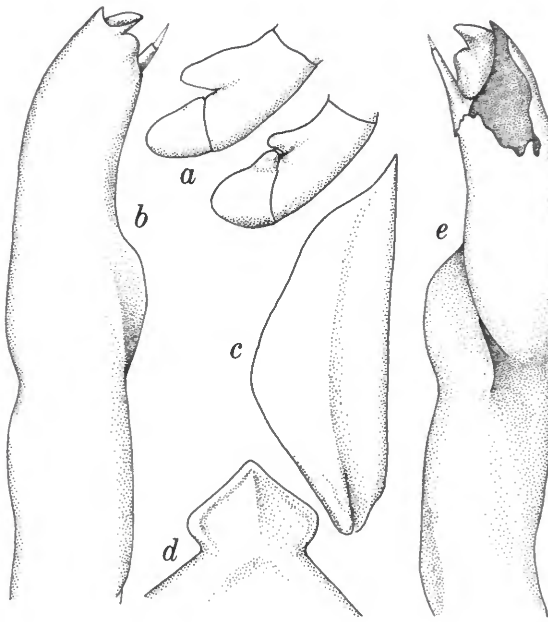


FIGURE 149.—*Procambarus (O.) angustatus* (holotype): *a*, basis and ischium of third and fourth pereiopods; *b*, lateral view of first pleopod; *c*, antennal scale; *d*, epistome; *e*, mesial view of first pleopod.

angle of podomere) and several tubercles in proximal half; ventral surface with 2 tubercles on distal margin, 1 on lateral condyle and other submedian. Merus with 2 spiniform tubercles dorsodistally; ventral surface with mesial row of 11 tubercles and only 2 representing lateral row. (See "Diagnosis" for description of first pleopod, Figure 149*b*,*e*.)

Female and second form male unknown.

TYPES.—Holotype, formerly ANSP 444 (♂I), now presumably lost.

TYPE-LOCALITY.—"Georgia inferiore, in aquae purae rivulos qui inter colliculos arenosos (*sandhills*) currunt" (LeConte, 1856:402).

RANGE.—Known only from streams in the sand hills of southern Georgia (see "Type-Locality"). A search for it over a period of some 30 years has resulted in failure. Consequently, I echo the lamentation of Hagen (1870:100), who stated: "It is a pity that he [LeConte] never gives the exact location."

GEORGIA SPECIMENS EXAMINED.—The holotype is the only specimen that I have seen.

SIZE.—Measurements were recorded in inches by LeConte (p. 402) as follows: "Long. 1.95. Cephalo-thorax .6. Thorax .25. Abdomen .8. Cauda .3. Antenna .9. Chela .6. latitud .2, forceps .3." Hagen (1870:50) stated that it was "... 1.95 inch long, hands 1.2 long ... ." The following are Faxon's (1885a:31) measurements:

Length, 47 mm. Carapax, 22 mm. Abdomen, 25 mm. From tip of rostrum to cervical groove, 16 mm. From cervical groove to posterior border of carapace, 6 mm. Length of rostrum, 8 mm.; acumen 3 mm. Width of rostrum at base, 3 mm.; between lateral spines 2 mm. Width of areola, 1.5 mm. Length of chela, 15 mm.; breadth of do., 4 mm.

REMARKS.—As noted above, I have devoted considerable effort, as have several friends attempting to assist me, in trying to locate additional specimens of this species not only in the Barrier Island Sequence and Vidalia Upland districts of the Coastal Plain Province but also in the lower Piedmont Province, all to no avail. Widespread in the area are populations of *P. (O.) enoplosternum* in which the males attain first form at a carapace length of as little as 14.8 mm, and at least some of these populations occur in clear streams flowing in sand hills. Except in the structure of the first pleopod, they differ in no important respect from LeConte's type of *Astacus angustatus*. The male pleopods of the two, however, are markedly different in three respects: in *P. (O.) enoplosternum* the cephalic process is longer and more prominent, and both a caudal process and a well-defined adventitious process are present; the latter two are lacking in *P. (O.) angustatus*.

Suggesting the possibility that the type of *P. (O.) angustatus* is an aberrant specimen of *P. (O.) enoplosternum* are two features (one each in two specimens) observed in the latter species. In one (Figure 153*m*) the cephalic process is so greatly reduced as to be essentially obsolete, and in another (Figure 153*u*) the caudal knob is equally as poorly developed as it is in the type of *P. (O.) angustatus*. In spite of these similarities in the pleopod, the differences outweigh them, and in view of the restricted ranges of other crayfishes in the *pictus* Group of the subgenus (including those of *P. (O.) pictus*, see Franz (1977b:17), and *P. (O.) youngi*), I might well have failed to sample a population that is indeed distinct from *P. (O.) enoplosternum*. I should add that without the secondary sexual characters, there are several species closely allied to the latter that would likely be considered conspecific! Thus it seems prudent to assume that the first pleopod of the type of *P. (O.) angustatus* was not an anomalous one and that either the species has a very restricted range or it is now extinct. Of interest is the assumption that this crayfish was presumably collected from the same general area as was the tree *Franklinia alatamaha*, which exists now only in cultivation.

Procambarus (Ortmannicus) enoplosternum Hobbs

FIGURES 13*e*, 137*b–d*, 138*c*, 150–154, 246

Procambarus enoplosternum Hobbs, 1947a:5–9, 12, 13, figs. 2, 5, 10, 12, 14 [not 13], 18, 20, 23–25, 32; 1947b:28, 29; 1958a: 72, 78–79, 83–86, 90, fig. 15; 1958b:160; 1958c:5, 9; 1959: 889, fig. 31.29; 1962:284, fig. 31; 1966b:68, 70; 1968b:K-8, fig. 25g.—Hobbs and Freeman, 1956:10.—Crawford, 1959:150, 151, 156, 162, 172, 177, 180, 181.—Hart and Hart, 1974:21, 28, 32, 33, 71, 88, 90, 91.—Peters, 1975:33.

Procambarus sp. A.—Hobbs, 1958a:72*, 76*, 79, 83–86, 90*, fig. 18.

Procambarus chacei Hobbs, 1958c:5–10*, figs. 14–26 [type-locality: Cedar Creek, 3 mi E of Lykes, Richland County, South Carolina; types: USNM, ANSP, IBM, MCZ, TU]; 1962:284*, fig. 28; 1966b:71; 1968b:K-8*, fig. 25c.—Anonymous, 1967c, tab. 3*.

Procambarus enoplosterum.—Hobbs III, 1969:42 [erroneous spelling].

Procambarus (Ortmannicus) enoplosternum.—Hobbs, 1972a:9; 1972b:64, 150, 154, fig. 50e; 1974b:55, fig. 218.

Procambarus (Ortmannicus) chacei.—Hobbs, 1972a:9, 1972b: 65*, 150*, 154*, 155, fig. 50g; 1974b:55*, fig. 219.

Procambaris enoplosternum.—Wharton, 1978:46* [erroneous spelling].

The above citations are believed to constitute a complete bibliography of the species. All of the references to "*enoplosternum*" except those of Hobbs and Freeman (1956), Crawford (1959), Peters (1975), and those on pages 28 and 91 in Hart and Hart (1974) are based on specimens from Georgia as are those references to "*chacei*" that bear asterisks.

SUMMARY OF LITERATURE.—This crayfish was described from specimens collected at two localities in the Ohoopee River basin in Georgia (Jacks Creek in Emanuel County and Rocky Creek in Toombs County). Not until 21 years later did any additional information on the species appear in the literature. Hobbs (1958a) presented a spot map of the distributions of *Procambarus enoplosternum* and *P.* sp. A (=*P. (O.) chacei*), showing six localities for the former and eight for the latter. He delineated their ranges as follows: *P. (O.) enoplosternum* "frequents the stream tributaries of the Ohoopee River ... in Georgia" (page 78) and *P.* sp. A "occurs in stream tributaries of the Wateree, Congaree, Edisto, and Savannah rivers in South Carolina and in two apparently isolated localities in the Ogeechee and Ocmulgee rivers in Georgia" (page 76). He also discussed their morphological and ecological affinities in commenting on the evolution of the *pictus* Group of the genus *Procambarus*. In the same year (1958c), he described the latter species, choosing Cedar Creek in Richland County, South Carolina, as the type-locality, and listing localities in Aiken, Bamberg, Calhoun, Colleton, and Lexington counties, South Carolina, and one locality each in Candler, Richmond, and Telfair counties, Georgia. He also stated that first form males had been collected in January, February, March, April, June, July, October, and November, and that ovigerous females had been found in March and July. Concerning its relationships, he stated (p. 9) that it

> appears to be more closely related to *P. enoplosternum* than to any other crayfish, and it is of interest that the ranges of the two overlap. While the range of *P. chacei* appears to be much larger than that of *P. enoplosternum* and extends both north and south of the latter, the two species have not been found together, and there is no evidence at the present that hybridization between them has occurred. A more exhaustive study of the two should be undertaken in the Altamaha, Ogeechee, and Savannah river systems.

Crawford (1959), in studying the entocytherid ostracods of Richland County, South Carolina, found six species associated with *P. (O.) enoplosternum*, and Hart and Hart (1974) reported eight species (six in Georgia) infesting it. Other than the record of a single locality in Richmond County, Georgia (Anonymous, 1967c), no further information concerning the species has been recorded.

Hobbs (1972a), in proposing several subgenera to express his concepts of relationships among the members of the genus *Procambarus*, assigned both species to the subgenus *Ortmannicus*, and later (1972b) included them in his key to the crayfishes of North and Middle America, and in his checklist (1974b) provided a synonymy for each along with a redefinition of their ranges. Reasons for synonymizing *P. (O.) chacei* with *P. (O.) enoplosternum* are presented in "Remarks" at the end of this treatment of the latter.

DIAGNOSIS.—Rostrum with marginal spines or tubercles usually well developed, median carina lacking. Carapace with 1 pair of cervical spines, very rarely with accessory ones. Areola 2.8 to 5.0 (average 3.6) times as long as broad and constituting 25.9 to 31.0 (average 27.6) percent of entire length of carapace (36.2 to 42.3, average 29.3, percent of postorbital carapace length). Antennal peduncle with usually prominent spine on ischium. Lateral half of ischium of third maxilliped lacking conspicuous mat of long plumose setae. Basis of cheliped without mesial spine. Mesial surface of palm of chela of male lacking beard but with mesialmost row of 8 to 11 (usually 9 or 10) tubercles. Male with simple hooks on ischia of third and fourth periopods, in first form male that on third overreaching basioischial articulation, that on fourth not reaching articulation and opposed by prominent swelling on cephalodistal extremity of corresponding basis. First pleopods asymmetrical and reaching coxae of third pereiopods, distal third of shaft bearing distinct hump some distance proximal to base of cephalic process; subapical setae flanking mesial, cephalic, and lateral bases of cephalic process, largely obscuring it and central projection; mesial process subspiculiform and directed caudodistally; cephalic process hooding central projection, its acute tip situated distomesial to latter, and di-

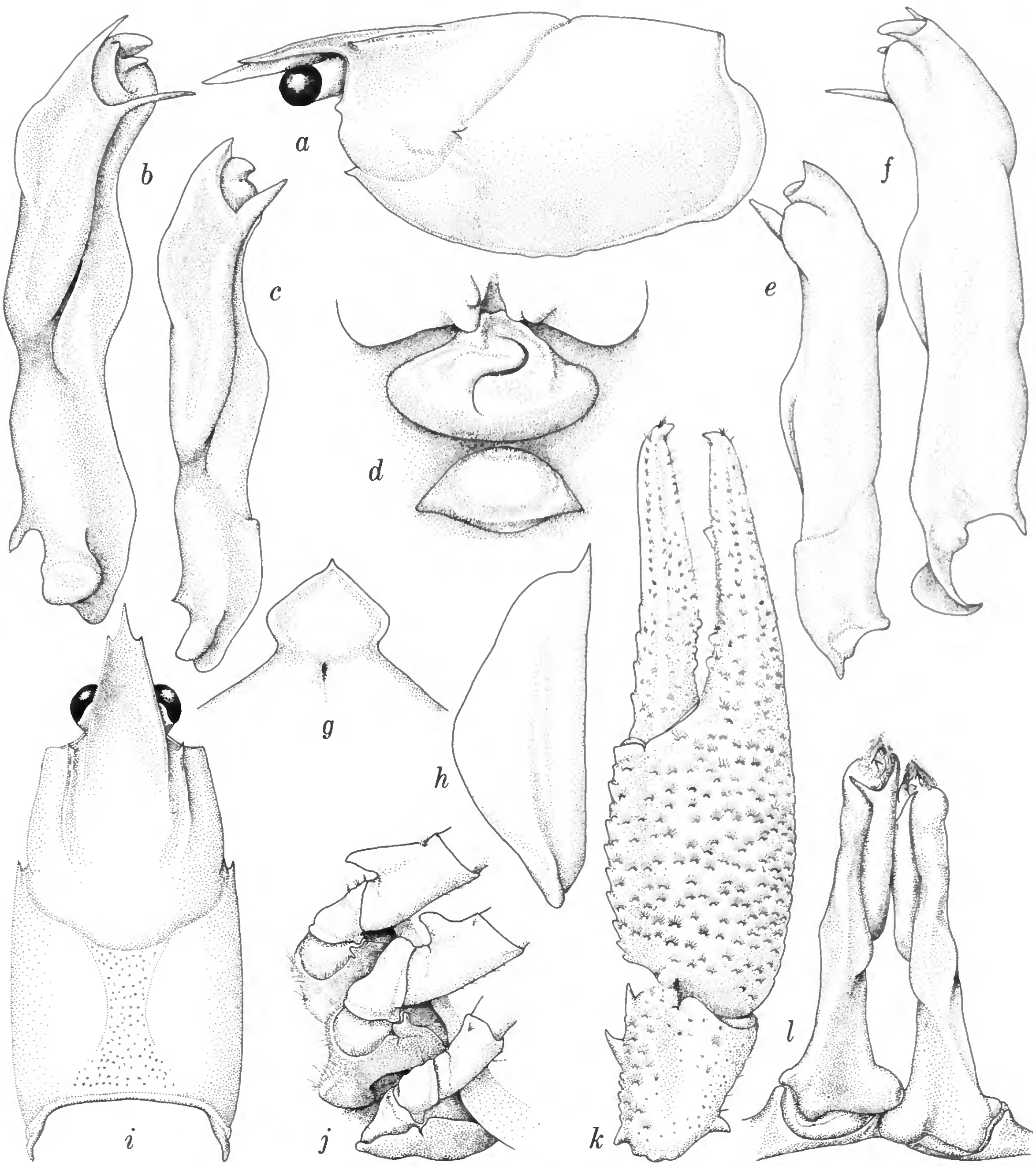


FIGURE 150.—*Procambarus (Ortmannicus) enoplosternum* (all from holotype except *c*, *e*, from morphotype, *d*, from allotype, and *l*, from paratopotypic male, form I): *a*, lateral view of carapace; *b*, *c*, mesial view of first pleopod; *d*, annulus ventralis; *e*, *f*, lateral view of first pleopod; *g*, epistome; *h*, antennal scale; *i*, dorsal view of carapace; *j*, proximal podomeres of third, fourth, and of fifth pereiopods; *k*, dorsal view of distal podomeres of cheliped; *l*, caudal view of first pleopods.

rected caudodistally; central projection strongly sclerotized, beaklike, and directed caudally to caudodistally; caudal element consisting of (1) narrow, compressed, corneous, usually curved tooth (distinctly smaller than central projection) directed caudally and flanked mesially by (2) curved, corneous, ridgelike adventitious process, and (3) swollen, rounded caudal knob on caudodistal extremity of shaft. Female with sternum cephalic to annulus ventralis bearing paired simple prominences (contiguous or separated by distinct gap) extending caudally, or multituberculate, rarely lacking prominences or tubercles; annulus ventralis subcampanulate to ovate in outline, with surface usually weakly sculptured, lacking median depression, and caudomedian area not conspicuously elevated (ventrally) or produced; sinuous sinus reaching neither cephalic nor caudal margins of annulus; postannular sclerite between one-half and two-thirds as wide as annulus and distinctly arched ventrally; first pleopod present.

COLOR NOTES.—The descriptions of two color patterns are included because of the rather striking differences that have been observed in several populations. Three variations are depicted in Figure 137*b–d*.

Topotypes (similar to Figure 137*d*): Carapace basically bearing reticulate pattern of charcoal over orange cream to cream with charcoal to black markings. Cephalic section of carapace with dark orange cream median longitudinal stripe extending from acumen to cervical groove; postorbital ridges black, and black stripe running from orbit posteriorly turning caudodorsally posterior to postorbital ridges, where thickening along anteromesial sides of mandibular adductor regions and joining in fine line interrupting median longitudinal stripe; antennal area with irregular cream spot and pinkish submarginal spot extending across anterior mandibular and anteroventral branchiostegal regions; hepatic region mostly dark with cream tubercles and spots. Caudal section of carapace with light median longitudinal stripe protruding into body of dark charcoal bar of saddle; horns of latter poorly defined except for 2 pairs of large black spots; branchiostegites ventral to level of latter spots grayish tan with irregular pinkish cream splotches; caudal ridge and flange black to bluish brown. Abdominal terga purplish red, with cephalic part of each darker and with rather indistinct transverse lines near midlength broadening and covering posterior part of corresponding pleura; latter with pinkish area anteriorly fading to pinkish cream on ventral margin. Cephalic section of telson mostly mauve tan but with pair of pale oblique spots anteriorly and charcoal over lateral sixth, caudal section suffused with reddish brown. Uropods generally mauve tan proximally, with increasing reddish brown suffusion distally, but mesial ramus with charcoal basally and along lateral margin; in addition, locking ridge on ramus white, sharply separating charcoal area from mauve tan region; lateral ramus also charcoal proximomesially and along lateral margin. Antennular and antennal peduncles bluish tan mottled in charcoal; flagella olive; antennal scale with dark lateral margin and only slightly paler area mesial to lateral thickened part. Chelipeds olive tan with black tubercles; major tubercles on merus and carpus white tipped. Remaining pereiopods bluish green to pale blue from base of ischium distally. Ventral surface of body bluish cream.

Savannah Basin and Ogeechee and Little Ocmulgee Rivers (Figure 137*b*, *c*): Carapace basically yellowish cream, conspicuously marked with shades of gray to almost black. Cephalic region with median longitudinal light stripe flanked laterally by narrower dark ones joining similarly colored areas over mandibular adductor regions; pale postorbital ridge with narrow black line abutting it ventrolaterally, line also joining dark area over mandibular adductor region; orbital, antennal, and mandibular regions mostly yellowish cream, with charcoal line extending from anterior margin of antennal region caudoventrally, expanding over ventral part of hepatic region; more dorsal part of latter with horizontal dark line continuous with ventral margin of mandibular adductor region. Thoracic area with conspicuous, almost black saddle, horns of which approaching cervical groove and bar with shallow anteromedian notch; bar flanked anteriorly and horns dorsally by rather narrow, cream area separating saddle from dark region across the branchiostegites and areola; branchiostegites ventral to horns of saddle also yellowish cream with irregular charcoal splotches; anteroventral branchiostegal area with light spot abutting cervical groove, otherwise ringed with charcoal; caudal flange dark gray; cervical spine cream. Abdomen basically olive with pinkish suffusion dorsally; all terga with broad, dark charcoal transverse band anteriorly; bands continuing ventrally onto anterior parts of corresponding pleura; narrower, much less conspicuous secondary band extending across midlength of second through fifth terga continuous with dark, posterior region of corresponding pleura; all pleura with pinkish cream area. Telson mostly pinkish tan, with small oblique cream spots anteriorly abutting dark lateral markings. Uropods pinkish tan except for charcoal areas (opposite dark spots on telson) on mesial ramus and mesial part of lateral ramus. Antennular and antennal peduncles cream mottled with charcoal; flagella olive tan; antennal scale cream with dark lateral margin and brownish area along mesial side of lateral thickened part. Chelipeds cream basally, becoming orange tan on carpus; dark irregular splotches present from distal third of merus to bases of fingers; many tubercles black, major ones tipped in white; tips of fingers cream. Remaining pereiopods dark cream suffused with pink, and grayish tinge present at articulations. Ventral surface of body pinkish cream to white.

TYPES.—Holotype, allotype, and "morphotype," USNM 82263 (♂I, ♀, ♂II); paratypes, MCZ, USNM, TU.

TYPE-LOCALITY.—Rocky Creek, 6 miles south of Lyons on U.S. Highway 1, Toombs County, Georgia.

RANGE.—This crayfish ranges from the Wateree River basin in South Carolina southward to the Little Ocmulgee-Altamaha Basin in Georgia. In the latter, it appears to be confined to the Coastal Plain Province, where it occurs from the Fall Line Hills through the Vidalia Upland districts, and in the Barrier Island Sequence District it is known from a few localities.

SPECIMENS EXAMINED.—I have examined a total of 1110 specimens, 559 from South Carolina and 551 from the following localities in Georgia. *Appling County*: (1) trib to Ten Mile Creek 1.7 mi SW of Tattnall Co line on St Rte 144, 1♀, 1j♂, 1j♀, 23 Mar 1959, R. H. Gibbs, collector. *Bryan County*: (2) Canoochee River near Clyde Rd, 1♂I, 26 Aug 1931, H. van der Shalie; (3) Ogeechee River opposite Jones Lake, 1♀, 24 Aug 1937, HS. *Bulloch County*: (4) Ogeechee River at St Rte 119, 1♂I, 2♂II, 3♀, 1j♂, 19 Apr 1977, C. E. Carter, C. W. Hart, Jr., J. E. Pugh, HHH. *Candler County*: (5) Canoochee River 4 mi W of Metter on St Rte 46 (Hobbs, 1958c:9), 1♂I, 24 Mar 1950, D. C. Scott. *Chatham County*: (6) Ogeechee River at mouth of McCrimmon Creek, 1♂I, 2♀, 26 Aug 1931, HS. *Dodge County*: (7) Little Ocmulgee River near Jay Bird Springs on St Rte 165, 2♂II, 2♀, 22 Apr 1966, E. T. Hall, Jr., HHH; 1♀, 21 Jun 1975, D. J. Peters, JEP, HHH; (8) Little Ocmulgee River 1.6 mi N of Chauncey on St Rte 165, 6♂I, 6♂II, 9♀, 1j♂, 2j♀, 21 Apr 1977, CEC, JEP, HHH. *Emanuel County*: (9) Ohoopee River 15 mi S of Swainsboro, 2♂I, 7♂II, 5♀, 4j♂, 2j♀, 6 Sep 1929, E. P. Creaser; (10) Jacks Creek at Lexsy, US Hwy 1 (Hobbs, 1947b:9), 1♂II, 1♀, 1j♀, 23 Aug 1937, HHH; 7♂II, 7♀, 2 Jan 1938, HHH; 4♂II, 3♀, 2 May 1946, HHH; (11) trib of Ohoopee River 15.2 mi W of Swainsboro on US Hwy 80, 1♀, 1j♂, 1j♀, 25 Mar 1950, E. C. Raney; (12) Jacks Creek on unnumbered road near St Rte 46, 1♂I, 1♂II, 1♀, 2j♂, 1j♀, 20 Jul 1971, ETH, B. A. Caldwell; (13) creek 11 mi N of St Rte 292 on US Hwy 1, 1♂I, 2♂II, 3♀, 3j♂, 3j♀, 20 Apr 1977, CEC, JEP, HHH. *Evans County*: (14) Canoochee River on US Hwy 301 at Claxton, 1♂II, 1♀, 1j♂, 1j♀, 12 Aug 1976, M. W. Walker, K. W. Martin. *Johnson County*: (15) midway between Dublin and Swainsboro along railroad, 13j♂, 5j♀, 5 Sep 1929, EPC; (16) 11 mi NE of Wrightsville on US Hwy 319, 1♂II, 1j♂, 2j♀, 1♀ with young, 18 Aug 1952, G. B. Hobbs, HHH; (17) Buckeye Creek 2.8 mi E of Washington Co line on St Rte 57, 1j♂, 26 Apr 1966, ETH, HHH; (18) 0.5 mi S of Washington Co line on St Rte 15, 1♂I, 16 Jun 1972, DJP, JEP, HHH; (19) Ohoopee River 2.9 mi SW of Wrightsville on US Hwy 319, 4♂I, 1♂II, 5♀, 2j♂, 19 Jun 1975, DJP, JEP, HHH; (20) Big Cedar Creek at St Rte 15, 1♂I, 1♂II, 1♀, 2j♂, 3j♀, 25 Apr 1966, ETH, HHH. *Laurens County*: (21) 8.6 mi N of St Rte 46 on US Hwy 441, 3♂I, 1j♂, 22 Mar 1961, P. C. Holt, V. F. Holt; (22) 3.4 mi S of St Rte 149 on US Hwy 441, 2♂II, 2♀, 5 Nov 1967, J. J. Sullivan; (23) 20.6 mi S of US Hwy 80 on St Rte 19, 1♂II, 4♀, 20 Jun 1975, DJP, JEP, HHH; (24) Crooked Creek 0.9 mi NE of Bleckley Co line on St Rte 26, 1♂I, 1♂II, 1♀, 27 Mar 1959, RHG; (25) Stitchihatchee Creek on St Rte 338 at Dexter, 1♂II, 1♀, 15j♂, 7j♀, 21 Apr 1977, CEC, JEP, HHH. *Long County*: (26) Goose Run Creek 7.7 mi NW of McIntosh Co line on St Rte 99, 1♂II, 1♀, 1 ovig ♀, 28 May 1969, ETH,

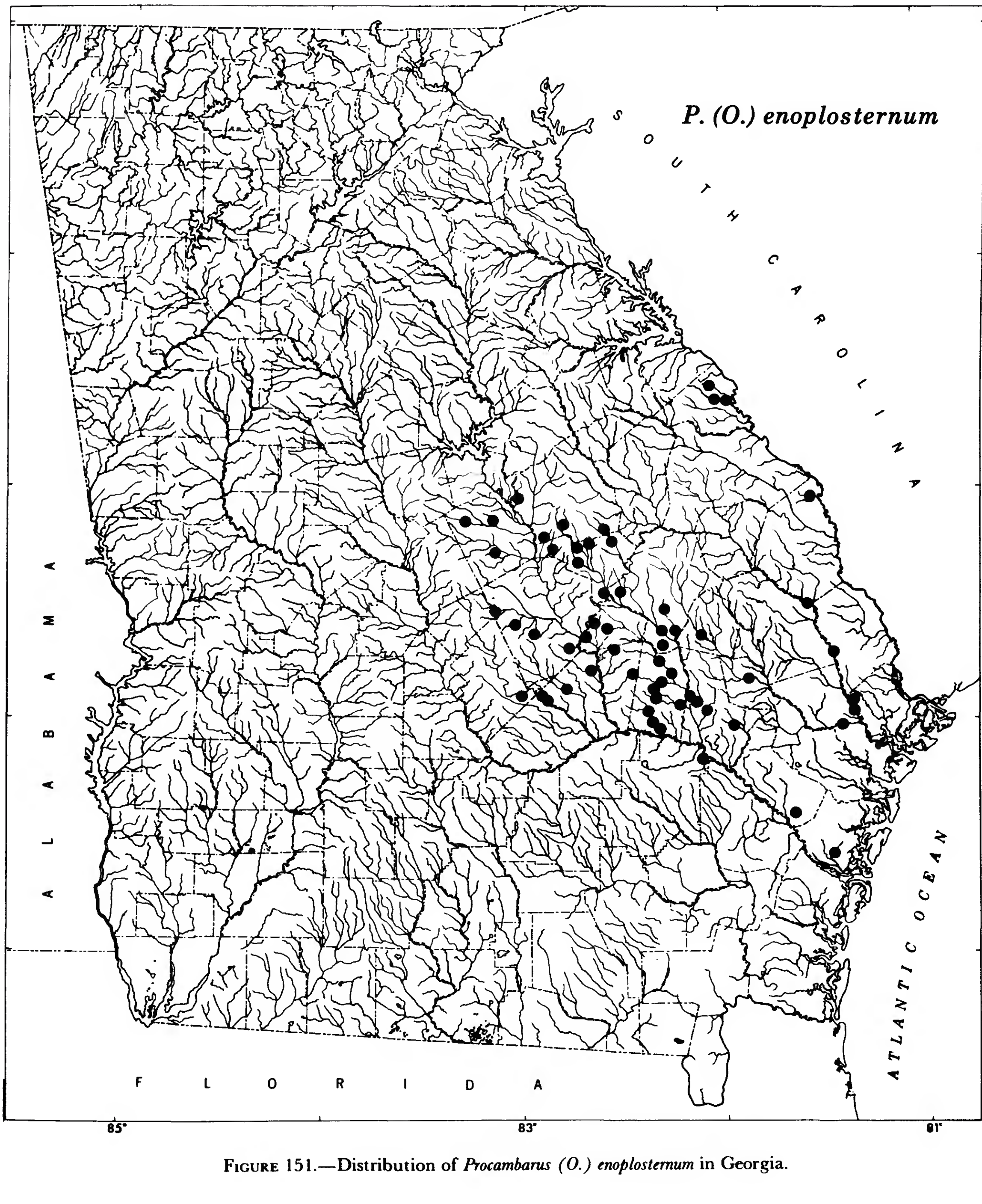


FIGURE 151.—Distribution of *Procambarus (O.) enoplosternum* in Georgia.

HHH. *McIntosh County*: (27) Buffalo Creek 6.5 mi W of US Hwy 17 on St Rte 251, 1♂I, 1♂II, 1j♂, 1j♀, 1 ovig ♀, 28 May 1969, ETH, HHH. *Montgomery County*: (28) 1.3 mi S of Treutlen Co line on US Hwy 221, 1♂I, 2♀, 10j♂, 2j♀, 22 Apr 1966, ETH, HHH; (29) Rocky Creek at Higgston, 1♂II, 26 May 1969, ETH, HHH. *Richmond County*: (30) Butler Creek at St Rte 21, 1j♂, 1j♀, 13 Feb 1967, D. Schultz and Holsomback; (31) Rocky Creek just below Milledgeville Rd, 1♂I, 26 Apr 1941, O. K. Fletcher; (32) King's Wood in Augusta (Hobbs, 1958c:9), 1♂I, 1♂II, 10♀, 5j♀, 1 ovig ♀, 23 Mar 1948, ECR; (33) Butler Creek at railroad 0.3 mi E of US Hwy 25 in Augusta, 2♂I, 1♀, 16 Apr 1977, CEC, CWH, JEP, HHH; (34) Butler Creek at St Rte 56, 1♂I, 1♀, 1 ovig ♀, 17 Apr 1977, CEC, CWH, JEP, HHH. *Screven County*: (35) Ogeechee River at Bulloch Co line on St Rte 24, 1♀, 1j♂, 2j♀, 18 Apr 1977, CEC, CWH, JEP, HHH; (36) Rocky Creek 5 mi S of Burke Co line on Rte S1321, 1♂I, 17 Apr 1977, CEC, CWH, JEP, HHH. *Tattnall County*: (37) Brazells Creek 2.3 mi W of Reidsville, 2♂I, 1♀, 9 Jun 1949, R. D. Suttkus, RHG; 5♂II, 7♀, 3j♂, 2j♀, 30 Apr 1950, D. C. Scott; (38) Thomas Creek 2.4 mi SE of Reidsville on St Rte 23, 1♂II, 1♀, 6j♂, 6j♀, 31 Dec 1956, GBH, HHH; 1♂II, 4♀, 2j♀, 1 ovig ♀, 27 May 1969, ETH, HHH; (39) 12 mi N of Appling Co line on St Rte 169, 1♂II, 2♀, 3j♂, 4j♀, 18 Apr 1963, PCH, VFH; (40) roadside ditch 1.8 mi SW of Toombs Co line on US Hwy 280, 1♂I, 1♀, 2j♀, 21 Jun 1975, DJP, JEP, HHH; (41) 1.9 mi NE of Reidsville on US Hwy 280, 2♂I, 2♀, 21 Jun 1975, HHH. *Telfair County*: (42) Little Ocmulgee River 4.7 mi N of Helena on Rte S576, 3♂I, 4♂II, 6♀, 5j♂, 2j♀, 23 Apr 1966, ETH, HHH; (43) Little Ocmulgee River 1.2 mi N of McRae on US Hwy 280 (Hobbs, 1958c:9), 4♂I, 1♂II, 5♀, 25 Mar 1950, ECR. *Toombs County*: (44) ponds on Pendleton Creek 5 mi S of Oak Park, 1♂I, 2♂II, 9♀, 5j♂, 4j♀, 6 Sep 1929, EPC; (45) ditch, trib to Swift Creek near Lyons, 1♂II, 6 Sep 1929, EPC; (46) type-locality, 1♂II, 1♀, 1j♂, 1j♀, 2 Jan 1938, HHH; 4♂I, 6♂II, 4♀, 2j♂, 1j♀, 28 Aug 1938, HHH; 4♂I, 5♂II, 4♀, 2j♂, 3j♀, 9 Jun 1946, HHH; 2♂I, 6♀, 1j♀, 20 Apr 1977, CEC, JEP, HHH; 1j♂, 5 Oct 1977, T. A. English, Jr., HHH; (47) Cobb Creek 6 mi N of Altamaha River on US Hwy 1, 1♂I, 16 Jul 1952, D. C. Scott; 1♂I, 1♀, 2 Jun 1952, RHG; (48) Pendleton Creek at St Rte 292, 2j♀, 20 Jul 1971, BAC, MWW; (49) Cobb Creek at St Rte 56, 4♂I, 1♂II, 2♀, 1 ovig ♀, 22 Jun 1975, DJP, JEP, HHH; (50) Cobb Creek at St Rte 107, 12j♂, 11j♀, 5 Oct 1977, TAE, HHH. *Treutlen County*: (51) 16 mi SE of East Dublin on St Rte 29, 1♂I, 2♂II, 4♀, 13j♂, 6j♀, 22 Apr 1966, ETH, HHH; (52) 19.5 mi SE of East Dublin on St Rte 29, 1♂I, 3♂II, 6♀, 3j♂, 3j♀, 22 Apr 1966, ETH, HHH. *Washington County*: (53) Deep Creek 3.8 mi E of Wilkinson Co line on St Rte 57, 1♀, 26 Apr 1966, ETH, HHH; (54) Ohoopee River 5.2 mi S of Tennille, 1♂II, 1j♂, 1j♀, 11 Nov 1961, C. H. Wharton; (55) Nealey Creek 4 mi SW of St Rte 242 on Co Rd 187, 2♂I, 3♂II, 16 Jun 1972, DJP, JEP, HHH; (56) Bluff Creek 1.4 mi E of Baldwin Co line on St Rte 24, 1♂I, 3♂II, 1♀, 15 Jun 1972, DJP, JEP, HHH. *Wheeler County*: (57) Alligator Creek 1 mi SW of Alamo on US Hwy 280, 2♂I, 1♀, 5 Nov 1967, JJS; 5♂I, 6♂II, 6♀, 1j♂, 1j♀, 21 Jun 1975, DJP, JEP, HHH; (58) roadside ditch 7.4 mi SE of Laurens Co line on St Rte 19, 2j♀, 20 Jun 1975, DJP, JEP, HHH. *Wilkinson County*: (59) trib to Maiden Creek 8.4 mi E of Twiggs Co line on St Rte 96, 3♂II, 3♀, 4j♂, 6j♀, 26 Apr 1966, ETH, HHH; (60) 8.1 mi E of Irwinton on St Rte 57, 1j♂, 26 Apr 1966, ETH, HHH; (61) Little Commissioner Creek, 1♂I, 28 May 1975, MWW, KWM; (62) Little Black Creek at St Rte 112, 1♀, 3 Apr 1978, DJP, JEP, HHH.

VARIATIONS.—Perhaps the most conspicuous variation in this crayfish is the body size of the adults in different populations. Although exceptions exist among collections available to me, members of populations occurring in the larger streams mature at a smaller size than do those in many of the smaller creeks. For example, in first form males from the vicinity of the type-locality, the carapace length is at least 25 mm, and, in most, more than 30 mm. In contrast, in males from the Little Ocmulgee, Ogeechee, and Savannah rivers, few attain a carapace length of more than 25 mm, and none of my specimens as much as 30 mm. The smallest first form male, having a carapace length of 14.8 mm, was collected in the Canoochee River in Candler County. Variations also occur in the color pattern (Figure 137*b–d*); the most obvious (other than variations resulting from adaptations to light and dark backgrounds) is in the development of the horns of the saddle spanning the thoracic section of the carapace. In specimens from most of the range, the saddle is readily evident, consisting of an almost concolorous transverse bar and paired horns; in others the transverse bar is occasionally much lighter than the horns, and sometimes, particularly in individuals frequenting the Ohoopee River basin, the horns are pale except anteriorly and posteriorly, leaving two pairs of very dark spots on the lateral surfaces of the branchiostegites. Marginal spines, occasionally reduced to tubercles, are always present on the rostrum, but the slope of the lateral margins of the latter varies greatly (Figure 152). In some localities (notably those in the Little Ocmulgee and Ogeechee rivers and the Savannah

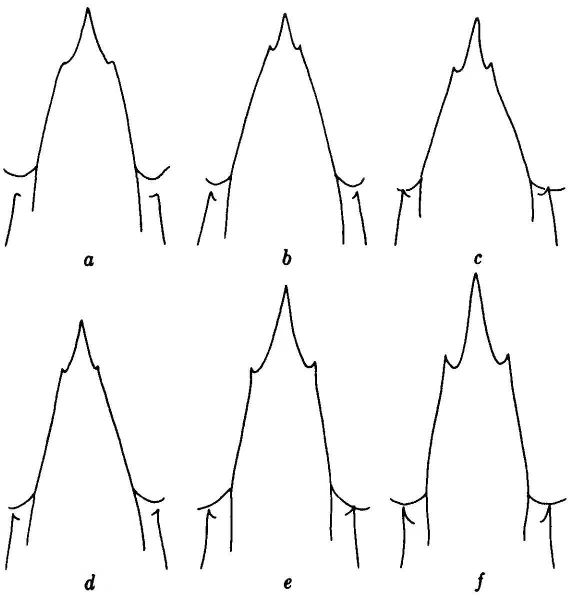


FIGURE 152.—*Procambarus (O.) enoplosternum*, variations in rostrum in Georgia: *a*, Tattnall Co; *b*, *d*, Montgomery Co; *c*, Emanuel Co; *e*, Screven Co; *f*, Wheeler Co.

watershed) all of the members have margins that are subparallel or convex laterally, and usually the acumen is proportionately long in those individuals having convex rostral margins. Elsewhere the rostrum tapers anteriorly from the base. Among the specimens I have examined, only one was observed to possess more than a single cervical spine on each side. This juvenile male from Johnson County had two on the left and three on the right. The usual variations found in the chelipeds are for the most part not noteworthy; but in the larger males the palm of the chela usually becomes somewhat inflated, thus appearing quite distinct from the slender elongate chelae typical of the smaller individuals, including the first form males. The usual differences in proportions observed in the chelae of the males and females of the subgenus exist (cf. Figures 138*c*, 150*k*), and, as in a number of other related species, the minute denticles on the opposable margins of the fingers occur in single rows in females and in juvenile males, whereas a band of denticles is present in the adult males. The first pleopods of the male also exhibit a rather broad spectrum of variation (Figure 153). Among the differences noted are the degree of curvature of the distal part of the appendage and the related development of the hump on the cephalic surface, which is more conspicuously set off from the shaft in some populations than in others (cf. Figure 153*p*,*u*). The cephalic process is also highly variable, particularly the lateral part that in some populations shields more of the lateral base of the central projection (Figure 153*x*) than it does in others (Figure 153*h*). Although the length of the cephalic process varies, I suspect that the extreme reduction shown in Figure 153*m* resulted from an injury during an earlier stadium. The central projection also exhibits differences in size and angle of disposition (Figure 153*a*,*k*,*u*). The configuration and degree of tumescence of the caudal knob also present striking contrasts in the pleopods of individuals from the same and different localities. The annulus ventralis varies from subcampanulate to oval in outline, and the ventral surface from a smooth convex one cut by a simple sigmoid sinus, to one that is subplane but shallowly dissected by grooves in addition to the sinus, and occasionally the cephalic region is somewhat elevated. The sternum cephalic to the annulus is decidedly inconstant in its surface contour (Figure 154): usually it is multituberculate or at least bears a pair of caudally projecting lobes, but in some specimens from both Long and Tattnall counties, the sternum is almost or completely smooth, resembling that of *P. (O.) litosternum*, a close relative.

SIZE.—The largest specimen available is a female, having a carapace length of 46.4 (postorbital carapace length 35.0) mm. Corresponding lengths of the largest and smallest first form males are 42.4 (30.4) mm and 14.8 (9.9) mm, and those of the smallest ovigerous female from Georgia, 24.1 (16.5) mm.

LIFE HISTORY NOTES.—Combining data on specimens from Georgia and South Carolina, first form males have been found throughout the year

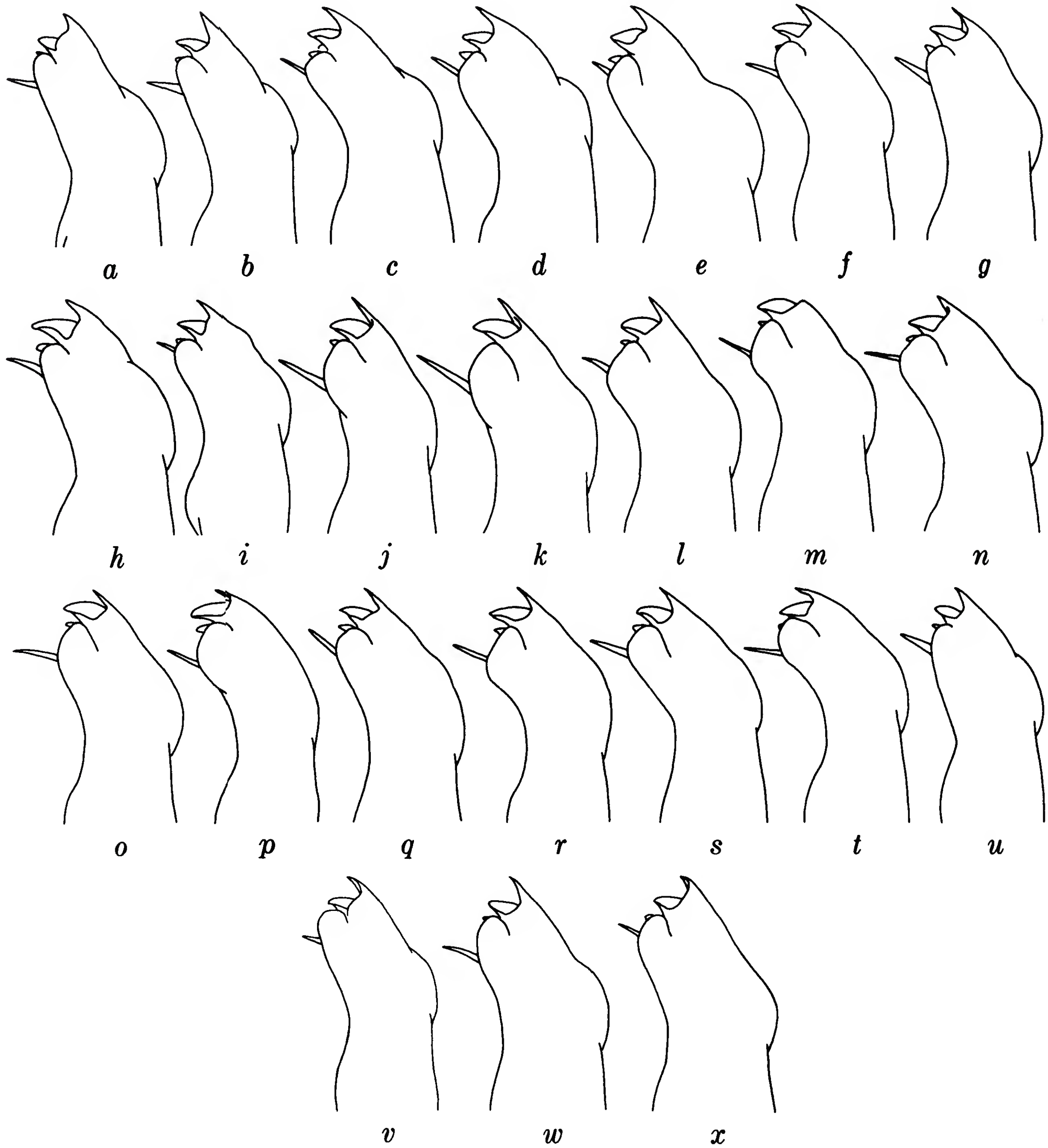


FIGURE 153.—*Procambarus (O.) enoplosternum*, variations in first pleopod of first form male (*a–c*, from South Carolina; all others from Georgia). Congaree Basin: *a*, *b*, Richland Co. Savannah Basin: *c*, Aiken Co; *d*, Richmond Co; *e*, Screven Co. Ogeechee Basin: *f*, Bulloch Co; *g*, Candler Co; *h*, Chatham Co. Canoochee Basin: *i*, Bryan Co. Ohoopee Basin: *j*, Washington Co; *k–m*, Johnson Co; *n*, Emanuel Co; *o*, Toombs Co. Oconee Basin: *p*, Washington Co; *q*, *r*, Laurens Co; *s*, Treutlen Co; *t*, Montgomery Co. Ocmulgee Basin: *u*, Telfair Co; *v*, Wheeler Co; *w*, Dodge Co. Altamaha Basin: *x*, McIntosh Co.

except in January (I have been unable to confirm the January record cited by Hobbs, 1958c:9) and December, during which only eight adults have been collected. In Georgia such males have not been taken in February or October. Ovigerous females were obtained in March, April, May, and June in Georgia, and in April, May, and July in South Carolina. A single female carrying young was found in Georgia in August, and others were collected in South Carolina during April and May. The records noted in the chart of "Seasonal Data" suggest that the egg-laying season occurs in the spring and early summer. Most of the adult females collected in April carried sperm plugs in their annuli ventrales.

The following data are available on ovigerous females from Georgia:

Carapace and postorbital carapace lengths (mm)	*Number of eggs*	*Diameter of eggs (mm)*
24.1 (16.5)	186	1.5–1.6
28.0 (19.1)	219	1.6–1.7
29.5 (21.7)	219	1.5–1.6
34.2 (24.3)	230	1.5–1.6

Seasonal Data (Georgia and South Carolina)

Sex/stage	*J*	*F*	*M*	*A*	*M*	*J*	*J*	*A*	*S*	*O*	*N*	*D*
♂I		1	15	49	33	29	8	6	3	8	6	
♂II	10	4	8	56	39	22	7	25	10		5	1
♀	10	6	30	80	47	28	8	65	14	8	10	1
♂j	22	7	12	76	14	5	4	8	24	21	4	7
♀j	18	14	11	61	18	8	13	39	12	12	16	8
♀ ovig			1	8	6	1	2					
♀ with young				3	2			1				

Ecological Notes.—Although most of the specimens of this crayfish that I have seen were collected in sluggish to moderately flowing streams, a few were obtained from pools in roadside ditches, and in two localities they were dug from burrows. They have been found in sand-bottomed streams in deep shade, where the only cover available to them consisted of tree litter, exposed roots of shoreline plants, and undercut banks. In stream beds with rocks, they were found in shallow excavations beneath them. In many streams within their range, the right-of-way of roads has been cleared of trees, and where unfiltered sunlight reaches the stream, often dense growths of both emergent and submergent macrophytes almost obliterate the substrate from view. The channels in such habitats become narrower, resulting in currents that are quite rapid. In these vegetation-choked streams, this crayfish has been found to occur most commonly among the plants and organic debris flanking the channels. It was also found in lesser numbers, especially the young, in areas where the current is sluggish or even where there is no perceptible flow. In April 1977, specimens were collected among terrestrial vegetation in the inundated flood plain of the Ogeechee River some seven to 10 meters away from the riverbed itself. There was no evidence of burrows in the shallow water, so presumably these individuals had wandered shoreward from the streambed during the flood stage.

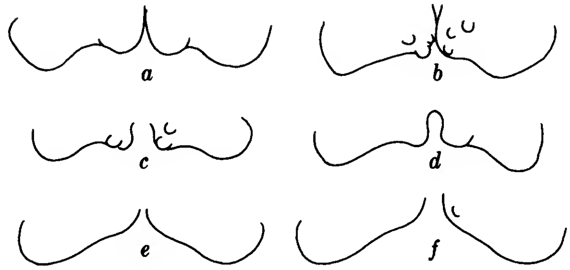


Figure 154.—*Procambarus (O.) enoplosternum*, variations in sternum immediately cephalic to annulus ventralis. Oconee Basin: *a*, *b*, Wheeler Co. Ocmulgee Basin: *c*, Telfair Co. Ohoopee Basin: *d*, Emanuel Co; *e*, Tattnall Co. Altamaha Basin: *f*, Long Co.

Under the bridge over the Ohoopee River, 2.9 miles southwest of Wrightsville on U.S. Highway 319, Johnson County, a number of open and plugged burrows were found on the river bank near, but some half to one meter above, the water level in the river. Occupying one of those excavated were a first form male and a female, and females were found in a few others. These burrows were in sandy soil with such a small amount of clay that, in the process of opening the simple unbranched tunnels, sand sloughed from the walls, filling the lower part of the gallery faster than it could be removed. In a cleared roadside ditch 1.9 miles northeast of Reidsville on U.S. Highway 280, Tattnall County, a male and female were found together in a simple burrow that had been plugged, and in another a female with well-developed cement glands was collected.

Finding members of this species in burrows in a roadside ditch containing no standing water demonstrates a capability—to be able to exploit temporary lentic habitats—that has not been observed in its closest relatives *P. (O.) epicyrtus*, *P. (O.) litosternum*, *P. (O.) pubescens*, *P. (O.) hirsutus* Hobbs (1958b:160), and *P. (O.) pictus* (Hobbs, 1940a:419). Perhaps this ability has enabled *P. (O.) enoplosternum* to extend its range to span those of all of them except that of *P. (O.) pictus*.

Georgia Crayfish Associates.—*Procambarus (O.) enoplosternum* has been collected with the following crayfishes (the numbers of times they have been found together are noted in parentheses): *Cambarus (D.) latimanus* (4), *C. (D.) striatus* (3), *C. (L.) diogenes diogenes* (1), *Faxonella clypeata* (6), *Procambarus (H.) advena* (1), *P. (H.) caritus* (1), *P. (H.) pygmaeus* (2), *P. (H.) truculentus* (2), *P. (L.) barbatus* (2), *P. (O.) acutus acutus* (8), *P. (O.) litosternum* (2), *P. (O.) lunzi* (1), *P. (O.) seminolae* (2), *P. (Pe.) petersi* (1), *P. (Pe.) spiculifer* (6), *P. (S.) howellae* (9), and *P. (S.) troglodytes* (3).

Remarks.—In describing *Procambarus (O.) chacei*, which is here designated a junior synonym of *P. (O.) enoplosternum*, Hobbs (1958c:9) pointed out its close affinities to the latter and stated that a thorough study of the two should be undertaken in Georgia, where their ranges overlapped. On the basis of the specimens available to him at that time, the two were easily separable on the basis of the structure of the cephalic process of the first pleopod of the first form male and the ratio of the length to the width of the areola, which in *P. (O.) chacei* was 2.8 to 4.0 times as broad as long and in *P. (O.) enoplosternum*, 4.5 to 5.0. Furthermore the Georgia specimens of *P. (O.) chacei* had a complete saddle marking the thoracic section of the carapace, and the annuli ventrales appeared to be decidedly different as did the structure of the cheliped (cf. illustrations of the two in Hobbs, 1947a and 1958c). With the acquisition of a much larger and more representative series of specimens, the differences that had been noted earlier fell into a mosaic pattern. While local populations in Georgia (those occurring in the Savannah Basin and the Little Ocmulgee and Ogeechee rivers proper) share more in common with specimens from Richland County, South Carolina (encompassing the type-locality of *P. (O.) chacei*), intermediate forms occur in the Ohoopee and tributaries of the Ogeechee and Altamaha basins. The only character that seems almost always to allow the separation of the two occurs in the rostrum. In *P. (O.) enoplosternum* the margins are rather strongly convergent, whereas in populations formerly assigned to *P. (O.) chacei* they are convex or subparallel. This feature, which is somewhat variable and lends itself to subjective analysis, does not seem to me to warrant the recognition of separate species.

Procambarus (Ortmannicus) epicyrtus Hobbs

Figures 13*f*, 137*a*, 138*d*, 155–157, 247

Procambarus sp. C. Hobbs, 1958a:72, 74, 76, 78, 79, 83, 85, 86, 90, fig. 17.

Procambarus epicyrtus Hobbs, 1958c:1–5, 9, 10, figs. 1–13; 1962: 284, fig. 30; 1968b:K-8, fig. 25h.—Hart and Hart, 1974: 21, 88.—Wharton, 1978:46.

Procambarus (Ortmannicus) epicyrtus.—Hobbs, 1972a:9; 1972b: 64, 150, 154, fig. 50d; 1974b:55, fig. 220.

These references are believed to constitute a complete bibliography for the species, and, inasmuch as this crayfish is endemic in Georgia, all pertain to its occurrence in the state.

Summary of Literature.—Prior to the description of this crayfish, Hobbs (1958a, which appeared in March), in his study of the evolutionary history of the *pictus* Group, discussed its affinities and presented an illustration of the distal part of the first pleopod of the first form male. In that article, he stated that "*Procambarus* sp. C is known from a single stream tributary of the Ogeechee River in Screven County, Georgia." In July of the same year, he (1958c) presented a description of this crayfish, introducing the name *Procambarus epicyrtus*. No new data were added by him in his treatment of the *blandingii* Section (1962) or in his key to the Malacostraca of the southeastern United States (1968b). In structuring the infrageneric species groups in the large genus *Procambarus*, Hobbs (1972a) referred this crayfish to the subgenus *Ortmannicus* and (1972b: 64) stated that it occurs in "stream tributaries of the Oconee and Ogeechee rivers in Georgia." No additional information appeared in Hobbs' checklist (1974b). The most recent reference to the species was that of Hart and Hart (1974), who reported two entocytherid ostracods (*Ankylocythere ancyla* and *Entocythere elliptica*) infesting *P. (O.) epicyrtus* at the type-locality.

DIAGNOSIS.—Rostrum with marginal spines or tubercles, lacking median carina. Carapace with 1 pair of cervical spines. Areola 3.4 to 5.2 (average 4.3) times as long as broad and constituting 27.0 to 30.8 (average 29.0) percent of entire length of carapace (38.3 to 41.6, average 40.2, percent of postorbital carapace length). Antennal peduncle with spine on ischium. Lateral half of ventral surface of ischium of third maxilliped lacking conspicuous mat of long plumose setae. Basis of cheliped without mesial spine. Mesial surface of palm of chela of male with mesialmost row of 8 to 12 tubercles. Male with hooks on ischia of third and fourth pereiopods; in first form male that on third overreaching basioischial articulation, that on fourth not reaching corresponding articulation but opposed by prominent tubercle (actually swollen cephalodistal extremity of podomere, which occasionally bearing accessory tubercle) on corresponding basis. First pleopods asymmetrical and reaching coxae of third pereiopods; distal fourth of shaft strongly inclined caudally; cephalic surface of neither member of pair with distinct shoulder, although prominent bulge present; subapical setae flanking lateral, cephalic, and mesial sides of both cephalic process and central projection, largely obscuring both; mesial process long, slender, and directed caudally; cephalic process short or moderately long, acute, and hooding basal part of central projection, apex not reaching so far distally as that of central projection; latter consisting of corneous, beaklike projection directed caudodistally; caudal element consisting of (1) prominent globose caudal knob on distal caudolateral end of shaft, (2) conspicuous corneous caudal process, not much smaller than central projection, situated along proximomesial side of latter and directed caudally, and (3) adventitious process forming distinct ridge partly surrounding basal part of caudal process (at least crest of ridge corneous). Female with sternum cephalic to annulus ventralis highly variable, possessing or lacking tubercles and/or prominent projections extending caudally over cephaloventral face of annulus; latter with slightly elevated (ventrally) cephalolateral ridges flanked caudally by broad, shallowly excavate arc partly surrounding prominent, slightly asymmetrical, caudomedian protuberance; sinus originating in depression, undulating caudally onto top of protuberance; when caudal side of annulus depressed, elevated area extending caudally over postannular sclerite; latter about 0.7 times as wide as annulus; first pleopod present.

COLOR NOTES (Figure 137*a*).—Carapace basically reticulate charcoal over tannish mauve background, with charcoal to black markings. Cephalic section of carapace with median longitudinal mauve tan stripe extending from acumen to cervical groove; postorbital ridges black; longitudinal black line extending from orbit posteriorly onto dorsal hepatic region, parallel and slightly ventral to postorbital ridge; hepatic and mandibular regions with charcoal spots and cream tubercles; latter region with pinkish cream area along anterior margin. Thoracic section of carapace with median longitudinal stripe present but not so sharply defined as in cephalic region and not completely dividing bar of caudal saddle; latter consisting of broad charcoal bar and 2 pairs of black lateral spots representing remnants of horns; branchiostegites ventral to level of black spots pale mauve to bluish gray, with large white spots; caudal ridge edged in black, flange dark bluish gray. Terga of abdomen mauve tan except for narrow charcoal bands anteriorly and black

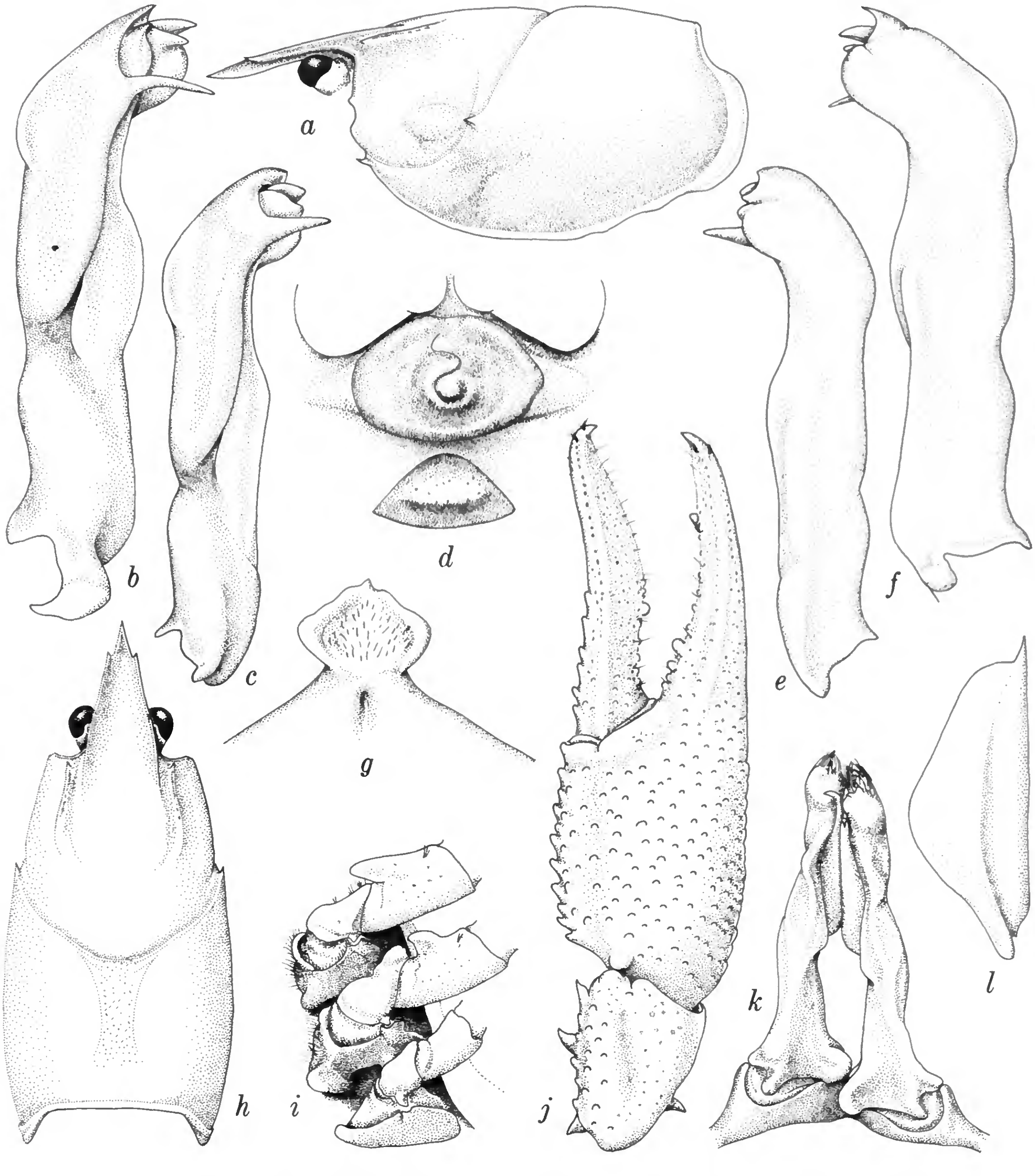


FIGURE 155.—*Procambarus (Ortmannicus) epicyrtus* (all from topotypic first form male except *c*, *e*, from topotypic second form male, and *d*, from topotypic female): *a*, lateral view of carapace; *b*, *c*, mesial view of first pleopod; *d*, annulus ventralis; *e*, *f*, lateral view of first pleopod; *g*, epistome; *h*, dorsal view of carapace; *i*, proximal podomeres of third, fourth, and fifth pereiopods; *j*, dorsal view of distal podomeres of cheliped; *k*, caudal view of first pleopods; *l*, antennal scale.

caudal marginal lines, latter continuing onto caudal margins of pleura. Pleura also mauve tan, with pinkish cream spot surrounded by reddish suffusion in mauve tan area. Telson, uropods, antennules, antennae, antennal scales, chelipeds, and other pereiopods as in *P. (O.) enoplosternum*. Ventral surface of body bluish cream.

TYPES.—Holotype, allotype, and morphotype, USNM 101286, 101287, 101288 (♂I, ♀, ♂II); paratypes, ANSP, IBM, MCZ, TU, USNM.

TYPE-LOCALITY.—South Ogeechee Creek, 6.8 miles south of Sylvania on U.S. Highway 301, Screven County, Georgia.

RANGE.—This crayfish is endemic to Georgia, where it occurs in the lower Ogeechee and Savannah river basins (not Oconee Basin as reported by Hobbs (1974b:55), a record based upon a mislabeled specimen purportedly from Wheeler County, now known to have been collected in Effingham County.) Insofar as is known, it is limited to the Vidalia Upland and Barrier Island Sequence districts of the Coastal Plain Province.

GEORGIA SPECIMENS EXAMINED.—I have examined a total of 304 specimens as follows. *Bryan County*: (1) Mill Creek 1.2 mi N of Ellabelle, 2j♂, 27 Dec 1971, G. K. Williamson, collector; (2) Little Creek on St Rte 204 approximately 1.5 mi SE of Seaboard-Coast Line RR, 1♀, 2j♂, 29 May 1969, E. T. Hall, Jr., HHH; 4♂II, 9♀, 2j♂, 7j♀, 22 Jun 1975, D. J. Peters, J. E. Pugh, HHH; (3) drainage ditch 1.5 mi NE of St Rte 204 on US Hwy 280, 1♀, 29 May 1969, ETH, HHH; (4) trib to Black Creek 5.8 mi SW of Blitchton, 1♂II, 7♀, 9 Jun 1949, R. D. Suttkus, R. H. Gibbs. *Bulloch County*: (5) Cone Branch 1.0 mi SSE of Ivanhoe, 6.2 mi SW of Guyton on St Rte 321, 1♂II, 8j♂, 1j♀, 11 Dec 1971, GKW. *Chatham County*: (6) Little Ogeechee River 5.7 mi SSE of Bloomingdale, 1♂I, 1♂II, 5♀, 2j♂, 3j♀, 18 Apr 1971, GKW. *Effingham County*: (7) vicinity of Pineora, 1♂II, 1♀, Mar 1967, J. J. Sullivan; (8) small creek off Pineora Rd approximately 12 mi SE of Guyton, 2♂I, 1♀, 5 Nov 1967, JJS; (9) Ebeneezer Creek 4 mi NW of Clyo, 1♀, 8j♂, 4j♀, Oct 1972, GKW; (10) under logs at Sisters Ferry, 1♂I, 2j♂, date ?, GKW; (11) Mill Creek at St Rte 17 about 2.5 mi N of Pineora, 4♂I, 6♂II, 4♀, 2j♂, 19 Apr 1977, C. E. Carter, C. W. Hart, Jr., JEP, HHH; (12) tribs to Little Ogeechee Creek 0.2 and 0.9 mi N of St Rte 30 on Rte 17, 1♂I, 3♂II, 8♀, 3j♂, 3j♀, 18 Apr 1977, CEC, CWH, JEP, HHH. *Jenkins County*: (13) trib to Buckhead Creek 5.5 mi N of Millen, 2♂I, 1j♂, 16 Sep 1955, R. D. Suttkus. *Screven County*: (14) type-locality, 8♂II, 6♀, 5j♂, 6j♀, 16 Mar 1952, E. C. Raney, R. Robbins; 1♂I, 6♂II, 16♀, 13j♂, 20j♀, 23 Dec 1956, G. B. Hobbs, HHH; 1♂I, 15♂II, 18♀, 17j♂, 15j♀, 18 Apr 1977, CEC, CWH, JEP, HHH; (15) trib to Ogeechee Creek at Oliver, 1♂II, Mar 1967, JJS; 1♂I, 5♂II, 6♀, 6j♂, 5j♀, 18 Apr 1977, CEC, CWH, JEP, HHH; (16) trib to Jackson Branch 6 mi SE of Buck Creek Church on Rte S9720, 1♂I, 2♂II, 9j♂, 6j♀, 18 Apr 1977, CEC, CWH, JEP, HHH.

VARIATIONS.—There are few variations worthy of note in this crayfish. The rostrum is consistent in possessing marginal spines or tubercles, but the degree of convergence of the margins and the length of the acumen are variable; the shorter acumens noted are probably often, if not always, results of injury. The areola is consistently broad and short, with room for as many as six or seven punctations across the narrowest part. The first pleopod of the first form male is remarkably uniform in structure; only the caudal process is noticeably different in length, but even that is always longer than it is in *P. (O.) enoplosternum*, the closest relative of *P. (O.) epicyrtus*. In the annulus ventralis of the females from Chatham County, the median elevated area is produced in a subacute apex, and the median part of the postannular sclerite is subconical. Variations of the caudal part of the sternal plate immediately cephalic to the annulus are depicted in Figure 157; the most ornate occurs in females from Screven County (Figure 157*a*), and the greatest diversity occurs in those from Bryan County, in some of which there is a median longitudinal carina (Figure 157*b, c*) or tubercle (Figure 157*d*).

SIZE.—The largest specimen examined is a female, having a carapace length of 50.8 (postorbital carapace length 37.4) mm. Corresponding lengths of the smallest and largest first form males are 26.2 (18.7) mm and 48.6 (35.5) mm, respectively. Neither ovigerous females nor ones carrying young have been observed by me.

LIFE HISTORY NOTES.—First form males have been collected in January, April, November, and December. Few or no collections have been made during other months. Females carrying eggs or young are not available. Thus virtually nothing is known of the life history of this crayfish.

ECOLOGICAL NOTES.—*Procambarus (O.) epicyrtus* is an inhabitant of lotic habitats, occurring in

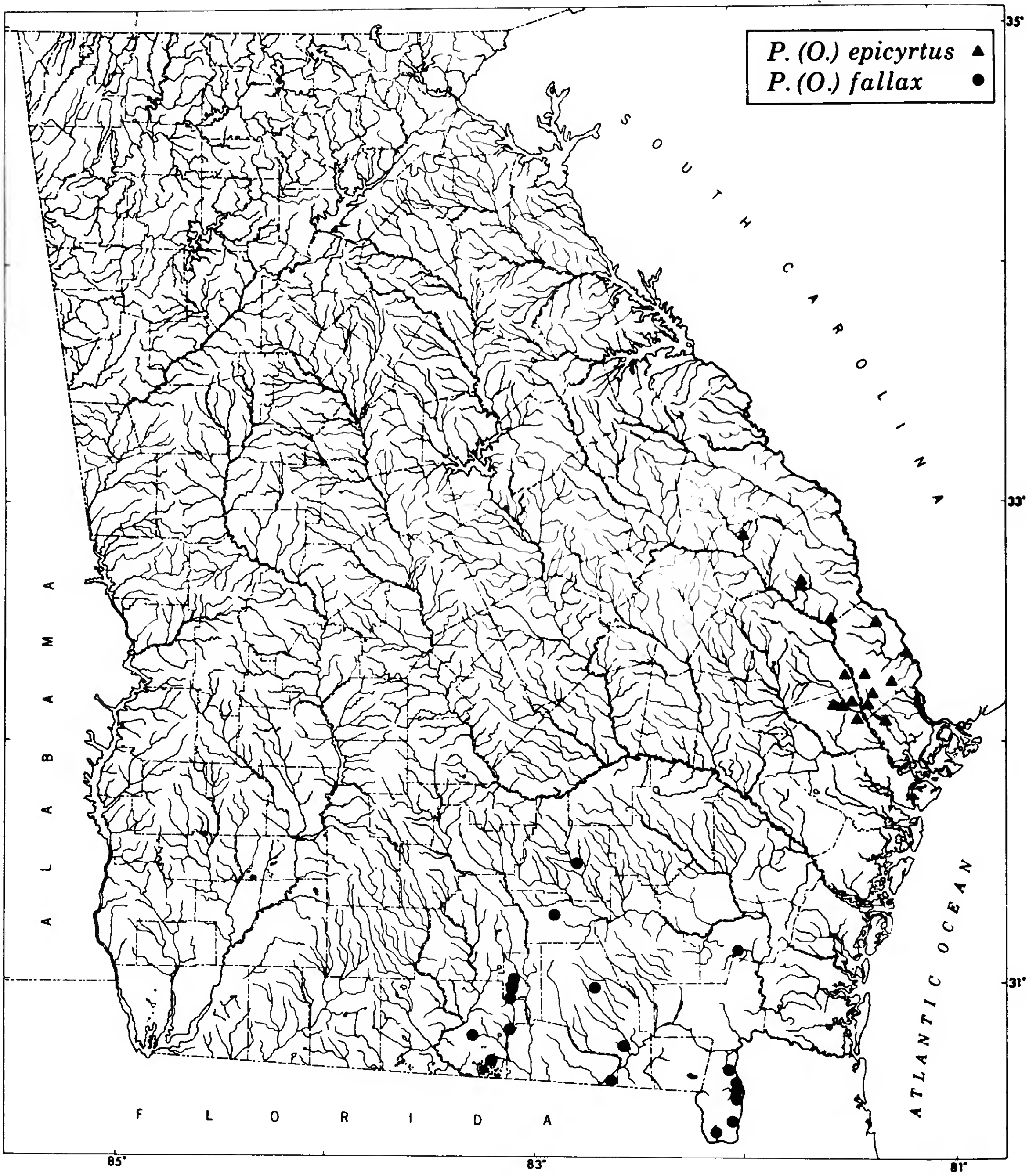


FIGURE 156.—Distribution of *Procambarus (O.) epicyrtus* and *P. (O.) fallax* in Georgia.

Seasonal Data

Sex/stage	*J*	*F*	*M*	*A*	*M*	*J*	*J*	*A*	*S*	*O*	*N*	*D*	*?*
♂I				9					2		2	1	1
♂II			10	31		5						7	
♀			7	41	2	16				1	1	16	
♂j			5	39	2	2			1	8		23	2
♀j			6	32		7				4		21	

streams of various sizes and in drainage ditches. In most of the habitats where it has been found, the water has been clear but coffee colored; the stream bottoms ranged from sand to clay, often overlain by deposits of organic matter. In some of the streams, there was a luxuriant growth of submergent and emergent macrophytes. Specimens have been taken from among the vegetation and in debris of various sorts, principally entangled limbs and other litter. Whether or not at least some members burrow is not known, but it seems probable that the females leave the open water prior to laying their eggs. Burrows in the stream banks are present in a number of the creeks in which this crayfish lives, but whether or not the tunnels were constructed or are used by *P. (O.) epicyrtus* remains to be determined.

Georgia Crayfish Associates.—Collected with *P. (O.) epicyrtus* were the following; numbers in parentheses represent in how many localities they were found together: *Procambarus (H.) advena* (1), *P. (H.) pygmaeus* (2), *P. (L.) barbatus* (3), *P. (O.) a. acutus* (1), *P. (O.) lunzi* (1), and *P. (S.) troglodytes* (2).

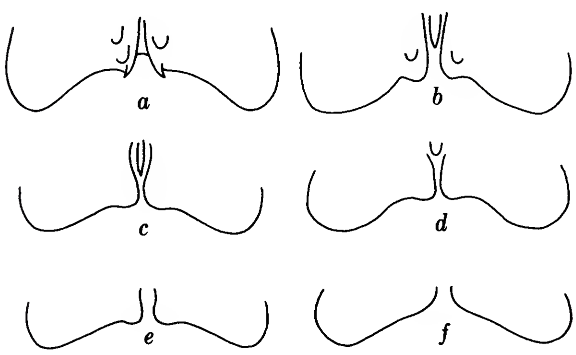


Figure 157.—*Procambarus (O.) epicyrtus*, variations in sternum immediately anterior to annulus ventralis: *a*, tributary to Ogeechee Creek at Oliver, Screven Co; *b–d, f*, Little Creek at St Rte 204, 6.9 mi E of US Hwy 280, Bryan Co; *e*, tributary to Little Ogeechee Creek 0.9 mi N of St Rte 30 on Rte 17, Effingham Co.

Procambarus (Ortmannicus) litosternum Hobbs

Figures 13*d*, 137*e*, 138*g*, 158–160, 250

Procambarus litosternum Hobbs, 1947a:4, 8–13, figs. 3, 4, 9, 11, 13, [not 15 as indicated], 16, 19, 21, 26, 29, 30; 1947b:29; 1958a:72, 78, 79, 83, 86, 90, fig. 12; 1958b:160; 1959:889; 1962:284, fig. 27; 1968b:K-10, fig. 25e.—Anonymous, 1972e:77.—Hart and Hart, 1974:21, 88.—Wharton, 1978: 46, 220.

Procambarus (Ortmannicus) litosternum.—Hobbs, 1972a:9; 1972b:64, 151, 154, figs. 29b, 50b; 1974b:57, fig. 221.

These references are believed to constitute a complete bibliography of the species, and, inasmuch as this crayfish is endemic to the state, all refer to Georgia.

Summary of Literature.—Accompanying the description of this crayfish by Hobbs (1947a) were notes on the type-locality, a statement of its affinities, and several locality records in the Canoochee and Ogeechee watersheds of Bulloch, Emanuel, and Jenkins counties. A key to the members of the *pictus* Subgroup was appended. In describing another member of the Subgroup, *Procambarus lepidodactylus* Hobbs (1947b), *P. (O.) litosternum* was included in an expanded key, and, in his analysis of the evolution of the *pictus* Group, Hobbs (1958a) discussed its range, certain morphological characters, and its relationships. In his key to the American crayfishes (1959), he noted that the range of the species encompassed the "Canoochee, Ogeechee, and Newport rivers in Ga." No additional information appeared in the literature until Anonymous (1972e) questionably identified two specimens from Pendleton Creek on State Route 292, Toombs County, as members of this species. Hobbs (1972a, b), in recognizing several subgenera of the genus *Procambarus*, assigned this crayfish to the subgenus *Ortmannicus*. Hart and Hart (1974) reported the infestation of members of this species in Evans County by two entocytherid ostracods, *Ankylocythere ancyla* and *Entocythere elliptica*.

DIAGNOSIS.—Rostrum with marginal spines or tubercles, lacking median carina. Carapace with 1 pair of cervical spines. Areola 3.2 to 4.8 (average 3.8) times as long as broad and constituting 26.3 to 30.5 (average 28.5) percent of entire length of carapace (36.4 to 41.6, average 38.6 percent of postorbital carapace length). Antennal peduncle with prominent spine, occasionally reduced to acute tubercle on ischium. Lateral half of ventral surface of ischium of third maxilliped lacking conspicuous mat of long plumose setae. Basis of cheliped without mesial spine. Mesial surface of palm of chela of male with mesialmost row of tubercles consistng of 7 to 12 (usually 9). Male with simple hooks on ischia of third and fourth pereiopods, in first form male that on third overreaching basioischial articulation, that on fourth not reaching articulation and opposed by prominent protuberance on cephalodistal end of corresponding basis. First pleopods asymmetrical and reaching coxae of third pereiopods, distal fourth of shaft bearing distinct cephalic hump subjacent to base of cephalic process; subapical setae flanking mesial, cephalic, and lateral bases of cephalic process and central projection, largely obscuring both, as well as caudal and adventitious processes; mesial process subspiculiform and directed caudodistally; cephalic process, with broad base and acute apex, hooding at least basal part of central projection and extending distally as far as or farther than latter; central projection strongly sclerotized, subtriangular, and extending caudodistally subparallel to cephalic process; caudal element consisting of (1) elongate, corneous caudal process projecting caudodistally from caudomesial base of central projection, flanked mesially by (2) strongly sclerotized tumescence bearing arched cristiform adventitious process, and (3) subtruncate caudal knob extending across caudodistal end of shaft, delimited caudolaterally by deep, almost straight, groove. Female with sternum cephalic to annulus lacking tubercles and caudally projecting prominences; annulus ventralis subcampanulate in outline, with ventral surface almost plane or with broad, subtriangular, median excavation; sinus forming sigmoid curve and reaching neither cephalic nor caudal margins of annulus; postannular sclerite at least three-fourths as wide as annulus and strongly arched ventrally; first pleopod present.

COLOR NOTES (Figure 137*e*).—Carapace mauve gray, with cream and brown to black splotches. Cephalic section with median longitudinal pinkish tan stripe poorly delimited, interrupted by brown splotches; no conspicuous markings present except pair of black spots in posterior gastric region and pale pinkish oblique mark extending from cephalic margin of antennal region posteroventrally across posterior mandibular area. Thoracic section of carapace with median longitudinal strip even less well defined than in cephalic section; saddle reduced to 2 pairs of black spots dorsolaterally marking cephalic and caudal parts of horns; caudal ridge and flange dark brown, latter fading ventrally to match pinkish tan on ventral part of branchiostegites, which also bearing few cream spots. Terga of abdomen largely pinkish tan, with paired, reddish charcoal to black markings anteriorly, these connected by narrow transverse line, and each tergum with caudal margin black; median area of terga slightly darker than lateral parts, suggesting broad, median, longitudinal dark stripe on abdomen; pleura pinkish brown, with centrally located pinkish cream spot. Telson and uropods marked like those of *P. (O.) epicyrtus* although dark areas not so intense. Similarly, antennules, antenna, antennal scale, chelipeds, and other pereiopods markedly resembling those of that species. Fingers of chelae with yellowish tips. Ventral surface of body pinkish cream.

TYPES.—Holotype, allotype, and "morphotype," USNM 82261 (♂I, ♀, ♂II); paratypes, USNM.

TYPE-LOCALITY.—Stream 5 miles northeast of Swainsboro (North Prong of the Canoochee River) on U.S. Highway 25, Emanuel County, Georgia.

RANGE.—This crayfish, endemic to Georgia, occurs in the Ogeechee, Canoochee, and Newport basins from Burke, Emanuel, and Jenkins counties downstream, probably almost to the lower

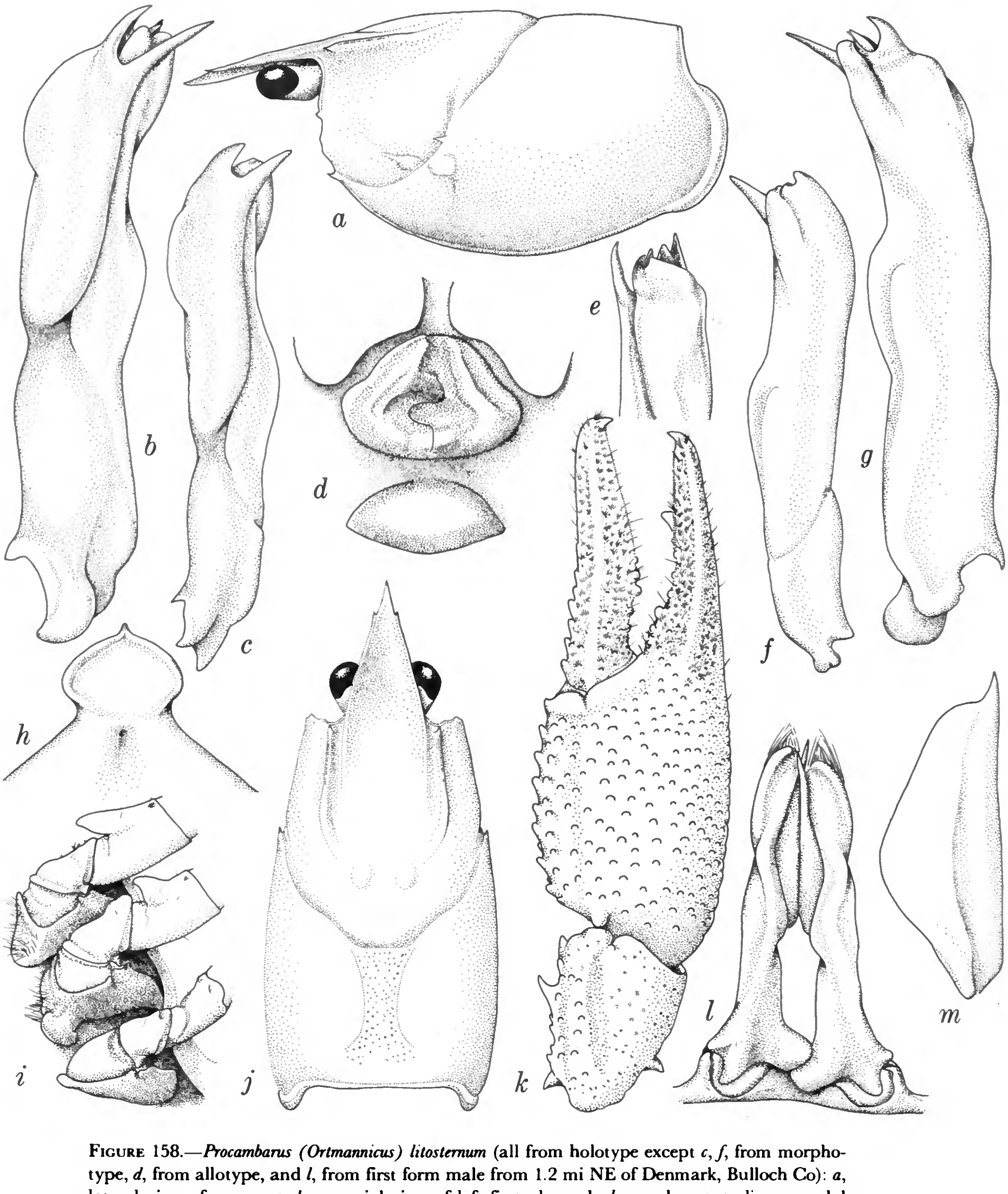


FIGURE 158.—*Procambarus (Ortmannicus) litosternum* (all from holotype except *c*, *f*, from morphotype, *d*, from allotype, and *l*, from first form male from 1.2 mi NE of Denmark, Bulloch Co): *a*, lateral view of carapace; *b*, *c*, mesial view of left first pleopod; *d*, annulus ventralis; *e*, caudal view of distal part of first pleopod; *f*, *g*, lateral view of first pleopod; *h*, epistome; *i*, proximal podomeres of third, fourth, and fifth pereiopods; *j*, dorsal view of carapace; *k*, dorsal view of distal podomeres of cheliped; *l*, caudal view of first pleopods; *m*, antennal scale.

parts of the rivers influenced by the tides. This area lies wholly within the Vidalia Upland and Barrier Island Sequence districts of the Coastal Plain Province.

GEORGIA SPECIMENS EXAMINED.—I have examined a total of 247 specimens from the following localities. *Bryan County*: (1) Savage Creek 2 mi S of Pembroke on St Rte 119, 1j♂, 2j♀, 27 Dec 1971, G. K. Williamson, collector; 1♂I, 9♂II, 2♀, 22 Jun 1975, D. J. Peters, J. E. Pugh, HHH; 4♂I, 1♂II, 1♀, 20 Apr 1977, C. E. Carter, JEP, HHH; (2) roadside ditch and conduit at south city limit of Pembroke on St Rte 119, 1♀, 22 Jun 1975, DJP, JEP, HHH. *Bulloch County*: (3) Lotts Creek 5.8 mi S of Statesboro on US Hwy 25 (Hobbs, 1947a: 12), 1♂II, 27 Mar 1939, H. H. Wallace, HHH; 1♂II, 1♀, 1j♂, 28 Mar 1950, W. J. Houck; 1j♂, 1j♀, 25 Jul 1950, WJH; (4) Lotts Creek 2.7 mi E of Emanuel Co line on US Hwy 80, 1j♂, 5 Oct 1977, T. A. English, Jr., HHH; (5) Wyatts Creek 14.2 mi S of Millen on US Hwy 25 (Hobbs, 1947a:12), 2♂I, 1♂II, 1♀, 2j♂, 2j♀, 17 Apr 1944, HHH; (6) trib to Lotts Creek 13 mi N of Claxton on US Hwy 25 (Hobbs, 1947a:12), 2j♂, 5j♀, 17 Apr 1944, HHH; (7) 1.2 mi NE of Denmark in spring-fed roadside ditch, 2♂I, 7♂II, 8♀, 9j♂, 25j♀, 14 Dec 1971, GKW; 1♂I, 5♂II, 6♀, 2j♂, 8j♀, 19 Dec 1971, GKW; (8) Black Creek 3 mi N of Denmark, 4♂II, 8♀, 2j♂, 2j♀, 22 Apr 1971, GKW; (9) Pole Branch 0.3 mi E of US Hwy 80 on St Rte 119, 1j♀, 19 Apr 1977, CEC, C. W. Hart, Jr., JEP, HHH; (10) roadside ditch 1.9 mi E of US Hwy 80 on St Rte 119, 1♀, 19 Apr 1977, CEC, CWH, JEP, HHH. *Burke County*: (11) Mill Creek 10.4 mi N of Millen on US Hwy 25 (Hobbs, 1947a:12, erroneously reported as Jenkins County), 2♂I, 9♂II, 9♀, 1j♂, 8j♀, 27 Mar 1939, HHW, HHH. *Candler County*: (12) Canoochee River 4 mi W of Metter on St Rte 46, 1♂II, 4♀, 2j♂, 1j♀, 24 Mar 1950, D. C. Scott; 2j♀, 25 Mar 1950, E. C. Raney; (13) Fifteen Mile Creek at St Rte 46, 1♀, 25 Mar 1950, ECR; 4♂I, 4♂II, 1♀, 3j♀, 16 Aug 1957, R. D. Suttkus; (14) Sams Creek at St Rte 46 W of Metter, 1♂I, 1j♂, 30 May 1969, E. T. Hall, Jr., HHH. *Emanuel County*: (15) type-locality, 2♂I, 3♂II, 6♀, 1j♂, 13 Apr 1944, HHH; (16) Fifteen Mile Creek 3.1 mi E of Twin City on US Hwy 80, 1♀, 5 Oct 1977, TAE, HHH. *Evans County*: (17) Thick Creek 5.5 mi N of Claxton on US Hwy 301 (Hart and Hart, 1974:21), 1♂I, 2♂II, 3♀, 7j♂, 6j♀, 23 Dec 1956, HHH; (18) Canoochee River just off US Hwy 301, 1j♂, 11 Aug 1976, K. W. Martin, M. W. Walker. *Jenkins County*: (19) Sculls Creek 9.6 mi S of Millen at US Hwy 25 (Hobbs, 1947a:12), 2♂I, 1♀, 2j♂, 3j♀, 27 Mar 1939, HHW, HHH; (20) Bay Gull Branch 11.6 mi S of Millen on US Hwy 25 (Hobbs, 1947a:12), 3♂II, 1♀, 17 Apr 1947, H. W. Fowler. *Liberty County*: (22) trib of Newport River at St Rte 38, 2♂I, 1♂II, 15 Jun 1948, RDS. *Screven County*: (23) Ogeechee River at Bulloch Co line at St Rte 24, 1♀, 19 Apr 1977, CEC, CWH, JEP, HHH. *Tattnall County*: (24) Billy Fork Creek 3 mi W of Evans Co line on US Hwy 280, 2♂I, 1♂II, 2♀, 4j♀, 22 Jun 1975, DJP, JEP, HHH.

VARIATIONS—As pointed out by Hobbs (1947a: 13), the rostrum is variable in length, reaching from the level of the end of the antennular peduncle to "scarcely reaching distal end of penultimate segment . . . . " Whereas the rostral margins may be gently or strongly convergent, the marginal spines are always present, although ranging from well-developed to vestigial acute tubercles. Similarly, the postorbital and cervical spines may be strong or weak. The first form males collected in Tattnall County differ from others observed in possessing a conspicuously shorter cephalic process on the first pleopod (Figure 160*d,h*), one that extends no farther distally than the level of the tip of the central projection. In specimens from elsewhere, the cephalic process distinctly overreaches the central projection. The apparent differences in the cephalic hump on the first pleopod in Figure 160 reflect, for the most part, the angle at which the appendages were positioned for illustration (to show both the central projection and caudal process); the hump is much better depicted in Figure 158*b,g*. The ventral face of the annulus ventralis exhibits a striking degree of variation, ranging from being virtually flat to slightly convex, or, more typically, traversed by a median longitudinal, caudally expanding depression (dorsally), and in at least one specimen bearing a well-defined posteromedian subconical protuberance. In most of the young females, the surface is plane, but similarly it is also almost flat in a number of the larger females—for example, in several from Jenkins and Tattnall counties. In large females from Bryan County the concavity is equally as prominent as it is in specimens from the type-locality (near the northern extremity of the range). An insufficient number of specimens is available to determine whether any of the variations noted above are regionally restricted.

SIZE.—The largest specimen that I have examined is a first form male, having a carapace length of 41.0 (postorbital carapace length 30.0) mm. Corresponding lengths of the smallest first form male and largest female are 28.1 (21.0) mm and 37.4 (28.9) mm, respectively.

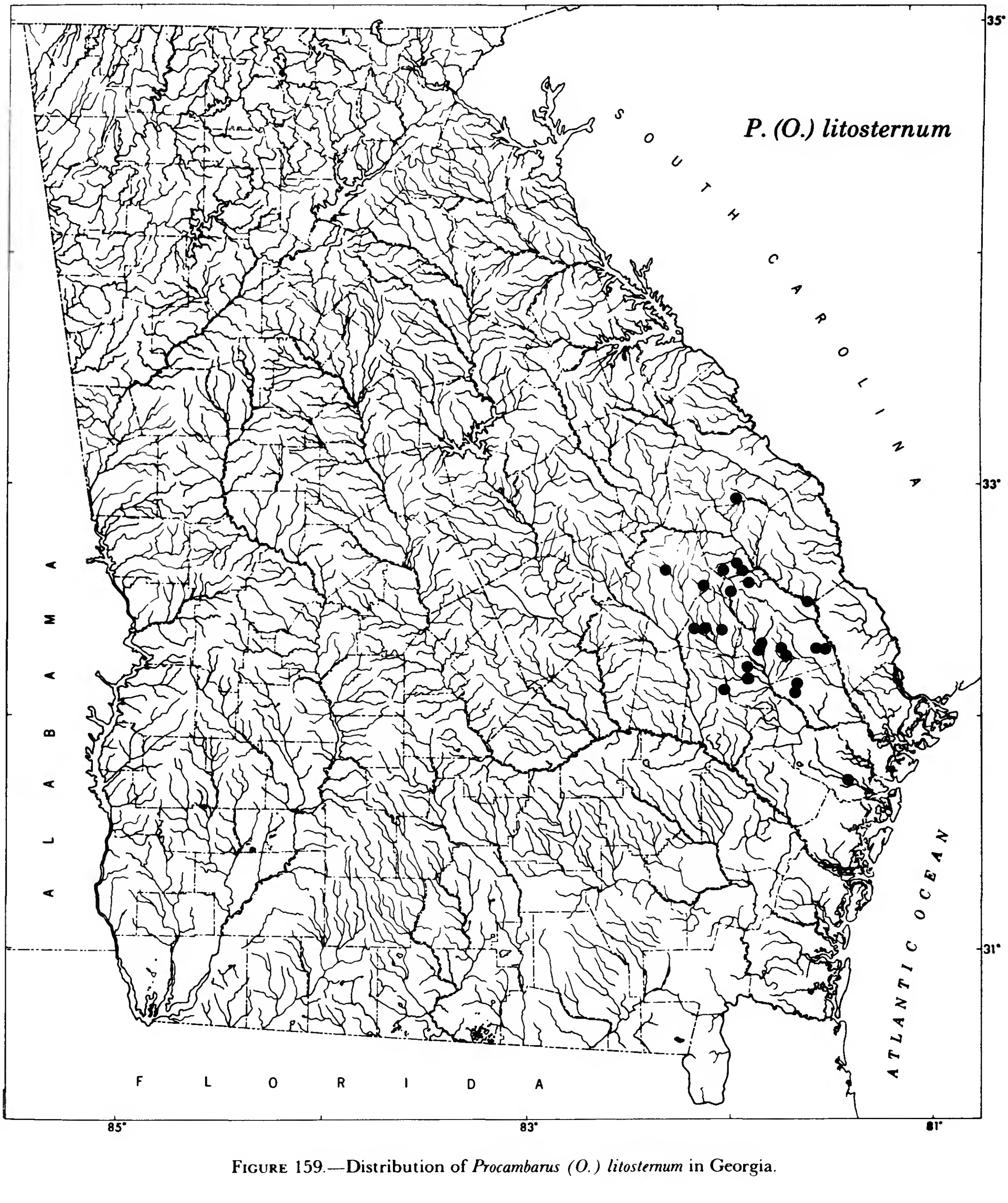


FIGURE 159.—Distribution of *Procambarus (O.) litosternum* in Georgia.

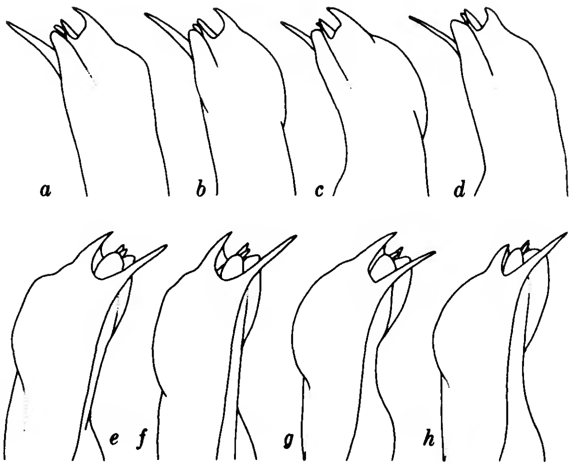


FIGURE 160.—*Procambarus (O.) litosternum*, variations in first pleopod of first form male (*a–d*, lateral view; *e–h*, mesial view): *a, e*, 2.0 mi S of Pembroke on St Rte 119, Bryan Co; *b, f*, tributary of North Newport River on St Rte 38, Liberty Co; *c, g*, 1.2 mi NE of Denmark, Bullock Co; *d, h*, Billy Fork Creek 3 mi w of Evans Co line on US Hwy 280, Tattnall Co.

LIFE HISTORY NOTES.—First form males have been found from March to June, August, and December. Neither ovigerous females nor ones carrying young have been collected. Thus virtually nothing is known about the life history of this crayfish. Few, if any, females have been collected during any months except March, April, and December; consequently no suggestion as to the probable egg-laying season can be made, and nothing is known of growth rates or longevity.

Seasonal Data

Sex/stage	*J*	*F*	*M*	*A*	*M*	*J*	*J*	*A*	*S*	*O*	*N*	*D*
♂I			2	8	3	5		4				4
♂II			12	12		11		4				14
♀			15	19	1	5		1		1		17
♂j			4	7	3		1	1		1		19
♀j			11	10	3	4	1	3				41

ECOLOGICAL NOTES.—Like its closest relatives, *P. (O.) enoplosternum*, *P. (O.) epicyrtus*, and *P. (O.) pubescens*, this crayfish is an inhabitant of lotic habitats, having been found most frequently in sluggish to moderately flowing, sand-bottomed creeks, which are usually coffee colored and often choked with vegetation. It was found in a spring-fed roadside ditch in Bulloch County, and in Savage Creek (Figure 7*e*), Bryan County, the stand of *Pontederia* was so dense that using a dip net to collect specimens was exceedingly difficult, and only under the highway bridge was it possible to use a seine. In June 1977, following a long dry period, the creek had ceased to flow, and fish were dying in the few remaining pools. Crayfish were still present in some of them, and freshly constructed chimneys marking burrows were abundant in the stream bed. Nowhere have I observed freshwater sponges in such abundance as at this locality. Sharing the pools there with *P. (O.) litosternum* were *P. (H.) pygmaeus* and *P. (S.) troglodytes*. Burrowing in the adjacent dry ditch that is at least occasionally flooded when the water in the creek reaches higher levels were *P. (L.) barbatus* and *P. (H.) advena*. Burrows of the latter were positioned where it is probable that they are seldom inundated.

GEORGIA CRAYFISH ASSOCIATES.—Collected with *P. (O.) litosternum* were the following (number of times found together in parentheses): *Faxonella clypeata* (2), *Procambarus (H.) advena* (2), *P. (H.) pygmaeus* (3), *P. (H.) truculentus* (1), *P. (L.) barbatus* (6), *P. (O.) enoplosternum* (2), *P. (O.) lunzi* (1), and *P. (S.) troglodytes* (6).

Procambarus (Ortmannicus) pubescens (Faxon)

FIGURES 13*b*, 137*f*, 138*j*, 161–163, 253

Cambarus pubescens Faxon, 1884:109–110, 137; 1885a:17, 18, 31–33, 158, 167, 173, pl. I: fig. 3, pl. VIII: fig. 1a, 1a′; 1885b:358; 1898:646; 1914:412–413—Underwood, 1886: 372.—Hay, 1899b:959, 963.—Ortmann, 1902:277.—Harris, 1903a:58, 121, 138, 143, 152.—Hobbs, 1940a:389, 398, 423; 1940b:7; 1942c:56, figs. 5, 6; 1962:274; 1972a:2.

Cambarus (Cambarus) pubescens.—Ortmann, 1905a:101, 128.

Cambarus (Ortmannicus) pubescens.—Fowler, 1912:341 [by implication].

Procambarus pubescens.—Hobbs, 1942a:350; 1942b:122, 129, 130, 133, 142; 1947a:1–5, 8, 12, 14, figs. 1, 6–8, [not 14] 15, 17, 22, 27, 28, 31; 1947b:29; 1952a:212; 1958a:72, 76, 79, 84–86, 90, fig. 6; 1958b:160, 163, 164; 1959:889; 1962: 273, 284, fig. 29; 1966b:70; 1968b:K-10, fig. 25d.—Hoff, 1944:349, 356.—Anonymous, 1972c:27, 28, 30, 31, 33; 1975a:156.—Hart and Hart, 1974:21, 32, 88, 129.—Duke et al., 1978:40.—Wharton, 1978:220.

Procambarus pubscens.—Hobbs III, 1969:41 [erroneous spelling].

Procambarus (Ortmannicus) pubescens.—Hobbs, 1972a:9; 1972b: 64, 151, 154, 155, fig. 50c; 1974b:60, fig. 223.—Hobbs III, Thorp, and Anderson, 1976:3, 12, 37–39, figs. 16, 24.

Procambarus (Ortmanicus) pubescens.—Hobbs III, Thorp, and Anderson, 1976:59 [erroneous spelling].

These citations are believed to constitute a complete bibliography of the species, and all except Hobbs III, Thorp, and Anderson (1976) deal primarily with the occurrence of the species in Georgia or with specimens from the state. Only one record of the presence of *P. (O.) pubescens* in South Carolina (Hobbs, 1972b:151; no locality cited) was known prior to the work of Hobbs III, Thorp, and Anderson.

SUMMARY OF LITERATURE.—Faxon (1884) described this crayfish on the basis of a second form male and a female collected in McBean Creek (south of Augusta), which serves as a boundary between Burke and Richmond counties, Georgia, and two additional females were reported from the latter county. In 1898, he recorded its occurrence in Buckhead Creek at Millen, which is now in Jenkins County (Hobbs, 1947a:4). Publications between 1898 and 1940 introduced no new information, although two new combinations were proposed for the name of the animal (Ortmann, 1905a, and Fowler, 1912). Hobbs (1940a) pointed out its affinities with *P. (O.) pictus* and several of the Floridian troglobitic species, and, in a second publication (1940b), its relationship to *P. (O.) lunzi.* Hoff (1944) cited this crayfish as a host of two new entocytherids described by him from Georgia, but no specific localities were mentioned. Although Hoff's specimens were collected by me, I am unable to determine from which localities they came. In 1947(a), Hobbs provided a diagnosis of the species, described the previously unknown first form male, and listed several localities in Bryan, Burke, McDuffie, Screven, and Wilkes counties. His discussion of the evolution of the *pictus* Group of the genus *Procambarus* (1958a) included morphological comparisons of *P. (O.) pubescens* with its relatives, a spot map delineating its range in the Oconee, Ogeechee, and Savannah drainage systems, and a discussion of its affinities. The names of the four undescribed species treated in that study are as follows: *P.* sp. A and *P.* sp. C are *Procambarus (O.) chacei* (=*P. (O.) enoplosternum*) and *P. (O.) epicyrtus*, respectively (Hobbs, 1958c); and *P.* sp. B and *P.* sp. D are *P. (O.) hirsutus* and *P. (O.) ancylus*, respectively (Hobbs, 1958b). Keys, discussions of relationships, and a few illustrations were included in Hobbs (1959, 1962). No specific localities other than those of Faxon (1884, 1898) and Hobbs (1947a) were cited in the literature until Anonymous (1972c) reported the occurrence of *P. (O.) pubescens* at five stations within the Brier Creek basin in Burke, Jefferson, and McDuffie counties. Three additional ones were added by Hart and Hart (1974) in Burke County and one in Laurens. The most complete accounts of the species are those of Hobbs (1947a) and Hobbs III, Thorp, and Anderson (1976). The latter noted its presence in several localities in the Savannah Basin sections of Aiken and Barnwell counties, South Carolina, provided a diagnosis of the species, presented color and ecological notes, and summarized the life history data presented earlier by Hobbs (1947a). Duke et al. (1978) presented a brief account of the effects of cadmium on adenylate energy charge in this crayfish. The publications not mentioned in this brief discussion contain no original data.

DIAGNOSIS.—Rostrum with marginal spines, lacking median carina; acumen often obscured by pubescence on apical part of rostrum. Carapace with 1 pair of cervical spines. Areola 2.1 to 3.7 (average 2.9) times as long as broad and constituting 25.1 to 30.4 (average 27.5) percent of entire length of carapace (36.2 to 42.4, average 38.6, percent of postorbital carapace length). Antennal peduncle with prominent spine on ischium. Lateral half of ventral surface of ischium of third maxilliped lacking conspicuous mat of long plumose setae. Basis of cheliped without mesial spine. Mesial surface of palm of chela of male with mesialmost row of tubercles consisting

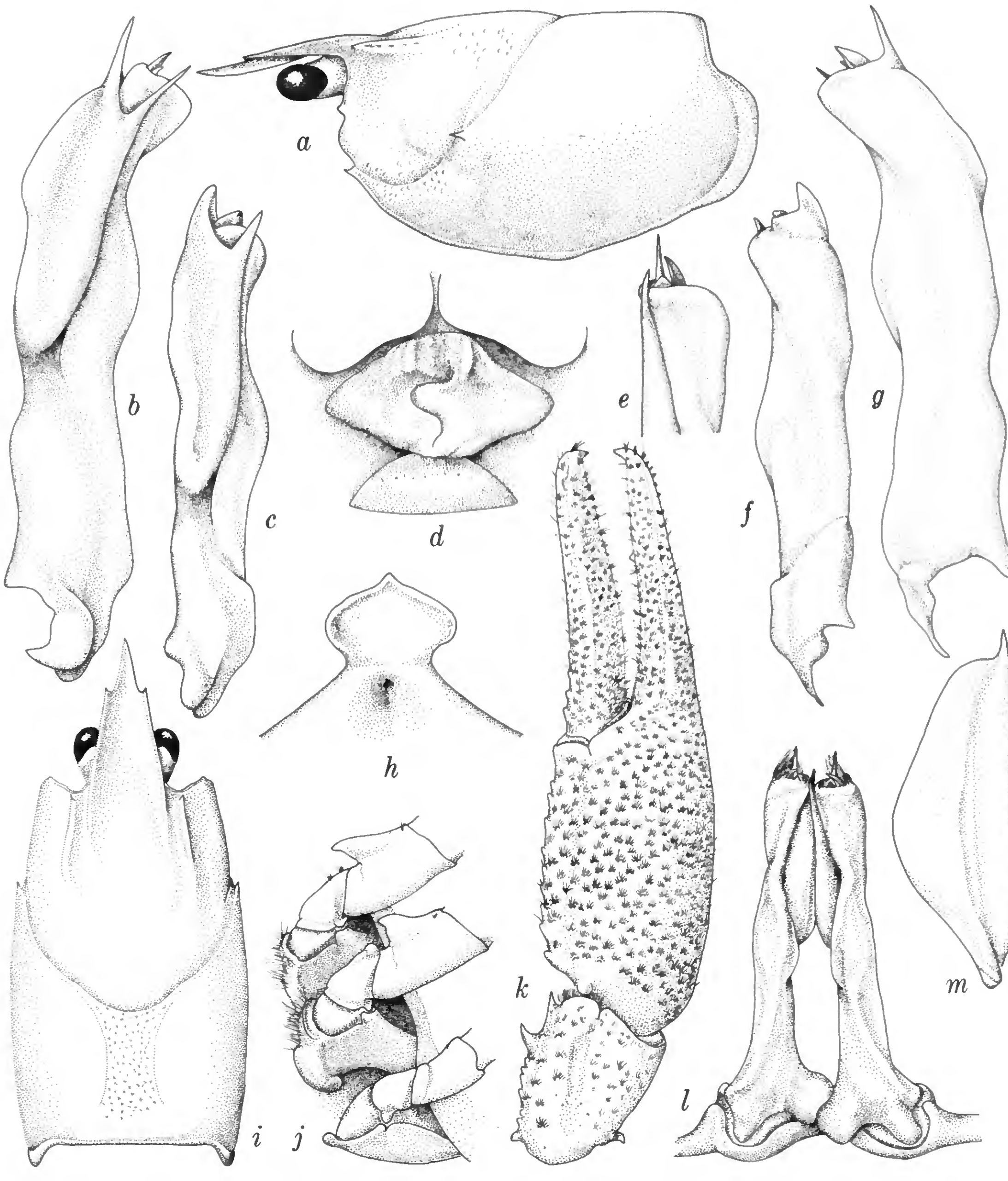


FIGURE 161.—*Procambarus (Ortmannicus) pubescens* (all from topotypic male, form I, except *c*, *f*, from topotypic second form male, and *d*, from topotypic female): *a*, lateral view of carapace; *b*, *c*, mesial view of first pleopod; *d*, annulus ventralis; *e*, caudal view of distal part of left first pleopod; *f*, *g*, mesial view of first pleopod; *h*, epistome; *i*, dorsal view of carapace; *j*, proximal podomeres of third, fourth, and fifth pereiopods; *k*, dorsal view of distal podomeres of cheliped; *l*, caudal view of first pleopods; *m*, antennal scale.

of 7 to 11 (usually 8 or 9). Male with simple hooks on ischia of third and fourth pereiopods, in first form male that on third overreaching basioischial articulation and that on fourth not reaching articulation but opposed by prominent protuberance on cephalodistal end of corresponding basis. First pleopods asymmetrical and reaching coxae of third pereiopods, distal fourth of shaft rather strongly inclined caudodistally and bearing prominent hump, distal extremity of latter situated at base of cephalic process; subapical setae flanking mesial, cephalic, and lateral sides of distal part of appendage and largely obscuring cephalic process and central projection; mesial process subspiculiform and directed caudodistally; cephalic process, usually far overreaching other terminal elements and quite far removed from central projection, slender, straight, and tapering to acute tip directed subdistally; corneous central projection rather short, compressed, subtriangular, and directed caudodistally and somewhat mesially; caudal element consisting of (1) prominent, but not strongly inflated, caudal knob, forming transverse rounded ridge across caudodistal end of shaft of appendage and infrequently sharply delimited caudolaterally, (2) caudal process consisting of small (occasionally vestigial or absent), corneous, obliquely set, triangular tooth situation at caudomesial base of central projection, and (3) low, corneous, ridgelike adventitious process (sometimes imperceptibly continuous with mesial part of caudal knob) extending along mesial side of caudal process. Female with sternum cephalic to annulus marked with median cleft often flanked by short, broadly rounded prominences jutting toward annulus and occasionally slightly overreaching its cephalic border; annulus ventralis almost always subovate, with greatest width in transverse axis, ventral surface usually moderately strongly sculptured with broad submedian longitudinal trough anteriorly flanked by low subparallel ridges, and with elevated posteromedian area; sigmoid sinus originating in trough and ending on posteromedian elevation anterior to caudal margin; postannular sclerite at least three-fourths as wide as annulus and arched ventrally; first pleopod present.

Color Notes (Figure 137*f*).—As in many of the Georgia crayfishes, two color phases exist: one consisting predominately of shades of blue, gray, and black and the other of brown, tan, orange, and black. The latter is described here. Carapace basically reticulate chocolate brown over orange tan, with conspicuous charcoal gray to black markings. Cephalic section of carapace with median longitudinal orange tan stripe extending from acumen to cervical groove flanked caudally by pair of almost black spots on mesial parts of mandibular adductor regions; antennal and mandibular, and sometimes hepatic, regions with small cream spot. Thoracic section with median longitudinal pale stripe less well defined than in cephalic section, but reaching caudal ridge, thus interrupting transverse bar of broad black saddle; horns of saddle deeply incised laterally near midlength; narrow light area subtending transverse bar anteriorly and continuing along dorsal margins of horns to level of incision; remainder of dorsal area with reticulate pattern matching that of cephalic section; caudal ridge and flange dark grayish blue and branchiostegites ventral to horn dark gray to brown, with cream to orange cream spots. Abdominal terga reddish brown on anterior two-thirds and grayish tan posteriorly, but first through fifth margined in black; lateral area of second through sixth with dark reddish brown spot; pleura of each segment with pink to red spot, flanked anteriorly and posteriorly by reddish brown covering most of each pleuron. Telson with reddish brown arc basally and broad, paired almost black areas on lateral fourth of cephalic section; caudal section and most of uropods brownish red; mesial ramus of uropod with blackish area proximally, fading along lateral margin; mesial blackish part set off sharply from reddish distal area by short translucent line; lateral ramus of uropod with blackish suffusion proximomesially and black edge along suture dividing proximal and distal sections. Antennular and antennal peduncles orange tan, mottled in charcoal; flagella olive tan; antennal scale also orange tan, with mottled charcoal lateral margin and charcoal suffusion along mesial side of thickened lateral part. Cheliped orange tan with black tubercles; major tubercles on merus and carpus with white to cream tips; fingertips only slightly paler than dark orange tan fingers. Remaining pereiopods pale olive to cream proximally and olive distal to ischium. Ventral surface of body pinkish cream.

TYPES.—Syntypes, USNM 3181 (♂II, ♀).

TYPE-LOCALITY.—McBean Creek, south of Augusta, Burke-Richmond county line, Georgia.

RANGE.—The Oconee, Ohoopee, Ogeechee, and Savannah river basins in Georgia and the latter basin in South Carolina. In the Savannah and Ogeechee watersheds, it invades the lower Piedmont Province; elsewhere it is confined to the Coastal Plain Province, frequenting streams in the Fall Line Hills and Vidalia Upland districts. An outlying population occurs in Black Creek, a tributary of the Ogeechee River in Bryan County (Barrier Island Sequence District).

GEORGIA SPECIMENS EXAMINED.—I have examined 601 specimens from the following counties (the numbers of localities in each are noted in parentheses): Baldwin (1), Bryan (1), Burke (22), Emanuel (1), Glascock (5), Gwinnett (?, see "Variations"), Hancock (1), Jefferson (4), Jenkins (3), Laurens (1), McDuffie (3), Oglethorpe (1), Richmond (6), Screven (2), Taliaferro (4), Warren (3), Washington (4), Wilkes (4), and Wilkinson (1). Data follow for those counties in which fewer than five localities are known. *Baldwin County:* (1) 0.3 mi N of Wilkinson Co line, 4♀, 22 Mar 1961, P. C. Holt, V. F. Holt, collectors. *Bryan County:* (2) Black Creek 3.7 mi SW of Blitchton on US Hwy 280 (Hobbs, 1947b:4), 1♂I, 4♂II, 8♀, 2j♀, 18 Dec 1939, G. B. Hobbs, HHH. *Emanuel County:* (3) stream from McKinney's Pond 7 mi SSW of Midville, 4♀, 4 Sep 1954, J. W. Crenshaw, W. Auffenberg; 2♀, 1954, Humphries. *Hancock County:* (4) Beaver Dam Creek 1.7 mi S of Powelton on St Rte 22, 1♂II, 1♀, 2j♂, 4 Oct 1977, T. A. English, Jr., HHH. *Jefferson County:* (5) Brushy Creek at St Rte 80, about 2 mi SE of Stellaville, 2♀, 2j♂, 5j♀, 29 Sep 1970, B. A. Caldwell, M. W. Walker; 2♀, 2j♂, 6j♀, 2 Oct 1972, GBH, HHH; (6) Brush Creek 0.4 mi S of Wrens on US Hwy 1, 2♀, 18 Sep 1947, E. A. Lachner, P. S. Handwerk; (7) Nails Creek at US Hwy 319, 3.7 mi N of Johnson Co line, 2♂I, 1♂II, 3♀, 1j♀, 16 Jun 1972, D. J. Peters, J. E. Pugh, HHH; (8) Salter Branch 1.4 mi W of Bartow on St Rte 242, 1♂II, 1♀, 16 Jun 1972, DJP, JEP, HHH. *Jenkins County:* (9) Buckhead Creek at Millen, 1♂II, 3♀, date ?, US Fish Commission; (10) Magnolia Springs below dam, 1♂I, 14 Feb 1948, Shaum and Grant; 15♂II, 14♀, 6j♂, 22j♀, 1 Feb 1952, D. C. Scott; (11) Chew Mill Creek 3.2 mi E of Burke Co Line on St Rte 17, 1j♂, 2j♀, 2 Oct 1972, GBH, HHH. *Laurens County:* (12) Rocky Creek 1.9 mi N of Bleckley Co line on St Rte 26 (Hart and Hart, 1974:21, 129), 2♂I, 4♂II, 1♀, 1♀ with young, 18 Aug 1952, GBH, HHH; 4♂I, 2♂II, 4♀, 1j♂, 7j♀, 21 Apr 1966, E. T. Hall, Jr., HHH; 1♂II, 6♀, 2j♂, 1j♀, 20 Jun 1975, DJP, JEP, HHH. *McDuffie County:* (13) trib to Sweetwater Creek 3.5 mi SE of Thomson on US Hwy 78 (Hobbs, 1947b:4), 2♂II, 1♀, 21 Jun 1940, GBH, HHH; (14) Little River, 1♂I, 2♀, 22 Jul 1948, D. C. Scott; (15) Brier Creek at St Rte 17, 2♂II, 2♀, 2j♂, 9j♀, 29 Sep 1970, BAC, MWW. *Oglethorpe County:* (16) trib to Long Creek 2.6 mi SE of Lexington, 1♀, 3j♂, 1j♀, 10 Oct 1953, R. D. Suttkus. *Screven County:* (17) Beaver Dam Creek 5 (not 3 as cited by Hobbs, 1947b:4) mi N of Sylvania on US Hwy 301, 1♂I, 6♂II, 4♀, 7j♀, 7 Sep 1938, GBH, HHH; 1♀, 1j♀, 14 Sep 1951, DCS; 4♂II, 6♀, 1j♂, 2j♀, 15 Sep 1955, RDS; 1♂I, 3♂II, 12♀, 1j♀, 2 ovig ♀, 17 Apr 1977, C. E. Carter, C. W. Hart, Jr., JEP, HHH; (18) Blue Spring near Sylvania, 1♂II, 5♀, 2j♀, 10 Aug 1951, DCS. *Taliaferro County:* (19) White Creek at St Rte 44, 1.8 mi NE of Green Co line, 1♂II, 3♀, 14 Jun 1972, DJP, JEP, HHH; (20) North Fork of Ogeechee River 3.6 mi E of Greene Co line on US Hwy 278 and 1.5 mi SW on Co Rd, 1♂I, 1♂II, 1♀, 14 Jun 1972, DJP, JEP, HHH; (21) South Fork of Little River at St Rte 22, 3♂II, 4♀, 1j♂, 5j♀, 1 Oct 1972, DJP, JEP, HHH; 4j♀, 4 Oct 1977, TAE, HHH; 2♂II, 4♀, 3 Apr 1978, R. J. Dubois, DJP, JEP, HHH; (22) South Fork of Ogeechee River at St Rte 22, 2♀, 3 Apr 1978, RJD, DJP, JEP, HHH. *Warren County:* (23) trib to Hart Creek 6.8 mi N of Camak on St Rte 80, 2♂I, 1♂II, 4♀, 1j♀, 27 Apr 1966, ETH, HHH; (24) trib to Goldens Creek 1.4 mi S of Warrenton on St Rte 80, 2♂I, 15 Jun 1972, DJP, JEP, HHH; (25) Reedy Creek 0.4 mi N of Jefferson Co line on St Rte 17, 1♀, 2j♂, 1j♀, 2 Oct 1972, GBH, HHH. *Washington County:* (26) Williamson Swamp Creek 1 mi N of Warthen, 1♂I, 6♀, 2j♂, 3j♀, 1 ovig ♀, 27 Apr 1966, ETH, HHH; (27) Hill Creek 5 mi E of Sandersville on St Rte 24, 3♂II, 1♀, 1j♂, 1j♀, 21 Jul 1971, BAC, MWW; (28) Williamson Swamp Creek 4.1 mi W of Jefferson Co line on St Rte 88, 2♀, 15 Jun 1972, DJP, JEP, HHH; (29) Cedar Creek 0.8 mi E of St Rte 15 on Rte 231, 1♀, 16 Jun 1972, DJP, JEP, HHH. *Wilkes County:* (30) Beaver Dam Creek 13 mi W of Washington on US Hwy 78 (Hobbs, 1947b:4), 1♂II, 6 Sep 1938, GBH, HHH; (31) Clark Creek 5.2 mi W of Tignall on Co Rd, 1♂II, 3j♂, 5j♀, 3 Oct 1972, GBH, HHH; (32) Clark Creek about 8.5 airmi NW of Washington, 2j♂, 4j♀, 3 Oct 1972, GBH, HHH; (33) Middle Fork of Fishing Creek 9 mi S of Lincoln Co line on St Rte 44, 2♂I, 1♀, 14 Jun 1972, DJP, JEP, HHH. *Wilkinson County:* (34) swampy creek 1.8 mi S of Baldwin Co line, 1♀, 1j♀, 22 Mar 1961, PCH.

VARIATIONS.—Among the more conspicuous variations of this crayfish is the shape of the rostrum. Usually it is subplane toward the apex

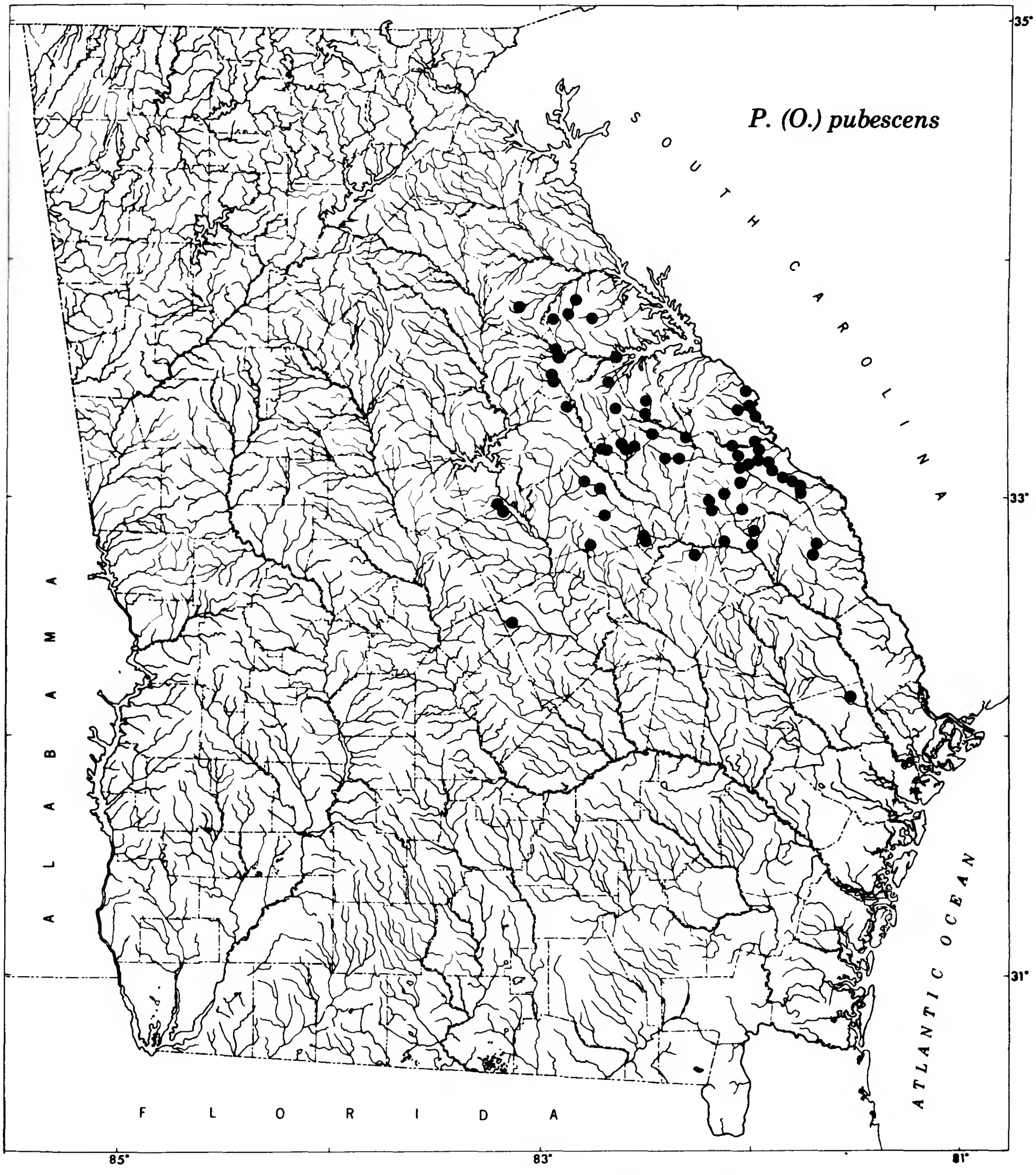


FIGURE 162.—Distribution of *Procambarus (O.) pubescens* in Georgia.

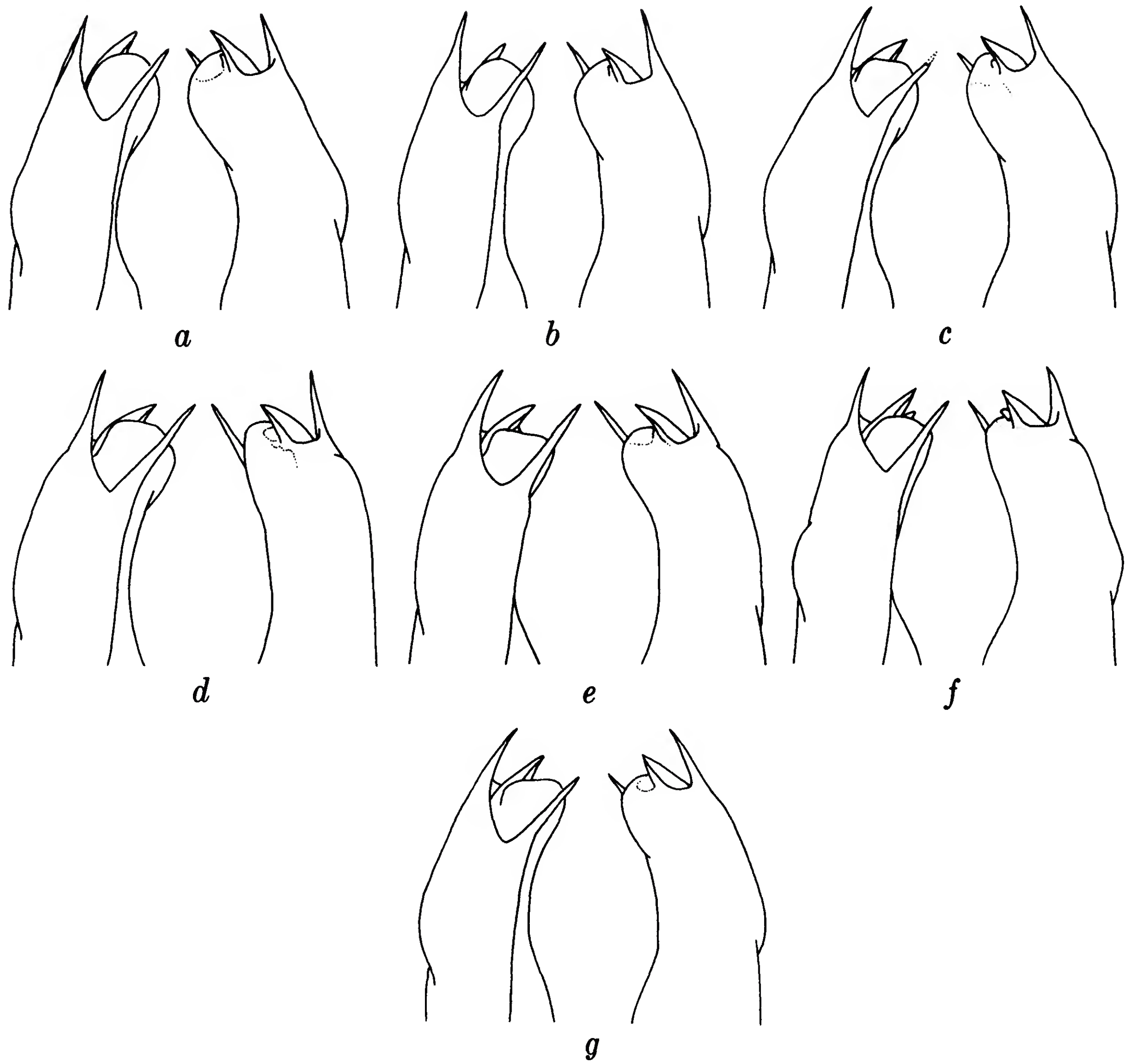


FIGURE 163.—*Procambarus (O.) pubescens*, variations in mesial and lateral views of first pleopod of first form male. Savannah Basin: *a*, Wilkes Co; *b*, Warren Co; *c*, McDuffie Co. Ogeechee Basin: *d*, Glascock Co; *e*, Jefferson Co; *f*, Jenkins Co. Oconee Basin: *g*, Laurens County.

and densely studded with anteriorly directed setae that obscure the acumen, but occasional individuals have been observed in which the pubescence is exceedingly limited. The rostral margins may be subparallel or gently convergent to the base of the acumen. Usually the cervical and postorbital spines are very well developed, but occasionally they are small. The usual differences occur in the number of spines and tubercles on the various podomeres of the cheliped but are not noteworthy. In contrast, whereas the opposable margins of the fingers of the chelae of the females are tuberculate and bear a single row of minute denticles, in the first form male a broad band of denticles largely obscures the comparatively small tubercles that are so clearly evident in the female. The caudal element of the first pleopod (Figure 163) of the first form male varies even in a single population: the caudal knob may be rather strongly sclerotized, bulge caudolaterally, and be set off from the other terminal elements by a well-defined transverse excavation; in some specimens, however, it is weakly sclerotized, bears no conspicuous bulge, and the limiting excavation flanking it caudally may be obsolete. The caudal process is small but well developed in specimens from much of the range; however, in those males from Glascock, Laurens, and Taliaferro counties (Upper Ogeechee and Oconee basins) it is much reduced or virtually obsolete. The adventitious process, like the caudal knob, is sometimes sharply defined, but at least ocasionally it is low and not distinctly set off from the caudal knob. The annulus ventralis is highly variable, more so in surface contour than in outline. In some individuals the ridges and elevations are much depressed: the anterolateral ridges flanking the median trough may be hardly recognizable, and the posteromedian elevation may be depressed to a degree that the posterior part of the annulus is almost flat, interrupted only by the sinuous sinus. The sternum immediately anterior to the annulus may or may not exhibit a distinct cleft flanked by slightly protruding prominences; such are conspicuously absent in the females from Glascock and Jefferson counties, and in these specimens not even the cleft is evident.

A female from 5.5 miles west of Loganville on U.S. Highway 78, Gwinnett County, is tentatively assigned to this species. In addition to the paucity of setae on the rostrum, the absence of a cervical spine, and the presence of small tubercles on the sternum immediately anterior to the annulus ventralis, the specimen was collected in a tributary to the Ocmulgee River, a basin from which no other member of the species has been found. I have attempted to obtain additional specimens in this locality, as well as in other nearby streams, but the only crayfishes encountered were members of *Cambarus (D.) latimanus* and *P. (Pe.) spiculifer*. Because I have been unable to confirm the presence of *Procambarus (O.) pubescens* in this locality, the latter is not included on Figure 162, nor is the single specimen listed among the "Georgia Specimens Examined."

SIZE.—The largest specimen available is a female, possessing a carapace length of 41.0 (postorbital carapace length 30.5) mm. Corresponding lengths of the smallest and largest first form males are 23.2 (16.3) mm and 36.4 (26.1) mm, and of the smallest ovigerous female, 25.5 (17.6) mm.

LIFE HISTORY NOTES.—First form males have been collected in February and during the months from April to September. Few adult males have been obtained during the remaining months, but I suspect that breeding males occur throughout the year. Ovigerous females have been found during April, June, July, August, and September, and two females carrying young were collected in August and another in September (Hobbs, 1947a:5). Data for the ovigerous females are as follows:

Carapace and postorbital carapace lengths (mm)	*Number of eggs*	*Diameter of eggs (mm)*
25.5 (17.6)	89	1.6
26.6 (19.3)	128	1.6–1.7
27.6 (19.6)	170	1.6
28.1 (19.0)	164	1.6–1.7
28.2 (19.4)	199	1.6–1.7
30.4 (21.3)	152	1.5–1.6
30.5 (21.6)	215	1.5–1.6
35.1 (24.6)	235	1.6
35.8 (25.0)	382	1.6
36.9 (26.9)	443	1.6

One of the females carrying young has a carapace length of 26.9 (postorbital carapace length 18.9) mm, and 80 second-instar young were clustered on her abdomen.

Seasonal Data

Sex/stage	*J*	*F*	*M*	*A*	*M*	*J*	*J*	*A*	*S*	*O*	*N*	*D*	*?*
♂I		1		13	1	11	1	3	6			1	
♂II		15	3	13		6	4	7	25	5		6	2
♀		14	9	54		9	6	16	37	13		14	6
♂j		6	1	7		5	1	7	14	16	1	7	
♀j		22	3	35		2	1	7	67	29		12	2
♀ ovig				4		2	2	2	2				
♀ with young								2	1				

ECOLOGICAL NOTES.—Previous accounts include those of Hobbs (1947a:5) and Hobbs III, Thorp, and Anderson (1976:38). The following summarizes most of what is known of the habitats exploited by this crayfish. *Procambarus (O.) pubescens* occurs in streams of various sizes (rivers to creeks that are less than a meter in width and a few centimeters deep), flowing with sluggish to moderately swift currents over sand, clay, silt-laden, and/or rock-littered beds that may or may not support macrophytes. In most of the streams from which I have collected it, the water was coffee colored, although that issuing from Magnolia Springs in Jenkins County was clear and considerably cooler during the summer months than that in most of the other streams where this crayfish has been found. In habitats where there are rocks in the stream bed, it occurs in shallow excavations under them. If vegetation is present, during the day the crayfish are usually concealed among the clumps or mats of plants or in the attendant organic litter. In all types of streams in which it has been found, *P. (O.) pubescens* is a denizen of tree litter entrapped either in the current or lee areas. Individuals also find cover along undercut banks and among exposed roots of shoreline trees and shrubs. Although I have not collected specimens from burrows, in segments of streams where the water flows over bare clay beds, I have seen the mouths of numerous tunnels and suspect that at least some of these excavations are occupied, if not also constructed, by members of this species. Rarely, except at night or immediately after I had routed an individual from its hiding place, have I seen *P. (O.) pubescens* in open water. At night I have observed individuals moving over areas of the stream where there was no ready cover available and on a number of occasions clinging to the leaves of *Vallisneria* undulating in the current.

GEORGIA CRAYFISH ASSOCIATES.—In Georgia, this crayfish has been found in the same locality with the following (the number of times they were found together is included in parentheses): *Cambarus (D.) latimanus* (41), *C. (D.) reflexus* (3), *C. (L.) diogenes diogenes* (1), *Procambarus (L.) barbatus* (1), *P. (O.) acutus acutus* (2), *P. (Pe.) petersi* (8), *P. (Pe.) raneyi* (6), *P. (Pe.) spiculifer* (2), *P. (S.) howellae* (1), and *P. (S.) troglodytes* (4).

The *seminolae* Group

Procambarus (Ortmannicus) fallax (Hagen)

FIGURES 14*e*, 136*e*, 138*e*, 156, 164, 248

Cambarus fallax Hagen, 1870:34, 97, 101, 107, pl. I: figs. 103-105.—Faxon, 1884:136; 1885a:8, 17, 19, 23-24, 29, 157, 167, 173, pl. II: fig. 4; 1885b:357; 1890:621; 1898:644; 1914:368, 413.—Underwood, 1886:369.—Lönnberg, 1894:125; 1895:3, 10, 11; 1898:350.—Hay, 1899b:959, 964.—Ortmann, 1902:277.—Harris, 1903a:58, 70, 97, 143, 152, 166.—Hobbs, 1937:154; 1942b:8, 9; 1962:273.—Carr, 1940:92.—Goodnight, 1941:70, 72, 73.—Kilby, 1945:84.

Cambarus Fallax.—Hagen, 1870:45-46 [lapsus calami].—Hobbs, 1972a:2.

Cambarus (Cambarus) fallax.—Ortmann, 1905a:102, 105.

Cambarus (Ortmannicus) fallax.—Fowler, 1912:341 [by implication].—Creaser, 1934:4 [by implication].

Procambarus fallax.—Hobbs, 1942a:342 [by implication]; 1942b:15, 18, 20, 21, 31, 45, 70, 71, 83, 93, 106, 109-118*, 123, 124, 128, 145, 152, 153, figs. 116-120; 1943a:52, 55, figs. 2, 5; 1959:889*; 1962:285*, fig. 40; 1968b:K-9*, fig. 25o; 1969a:118.—Hoff, 1944:340, 349.—Needham, 1949:453.—Dickinson, 1949:23.—Penn, 1950b:647, 649; 1954:296.—Crocker, 1957:71.—Hart, 1959:204.—Hoffman, 1963:368.—Hobbs III, 1969:41.—Holt, 1973b:88, 90, 93.—Hart and Hart, 1974:128, 131.—Franz, 1977a:91-93*.—Huner and Avault, 1977:21.

Procambarus (Ortmannicus) fallax.—Hobbs, 1972a:9; 1972b:64*, 150*, figs. 27e, 49h; 1974b:55*, fig. 235.—Hobbs, Hobbs, and Daniel, 1977:148.

Procambaris fallax.—Wharton, 1978:46* [erroneous spelling].

These citations include all references to the species that I have encountered in the literature. Those pages marked by asterisks note its occurrence in Georgia.

SUMMARY OF LITERATURE.—This species was described by Hagen (1870) on the basis of specimens that had been collected in an unknown locality in Florida by Dr. H. Bryant (see Faxon, 1885a:24). Not until 15 years later were specific localities in the state recorded (Faxon, 1885a:24).

Other localities in Florida were added by Faxon (1890, 1898, 1914) and Lönnberg (1895). The first remarks on the habitats of this crayfish were made by the latter (p. 3) as follows: "They lived in creeks, small lakes and ponds, very often hiding in the rich vegetation there or under logs, boards and so on. Sometimes I found them digging holes on the shore, at low water, and then those holes often went down to such a depth that the water came up into them." In these statements, Lönnberg was referring to both *P. (O.) fallax* and *P. (Leconticambarus) alleni* (Faxon, 1884:110). In summarizing its habitat distribution in the vicinity of Gainesville, Florida, Hobbs (1937) stated that it is "peculiar to ponds and lakes but is often found in habitats occupied by members of other species." The most complete account of the species, including geographical, ecological, and life history data, as well as remarks on its relationships, is that of Hobbs (1942b), who also recorded its presence in Echols County, Georgia (p. 112). In 1962 (p. 285), he stated that the species ranges "from the Suwannee and St Mary [sic] drainages (Ga.) south to DeSoto, Highlands, and Palm Beach counties, Florida," and in 1972 (b:64) noted a range extension: "Lotic and lentic habitats from the Satilla River drainage, Georgia, southward through peninsular Florida." Carr (1940), Penn (1950b), and Franz (1977a) reported that this crayfish is preyed upon by the striped swamp snake *Regina alleni*, the former two using the combination *Liodytes alleni*. Franz's account of the feeding behavior of rotating the crayfish so it can be devoured tail-first is noteworthy. Kilby (1945) found that the frog *Rana pipiens sphenocephala* also feeds upon this crayfish. The role of *P. (O.) fallax* as a host to several entocytherid ostracods was recorded by Hoff (1944), Hart (1959), and Hobbs III (1969), and to branchiobdellid worms by Goodnight (1941), Hoffman (1963), and Holt (1973b). The remaining citations include references to previous work or contain statements or discussions of relationships and proposed taxonomic changes. The bases for the latter are discussed in the introductory section of this study.

DIAGNOSIS.—Rostrum almost always with marginal spines, sometimes latter reduced to tubercles and rarely to angles at base of acumen; median carina absent. Carapace with 1 pair of cervical spines (rarely with 2 on either or both sides). Areola 5.5 to 8.8 times as long as broad and constituting 27.5 to 33.7 (average 30.7) percent of entire length of carapace (39.4 to 45.8, average 42.9, percent of postorbital carapace length). Antennal peduncle with spine on ischium. Lateral half of ventral surface of ischium of third maxilliped lacking conspicuous mat of long plumose setae. Basis of cheliped without mesial spine. Mesial surface of palm of chela of male with mesialmost row of 8 to 14 tubercles. Male with hooks on ischia of third and fourth pereiopods; that on fourth in first form male bituberculate, not overreaching basioischial articulation, and opposed by prominent tubercle on corresponding basis. First pleopods asymmetrical and reaching coxae of third pereiopods; distal fourth or fifth of shaft gently inclined caudally; cephalic surface of neither member of pair with distinct shoulder; subapical setae flanking lateral, cephalic, and mesial sides of cephalic process and central projection, largely obscuring both terminal elements; mesial process rather long, bladelike, directed distolaterally, and surpassing other terminal elements distally; cephalic process slender, basally hooding and extending caudodistally subparallel to central projection, apex not reaching so far caudally as that of latter; central projection corneous, elongate, compressed, directed caudodistally, but largely adnate with distomedian surface of shaft and only acute tip free; caudal element vestigial, forming corneous ridge along lateral side of central projection, well-defined process and caudal knob lacking. Female with sternum cephalic to annulus ventralis lacking projections or tubercles; annulus ventralis subcampanulate in outline, with ventrally elevated cephalic region bisected by narrow trough leading caudally into median depression or to declivity bearing tilted S-shaped (often reversed) sinus; postannular sclerite little narrower than annulus; first pleopod present.

COLOR NOTES (Figure 136*e*).—Carapace basi-

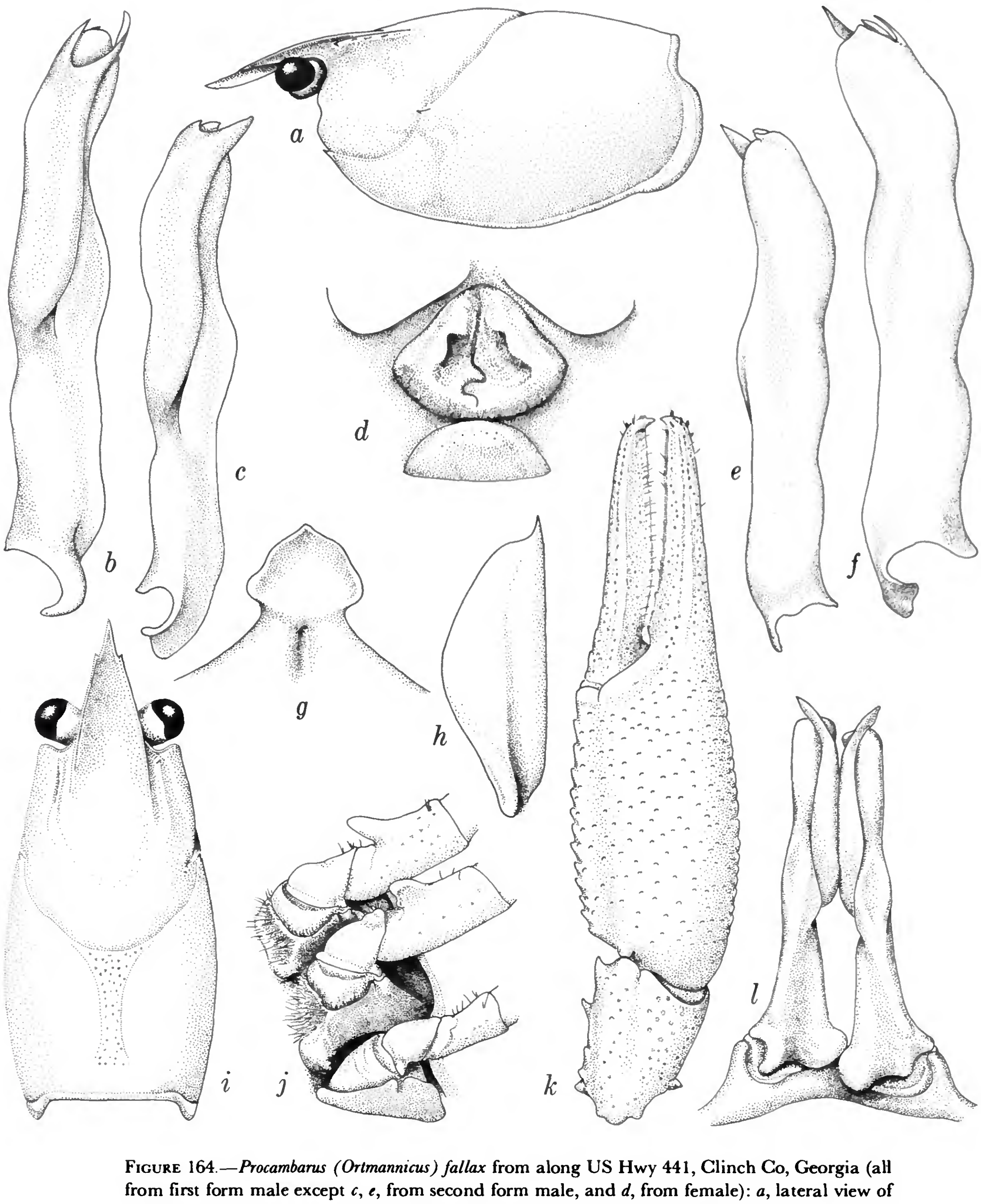


FIGURE 164.—*Procambarus (Ortmannicus) fallax* from along US Hwy 441, Clinch Co, Georgia (all from first form male except *c*, *e*, from second form male, and *d*, from female): *a*, lateral view of carapace; *b*, *c*, mesial view of first pleopod; *d*, annulus ventralis; *e*, *f*, lateral view of first pleopod; *g*, epistome; *h*, antennal scale; *i*, dorsal view of carapace; *j*, proximal podomeres of third, fourth, and fifth pereiopods; *k*, dorsal view of distal podomeres of cheliped; *l*, caudal view of first pleopods.

cally dark brown dorsally, fading to pinkish tan ventrally on branchiostegites, with light cream tan median longitudinal stripe extending from rostrum to caudal margin; cephalolateral area with oblique red stripe, flanked dorsally and ventrally by narrow cream lines, extending from antennal region along ventral hepatic area, and small cream spot immediately dorsal to cervical spine. Branchiostegites with paired longitudinal black stripe laterally, extending from cervical groove to caudal ridge and paired black spots caudodorsally, spots joined by black transverse band on caudal ridge. Abdomen with median, longitudinal broad brown stripe, flanked laterally by series of dark, obliquely oriented splotches situated anteriorly on first through fifth terga; pleura of second through sixth segments delimited basally by ventrally convex black marks, these together forming scalloped line. Prominent, irregular cream patches situated on each tergum between row of oblique splotches and scalloped line; pleura reddish tan mottled with cream, and with white spot abutting scallops anteroventrally. Telson olive tan with brown markings and with pair of oblique cream spots ringed in dark brown anteriorly; lateral quarters darker than median half; caudal section with narrow cream to white median longitudinal line. Uropod similarly olive tan with brown mottlings, and ridges and lateral margins of rami dark brown. Antennular and antennal peduncles olive mottled with brown; flagella dark olive; antennal scale olive to cream, with brown lateral margin and stripe along mesial margin of thickened lateral area. Third maxilliped pale olive, fading proximally to cream. Chelipeds olive to brown, mottled with dark brown from distal two-thirds of merus distally to corneous tips of fingers, tubercles and fingers very dark; ventral surface paler. Ventral surface of body cream.

TYPES.—Syntypes, MCZ 3526 (♂I, ♂II), BSNH (♂II, ♀), USNM 63294 (♂II, ♀).

TYPE-LOCALITY.—Florida. Restricted to Saint Johns River at Welaka, Putnam County, Florida, by Hobbs (1974b:55).

RANGE.—Tributaries of the Satilla and Suwannee rivers in Georgia, southward through most of peninsular Florida. In Georgia, it is confined to the Satilla, Saint Marys, and Suwannee basins in the following districts of the Coastal Plain Province: Tifton Upland, Bacon Terraces, Okefenokee Basin, and Barrier Island Sequence.

SPECIMENS EXAMINED.—I have examined a total of 2923 specimens, of which 2752 were from Florida and 171 from the following localities in Georgia. *Atkinson County:* (1) 2 mi W of Pearson, 1♀, 18 Apr 1947, H. W. Fowler, collector. *Brantley County:* (2) Buffalo Creek 6 airmi SW of Nahunta on unnumbered rd, 1♂II, 20 Apr 1974, C. R. Gilbert. *Charlton County:* (3) Saint Marys River 16 mi S of Folkston on St Rte 23, 1♂I, 4♂II, 4♀, 1j♀, 27 Mar 1940, E. C. Raney; 3♂II, 3 Sep 1962, ECR; (4) 23.3 mi S of Folkston, 1♂II, 27 Mar 1940, ECR; (5) 9 mi N of Saint George on St Rte 23, 4♂I, 3♂II, 6♀, 2j♂, 3j♀, 18 Apr 1963, P. C. Holt, V. F. Holt; (6) Green Branch 8.5 airmi S of Saint George on Co Rd, 1♂I, 1♀, 21 Jul 1975, J. Germann; (7) Tiger Branch 12 airmi SW of Saint George, 1♂II, 1♀, 3 Oct 1974, JG; (8) Cornhouse Creek 8.3 airmi SSW of Folkston on St Rte 23, 2♂I, 4♂II, 1j♀, 8 Jun 1976, JG; (9) slough of Harris Creek 3.3 mi N of Saint George on St Rte 23, 1 ovig ♀, 21 Jul 1975, JG. *Clinch County:* (10) temporary pools 5 mi S of Homerville off US Hwy 441, 3♀, 4 Nov 1967, J. J. Sullivan; (11) swamp N of Fargo, 1j♀, 25 May 1941, G. B. Hobbs, HHH; (12) roadside ditch about 12 mi N of I-10 on US Hwy 441 [either the mileage or state and county are incorrect for Interstate Highway 10 is more than 12 miles south of the Georgia line], 9♂I, 4♂II, 7♀, 2j♂, 11j♀, 26 Jul 1966, W. F. Smith-Vaniz. *Coffee County:* (13) Seventeen Mile Creek at St Rte 32, 5♂II, 3♀, 1j♂, 13 Sep 1972, R. M. Gaddis, M. W. Walker. *Echols County:* (14) stream 0.4 mi N of Florida line on US Hwy 441, 4j♂, 8j♀, 27 Oct 1938, F. N. Young, Jr., HHH; 2♂I, 8♂II, 2♀, 29 Mar 1977, H. K. Wallace, HHH. *Lanier County:* (15) Lakeland, 1♀, 2j♀, 23 Feb 1930, O. C. Van Hyning; 1♀, 1j♀, 25 Oct 1946, HWF; (16) Bank Lake 1.5 mi S of Lakeland, 1♂I, 3♀, 12 Sep 1929, E. P. Creaser. *Lowndes County:* (17) ditch 3 to 4 mi S of Valdosta, 1♀, 1953, B. Fulford; (18) ditch 1.5 mi S of Valdosta on old Clyattsville Rd, 2♂I, 2♂II, 4♀, 4j♂, 2j♀, 1953, M. E. Carter; (19) Twin Lakes at town of Twin Lakes on US Hwy 41, 2j♀, 13 Sep 1929, EPC; 1♂I, 25 Mar 1959, R. L. Gibbs; (20) Lanier-Lowndes Co line, 3♂I, 1♂II, 2♀, 5 j♂, 3j♀, 23 Mar 1961, PCH, VFH; (21) Grand Bay Creek 11 mi E of Valdosta on US Hwy 84, 3♂I, 2♂II, 5♀, 1j♂, 3j♀, 4 Nov 1967, JJS.

VARIATIONS.—Variations of a conspicuous nature are rare among the Georgia members of this species. With few exceptions, in specimens in which the marginal spines on the rostrum are reduced to tubercles, there is evidence of abrasion of other spines on the carapace. Most specimens from Charlton County (Saint Marys Basin) possess areolae constituting more than 30.7 percent of the total length of the carapace, reflecting a shorter rostrum resulting from abrasion or earlier injury of the acumen. In addition most members of the species from the Saint Marys watershed also possess areolae that are broader than the average (less than 6.8 times as long as wide) but in occasional ones the areola is as much as 7.8 times as long as broad. A very small proportion of the specimens from Georgia exhibits what I consider to be an atavistic trait in possessing a second well-developed cervical spine, a character that appears typically only in members of the subgenus *Pennides* and in some Middle American representatives of the subgenus *Austrocambarus*. Among the secondary sexual characters of the first form male, only the hook on the fourth pereiopod exhibits a noteworthy variation: the terminal tubercle adjacent to the shaft of the ischium is much more strongly developed in some specimens than in others, and in a few it is so poorly defined that the hook may appear not to be bituberculate. The median part of the annulus ventralis exhibits considerable individual variation: in some specimens there exists a distinct submedian depression, while in others there is a gradual sloping (cleft by the anteromedian groove and sinus) from the cephalomedian elevation caudally.

Size.—The largest specimen from Georgia is a female that has a carapace length of 34.3 (postorbital carapace length 24.6) mm. Corresponding lengths of the smallest and largest first form males are 15.1 (10.5) mm and 26.9 (20.0) mm. The only female collected in Georgia that was carrying eggs (or young) has corresponding lengths of 20.5 (14.1) mm.

Life History Notes.—Although few data are available that aid in an understanding of the life history of the species in Georgia, considerably more information may be gleaned from the collections made in Florida. Even so, the life cycle is by no means known. First form males were obtained in Georgia in March, April, June, July, September, and November; in Florida they were found during every month of the year (Hobbs, 1942b:112). The only ovigerous female that I have examined from Georgia was collected in July; in Florida such females have been found during every month of the year, and females carrying young were found in March, April and June. The ovigerous female, collected in Charlton County on 21 July 1975, carried 84 eggs, ranging from 1.4 to 1.5 mm in diameter. (See "Size" for measurements.)

Seasonal Data (Florida and Georgia)

Sex/stage	*J*	*F*	*M*	*A*	*M*	*J*	*J*	*A*	*S*	*O*	*N*	*D*	?
♂I	29	37	91	37	11	27	29	5	20	19	20	6	10
♂II	39	66	126	41	7	22	20	2	28	77	69	31	30
♀	66	155	184	95	36	34	37	5	48	91	100	36	74
♂j	36	62	44	18	6	6	78	3	33	33	29	25	15
♀j	57	78	59	33	22	21	74	7	39	42	40	26	11
♀ ovig	1	6	75	7	3	8	3	2	2	5	2	1	2
♀ with young			42	3		3							1

Ecological Notes.—Most of the account of the ecological distribution of this crayfish presented by Hobbs (1942b:113–114) is applicable to its occurrence in Georgia and is quoted here:

> *P. fallax*, unlike many of the Florida species, is not restricted to one particular type of habitat, and it shows little, if any, correlation with any one type of lake or pond, so long as there is sufficient vegetation to afford hiding places and there is water most of the year.
>
> Practically all of the streams within the range of *fallax* seem to be inhabited by it, in at least some of their reaches. In larger calcareous streams and many of the spring runs *P. fallax* is abundant. Even in some of the helocrene springs small specimens have been taken from the leaves which have fallen into the rill courses. Many of the acid flatwoods streams are inhabited by *fallax*, and in several instances this species has been taken from sand bottomed creeks.
>
> Although *P. fallax* inhabits both lotic and lentic situations in the northern and central parts of its range, it becomes more restricted to lotic habitats as it approaches the southern limits. It is most often found in the quieter reaches of a stream . . . . In general there seems to be a high degree of correlation between the abundance of *fallax* and the amount of vegetation. In some of the sand bottomed creeks with a sparse flora, *fallax* is absent, but where the creek becomes more sluggish and plants become more abundant, *fallax* is usually common. Never have I taken this species from a sand bottomed stream where there was no vegetation.

> This species probably does not burrow by preference but when the water table is lowered in dry seasons, *fallax* usually contructs a simple burrow with only one passage slightly slanting from the vertical; at the bottom, which may or may not be below the permanent water table, a slightly enlarged chamber occurs; it is here the crayfish is always found when it is dug from the burrow.

During dry seasons it has been found burrowing in pond basins and in ditches.

On several occasions in Florida, this crayfish was found moving over land in fields and hammocks, and a first form male was found at a light, used to attract insects, some 200 meters from the nearest body of water, a lake in Marion County, Florida (Hobbs, 1942b:113–114).

Members of the species have perhaps been taken in greatest numbers from the roots of water hyacinths (*Eichornia crassipes*) both in streams and lentic habitats. One afternoon in March, among the several hundred individuals caught (by lifting mats of hyacinths from a lake in Florida with the aid of a tray possessing a quarter-inch (6.5 mm) mesh hardware cloth) were 58 ovigerous females and 41 that were carrying young.

Although the few collections of crayfishes from the Okefenokee Swamp proper have not revealed the presence of this crayfish, I suspect that it will be found to be common. As pointed out by Hobbs (1942b:113–114), it has been found in sphagnum bogs, in which the pH of the water was less than 5, and in parts of the swamp where sufficient light reaches the waterways to support luxuriant plant growth, this species should occur in numbers.

Georgia Crayfish Associates.—The following crayfishes have been collected with *P. (O.) fallax* in one or more localities in Georgia (the number of times they have been found together is noted in parentheses): *Procambarus (H.) pygmaeus* (2), *P. (O.) seminolae* (6), *P. (Pe.) spiculifer* (1), and *P. (S.) paeninsulanus* (3).

Procambarus (Ortmannicus) leonensis Hobbs

Figures 14*d*, 136*g*, 138*f*, 165, 249

Procambarus leonensis Hobbs, 1942b:9, 15, 20, 21, 66, 87, 106, 110–112, 114–118, 123, 152, 155, figs. 121–125; 1943a:49–53, 55, figs. 1, 6, 7, 10, 12–14, 16, 17, 22, 26, 29, 31; 1945b: 254; 1959:889; 1962:285, fig. 29; 1966b:70; 1968b:K-9, fig. 25n.—Hoff, 1944:340, 356.—Hart, 1959:203, 204.—Hobbs and Hart, 1959:149, 154, 158–160, 163, 164, 167, 168, 171, 174, 176, 178, 185, fig. 12.—Caine, 1974b:3, 5, 7, 9–10, 14–15, 17, 19, 20, 22–26, 29, 30, 32–34, 36–39, 43, 45, 47–54, 56, 60, 69, figs. 1c, 4c, 5a.—Hart and Hart, 1974:27, 88, 128.—Franz, 1977a:93.

Procambarus (Ortmannicus) leonensis.—Hobbs, 1972a:9; 1972b: 63, 64, 151, 154, fig. 50a; 1974b:57, fig. 236.

The above is believed to constitute a complete bibliography for the species. Inasmuch as representatives have not been found in Georgia, none of the citations include references to the state.

Summary of Literature.—Due to the delay in publication of the full description of this crayfish (Hobbs, 1943a), the brief diagnosis of the species in his compilation of the crayfishes of Florida (Hobbs, 1942b:114) must be considered to constitute the original description, despite the fact that the account in the later publication is so designated therein.

Virtually all that is known about the species is included in Hobbs (1942b), Hobbs and Hart (1959), and Caine (1974b). The latter, in addition to discussing its habitat in Florida, presents comparative data concerning adaptations involving the following: temperature and stream velocity tolerances, oxygen levels and metabolism, substrate preferences, burrowing, and behavior. Entocytherid ostracods harbored by it are cited by Hoff (1944), Hart (1959), Hobbs (1966b), and by Hart and Hart (1974). Franz (1977a) suggested that it might serve as prey for the snake *Regina alleni*. Its assignment to the subgenus *Ortmannicus* was proposed by Hobbs (1972a), and its range was defined and illustrations were presented in Hobbs (1972b and 1974b).

Diagnosis.—Rostrum with marginal spines or tubercles, or at least angulate at base of acumen; median carina lacking. Carapace with 1 pair of cervical spines or tubercles. Areola 4.7 to 8.8 (average 6.3) times as long as broad and constituting 29.1 to 34.0 (average 30.8) percent of entire length of carapace (38.6 to 43.8, average 40.9 percent of postorbital carapace length). Antennal peduncle with spine or prominent tubercle on

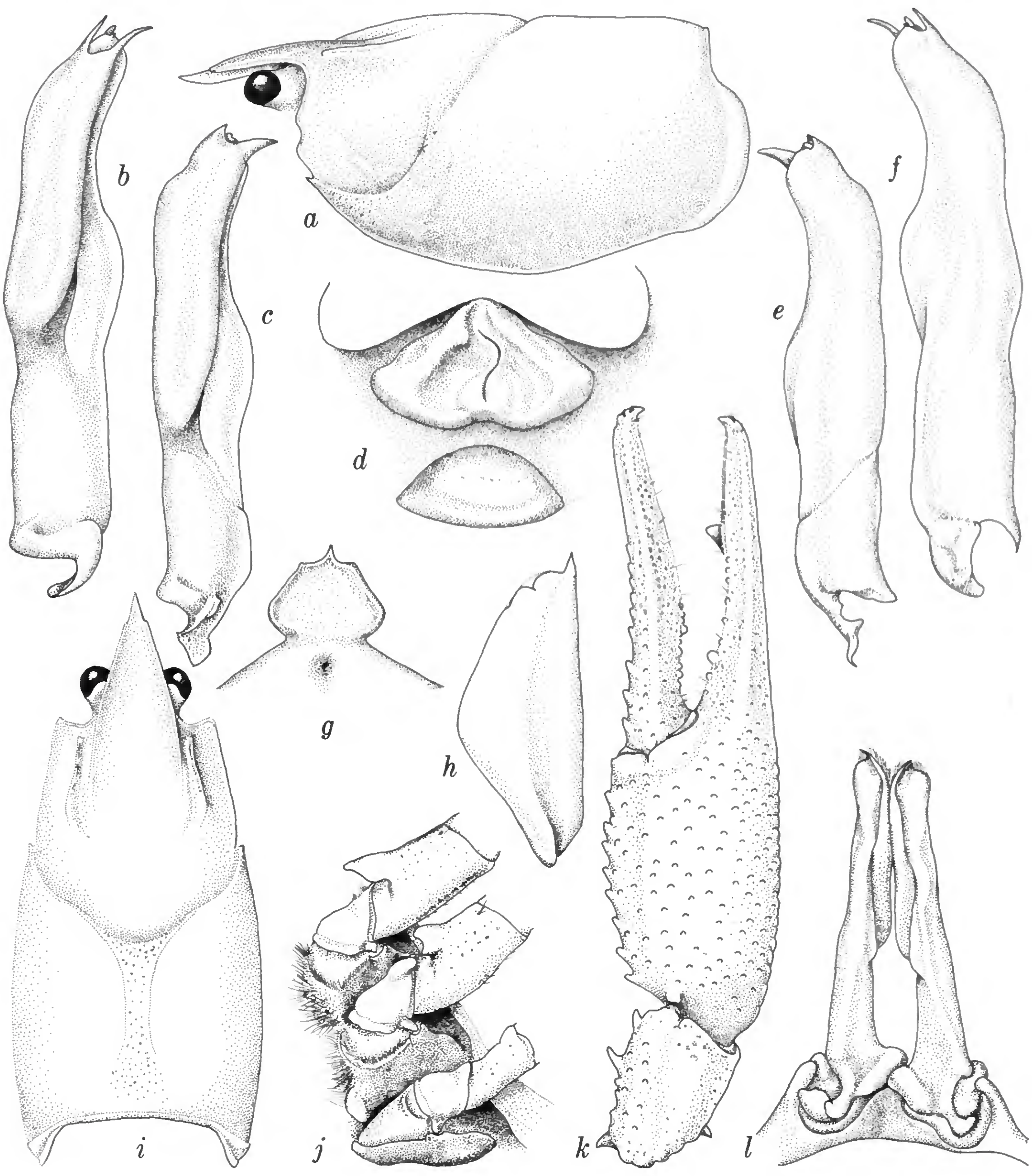


FIGURE 165.—*Procambarus (Ortmannicus) leonensis* (all from holotype except *c*, *e*, from morphotype, *d*, from allotype, and *l*, from first form male from Lake Bradford Slough, Tallahassee, Leon Co, Florida): *a*, lateral view of carapace; *b*, *c*, mesial view of first pleopod; *d*, annulus ventralis; *e*, *f*, lateral view of first pleopod; *g*, epistome; *h*, antennal scale; *i*, dorsal view of carapace; *j*, proximal podomeres of third, fourth, and fifth pereiopods; *k*, dorsal view of distal podomeres of cheliped; *l*, caudal view of first pleopods.

ischium. Lateral half of ventral surface of ischium of third maxilliped sometimes with moderately conspicuous tufts of plumose setae but never with dense mat obscuring entire surface. Basis of cheliped without mesial spine. Mesial surface of palm of chela of male with mesialmost row of 8 to 11 (usually 8 or 9) tubercles. Male with simple hood on ischium of third pereiopod, in first form male overreaching basioischial articulation, and that on fourth often bituberculate and opposed by obliquely set tumescent ventrodistal end of corresponding basis. First pleopods asymmetrical and reaching coxae of third pereiopods, distal part of shaft inclined caudally but cephalic surface lacking distinct hump; subapical setae obscuring cephalic process and central projection; mesial process subspiculiform and directed caudodistally and rather strongly laterally, not overreaching other terminal elements distally; cephalic process acute, situated cephalic to central projection and extending caudodistally subparallel to latter; caudal element represented by vestigial caudal process at caudal base of central projection; latter small, corneous, flattened, arising from central part of distal end of shaft, directed caudodistally but never reaching so far distally as cephalic process. Female with sternum cephalic to annulus ventralis lacking tubercles or caudally protruding prominences; annulus ventralis subcampanulate in outline and bearing broad, triangular median depression, flanked by caudally diverging ridges, frequently with caudomedian concavity; sinus in form of simple arc situated in median part of depression, not reaching cephalic or concave caudal margin of annulus; postannular sclerite about two-thirds as wide as annulus and arched ventrally; first pleopod present.

COLOR NOTES (based on specimen from Leon County, Florida; Figure 136*g*).—Carapace reddish brown dorsally; margins of rostrum, postorbital ridges, and arc covering and flanking cephalomedian part of cervical groove almost black. Orbital and mandibular regions with pale pinkish cream oblique stripe; reddish hepatic area with several small cream spots and streaks. Branchiostegites dark brown dorsally, fading to grayish tan ventrally, marked with many small irregular cream spots, and with 3 pairs of larger dorsolateral black spots: anterior pair abutting cervical groove, another lying almost against dorsal part of caudal flange, and third situated immediately mesial to latter pair, contiguous to reddish brown caudal ridge. Abdominal terga purplish brown, first through fifth with paired, narrow, almost linear dorsolateral spots anteriorly, flanked laterally by oval to subcircular paler spot, and caudal margins dark purplish red. Sixth with complex pattern of black lines. Pleura also purplish red, and second through sixth indistinctly set off from terga by black spot anteriorly, bleeding caudally; second pleuron with central pink spot, succeeding ones pale cephalically and caudally, with small pink spot at midlength near ventral margin. Cephalic section of telson with dark brown median and paired lateral stripes, otherwise purplish red; uropods also mostly purplish red, but basal segment very dark, with proximal pinkish cream spot, dark coloration also on lateral margin of mesial ramus and median ridges of both rami. Eyestalks and antennular and antennal peduncles straw colored, mottled with dark brown splotches, flagella of latter two olive tan; antennal scale pinkish tan, with reddish brown (almost black) lateral margin and only slightly paler longitudinal stripe along mesial side of rib, stripe fading onto lateral part of lamella. Third maxilliped reddish tan. Dorsal surface of cheliped tan to brown and mottled with irregular black splotches from basis to proximal part of fingers; latter very dark brown, with pale pinkish to yellowish tips; large tubercles on dorsodistal part of merus cream tipped, otherwise all tubercles on cheliped black. Remaining pereiopods dark olive gray dorsally from ischium through dactyl; merus and carpus slightly darker distally. Sternal area orange to pinkish cream.

TYPES.—Holotype, allotype, and "morphotype," USNM 81091 (♂I, ♀, ♂II); paratypes, MCZ, USNM, ANSP.

TYPE-LOCALITY.—Sinkhole pond, 3 miles southwest of Tallahassee on State Route 20, Leon County, Florida (now beneath runway at airport).

RANGE.—Between the Apalachicola and Suwannee rivers in Florida.

SPECIMENS EXAMINED.—This crayfish has not been collected in Georgia; however, it has been found so close to the Georgia line in Gadsden and Leon counties, Florida, that I do not doubt that it occurs in either the Aucilla or Ochlockonee river basin in the southwestern part of the state.

SIZE.—The largest specimen that I have measured is the holotypic first form male, which has a carapace length of 46.5 (postorbital carapace length 35.4) mm. Corresponding lengths of the smallest first form male are 27.2 (19.5) mm, and those of the smallest ovigerous female, 29.5 (22.5) mm.

LIFE HISTORY NOTES.—First form males were reported by Hobbs (1942b:115) to have been collected in January, April through June, August, and in November and December. Subsequently they have also been found in September. Ovigerous females have been found in April, May, August (Hobbs, 1942b), and September. Data on three of these females are as follows:

Carapace and postorbital carapace lengths (mm)	*Number of eggs*	*Diameter of eggs (mm)*
29.5 (22.5)	183	1.6–1.7
31.3 (23.4)	347	1.5–1.6
46.1 (34.5)	463	1.5–1.7

Seasonal Data (Florida)

Sex/stage	*J*	*F*	*M*	*A*	*M*	*J*	*J*	*A*	*S*	*O*	*N*	*D*
♂I				5	3	5			3		10	1
♂II		7	5	5	8	2		4	10	1	12	1
♀		11	4	12	10	4		4	13	2	19	2
♂j		20	2	2	105			5	36	12	6	
♀j		51	8	2	133			5	44	14	8	2
♀ ovig					2				1			

ECOLOGICAL NOTES.—Hobbs (1942b:116–117) presented the following account of the ecological distribution of the species in Florida.

Like *fallax*, *leonensis* occupies many types of habitats. It has been collected from swamp ponds, acid creeks, clumps of sphagnum, roadside ditches, sand bottomed streams, lakes, and burrows. Most of the mature specimens in my collection were taken from burrows; however, too little is known of the habits of this species to assume that unlike *fallax*, it burrows by preference when adult. More probably it is purely a coincidence that most of my collections were made either in dry weather or shortly thereafter. I know that this is the case for most of my collecting in Taylor County. In Franklin County this species was taken from a sand bottomed stream where *Hydrocotyl*, *Persecaria*, *Ceratophyllum*, and *Utricularia* were growing along the margins, and most of the specimens were taken among the roots of this vegetation. In Gadsden County *leonensis* was taken from a roadside ditch adjoining a small, clear, moderately swift stream. Some of the specimens were found in the open ditch, but several were taken from flooded burrows in its bottom. In Jefferson County this species was collected from burrows in the edge of a temporary pond. These burrows were simple and, although only about a foot deep, penetrated the water table. In Lafayette County specimens were dug from burrows in a roadside ditch which usually contains water. The burrows here penetrated to a depth of about one foot but did not reach the water table. From Leon County *leonensis* was taken from acid swamp pools, from burrows around open mud bottomed ponds, and from lakes and sloughs. Several of the lakes in Leon County are sporadically drained by subterranean outlets; at such times the entire lake goes dry except for a few small pools, and the crayfish may be found burrowing in the mud bottoms or may be taken in seines dragged through the pools. Judging from the relative abundance of burrows and the number of crayfish taken in the seines, this species must be common in these large lakes. In a small swamp stream near Tallahassee *leonensis* was taken from the edge of the water among *Eleocharis*, *Ludwigia*, and *Sphagnum*. In Liberty County it was collected from a sand bottomed creek. In three localities in Madison County this species was taken from small streams which were choked with vegetation. Two of these streams were flowing rather rapidly and had an abundant growth of *Vallisneria* and other aquatics. The other stream was rather sluggish and was continuous with a swamp pond supporting an abundant growth of *Castalia*. From Taylor County *leonensis* was taken in a shallow pool in a Cypress-Gum swamp, from roadside ditches, and from pools in the bed of a small, stagnant, swamp stream.

GEORGIA CRAYFISH ASSOCIATES.—Inasmuch as this crayfish has not been collected in Georgia, no associates are recorded.

Procambarus (Ortmannicus) lunzi (Hobbs)

FIGURES 14*c*, 136*d*, 138*i*, 166–168, 252

Cambarus lunzi Hobbs, 1940b:3–7, figs. 1–10; 1942b:129, 142, 144.

Procambarus lunzi.—Hobbs, 1942a:343; 1958a:73, 79, 80, 85, 86, 88, fig. 9; 1958b:160, 167; 1959:889; 1962:285, fig. 37;

1966b:70; 1968b:K-10, fig. 25m.—Hoff, 1944:349, 356.—Hart, 1959:203.—Hobbs III, 1969:41.—Hart and Hart, 1974:28, 63, 137.

Procambarus (Ortmannicus) lunzi.—Hobbs, 1972a:9; 1972b: 63*, 151*, 154*, 155, fig. 49f; 1974b:58*, fig. 234.

The above citations are believed to constitute a complete bibliography for the species. References to the occurrence of this crayfish in Georgia are marked with asterisks.

Summary of Literature.—This crayfish was described and illustrated on the basis of a male and female dug from a single burrow in Hampton County, South Carolina (Hobbs, 1940b). Not until thirty-four years later was the second form male illustrated (Hobbs, 1974b:fig. 234). In revising the genus *Cambarus*, Hobbs (1942a) assigned the species to the genus *Procambarus*. Its affinities were discussed by the same author in his account of the evolutionary history of the *pictus* Group of the genus *Procambarus* (1958a) and in his treatment of the *blandingii* Group (1962). The record from the type-locality remained the only one for the species until Hobbs (1972b:63) stated that it had been found in "lentic and sluggish lotic habitats and burrows between the Combahee River, South Carolina and the Altamaha River, Georgia." Restating the same information, Hobbs (1974b:58) recorded its range to include "Hampton and Beaufort counties, South Carolina, southward to McIntosh County, Georgia." Hoff (1944) described two new entocytherid ostracods harbored by the types of this crayfish, and Hart (1959) and Hobbs III (1969) repeated Hoff's records. Hart and Hart (1974), in addition to citing Hoff's work, found that *P. (O.) lunzi* served as a host to a third species of entocytherid, which they had retrieved from topotypes. Thus except for a statement of its habitat and range, the illustration of the first pleopod of the second form male, and its serving as a host to three ostracods, almost nothing has been added to our knowledge of the species since it was first described.

Diagnosis.—Rostrum with or without marginal spines or tubercles, lacking median carina. Carapace with 1 pair of small cervical spines or tubercles. Areola 6.3 to 13.0 (average 8.9) times as long as broad and constituting 31.4 to 34.8 (average 33.1) percent of entire length of carapace (40.5 to 46.4, average 43.1, percent of postorbital carapace length). Antennal peduncle with spine (rarely reduced to tubercle) on ischium. Lateral half of ventral surface of ischium of third maxilliped lacking conspicuous mat of long plumose setae. Basis of cheliped without mesial spine. Mesial surface of palm of chela of male with mesialmost row of tubercles consisting of 7 to 9 (usually 8). Male with simple hooks on ischia of third and fourth pereiopods, in first form male that on third overreaching basioischial articulation and that on fourth not reaching articulation but opposed by prominent protuberance on cephalodistal end of corresponding basis. First pleopods asymmetrical and reaching coxae of third pereiopods; distal part of appendage slightly inclined caudally and bearing conspicuous hump, distal extremity of which situated at base of cephalic process; subapical setae flanking mesial, cephalic, and lateral bases of cephalic process; mesial process spiculiform and directed caudolaterally around mesial half of tumescent distal part of shaft; cephalic process slender, directed caudodistally and extending farther distally than other terminal elements; caudal element obsolete; central projection consisting of rather conspicuous, acute, corneous blade arising from middle of distal end of shaft and directed caudally. Female with sternum cephalic to annulus ventralis bearing or lacking tuberculiform prominences, 1 or more of which extending caudally slightly over cephaloventral face of annulus; latter subovate, with greatest width in transverse plane, ventral surface weakly sculptured but almost always with distinct wide posteromedian depressed area, flanked anteriorly and anterolaterally by ridge, bearing variously contoured sinus; caudal end of latter frequently ending on small median elevation on or jutting from midposterior margin of annulus; tongue oriented either dextrally or sinistrally. Postannular sclerite, frequently partly hidden by caudal region of annulus, at least two-thirds as wide as annulus; first pleopod present.

Color Notes (Figure 136*d*).—Carapace red-

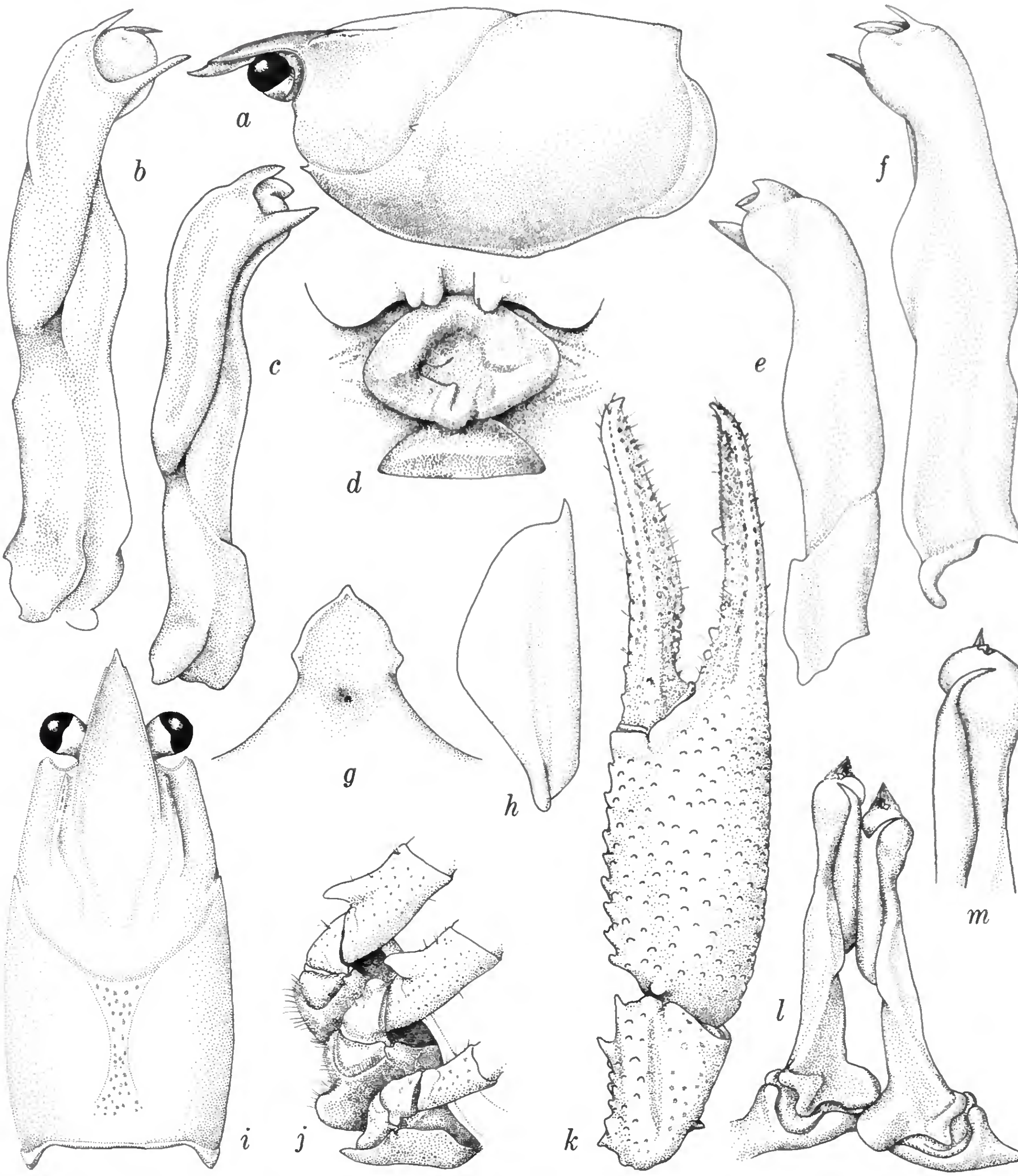


FIGURE 166.—*Procambarus (Ortmannicus) lunzi* from roadside ditch 2.3 mi S of Pembroke on St Rte 119, Bryan Co (all from first form male except *c*, *e*, from second form male, and *d*, from female): *a*, lateral view of carapace; *b*, *c*, mesial view of first pleopod; *d*, annulus ventralis; *e*, *f*, lateral view of first pleopod; *g*, epistome; *h*, antennal scale; i, dorsal view of carapace; *j*, proximal podomeres of third, fourth, and fifth pereiopods; *k*, dorsal view of distal podomeres of cheliped; *l*, caudal view of first pleopods; *m*, caudal view of distal part of first pleopod.

dish brown dorsally, with orange tan and black markings. Cephalic section with median longitudinal orange tan stripe extending from acumen to cervical groove, otherwise lacking conspicuous markings although becoming more pinkish ventrally. Thoracic section with orange tan median longitudinal stripe almost reaching charcoal caudal ridge. Saddle reduced to pair of black longitudinal stripes, representing horns, and pair of much less conspicuous dark markings lateral to caudal margins of branchiocardiac grooves and abutting black caudal ridge; flange and branchiostegite ventral to black stripe pinkish lavender with faint lavender cream spots. Abdomen with broad, median longitudinal brownish red stripe, flanked laterally by narrower pink one; each tergum with paired dark brown spots dorsolaterally. Bases of pleura with scalloped black line basally, otherwise reddish except for small centrally located pinkish spot. Markings on telson similar to those of *P. (O.) epicyrtus*; uropods reddish brown with dark brown keels and lateral margins on both rami. Antennular and antennal peduncles pinkish cream, marked with reddish brown; flagella olive tan. Antennal scale pinkish cream with reddish brown lateral border and similarly colored area mesial to lateral thickened part. Cheliped with merus greenish cream basally, changing to olive brown dorsally; carpus and chela brown with olive mottlings and bearing orange cream to brownish orange tubercles, major ones on merus and carpus cream tipped; ventral surface of both orange tan. Remaining pereiopods bright olive from base of ischium distally, distal part of each podomere darker green, dactyl almost emerald green. Ventral surface of body cream.

TYPES.—Holotype and allotype, USNM 79301 (♂I, ♀).

TYPE-LOCALITY.—Roadside ditch 1.4 miles southwest of Early Branch on State Route 28, Hampton County, South Carolina.

RANGE.—From the Ashepoo River drainage in Colleton County, South Carolina, southwestward to the Satilla (Turtle River) watershed in Georgia, including Sapelo and Saint Simons islands, Georgia. In both states it is apparently confined to the Coastal Plain Province, and in Georgia it is restricted to the Barrier Island Sequence and southeastern part of the Vidalia Upland districts.

SPECIMENS EXAMINED.—I have examined a total of 392 specimens of this species—164 from several localities in Beaufort, Colleton, Hampton, and Jasper counties, South Carolina, and 224 from the following places in Georgia. *Bryan County:* (1) drainage ditch 7.9 mi W of US Hwy 17 on St Rte 67, 1♂II, 3♀, 28 May 1969, E. T. Hall, Jr., HHH, collectors; (2) Ogeechee River at US Hwy 17, 1♂I, 1♀, 4 May 1970, R. W. Heard; (3) Savage Creek and connecting roadside ditches 1.9 to 2.3 mi S of Pembroke on St Rte 119, 3j♂, 3j♀, 27 Dec 1971, G. K. Williamson; 2♂I, 1♂II, 8♀, 6j♂, 5j♀, 20 Apr 1977, C. E. Carter, J. E. Pugh, HHH. *Chatham County:* (4) roadside ditch 3.2 mi SSW of Bloomingdale, 1♂II, 2♀, 2j♂, 2j♀, 30 Jan 1971, GKW, T. Roe; (5) cypress pond and ditch 3.5 mi SSW of Pooler on Quacco Rd, 7♂II, 8♀, 14j♂, 10j♀, 21 Jan 1971, GKW; (6) 2 mi NE of Richmond Hill on US Hwy 17, 8♂II, 4♀, 4j♂, 2j♀, 20 Jan 1972, GKW; (7) Ogeechee Creek at Bush Rd 12.6 mi WSW of Savannah, 1♀, 20 Jan 1972, GKW. *Effingham County*: (8) creek 12 mi SE of Guyton on Pineora Rd, 1♂I, 1♂II, 2♀, 5 Nov 1967, J. J. Sullivan; (9) cypress pond 4.5 mi SE of Pineora, 2♂II, 5♀, 5j♂, 1j♀, 14 Dec 1971, GKW. *Glynn County*: (10) 2.3 mi SW of US Hwy 17 on St Rte 99, 1♂I, 1♂II, 2j♀, 28 Dec 1971, GKW; (11) pools on Demene Rd, Saint Simons Island, 1j♂, 4 Jul 1962, G. C. Miller; 1j♀, 4 Aug 1963, GCM. *Liberty County:* (12) roadside ditch 11.8 mi N of Eulonia on US Hwy 17, 1♀, 19 Dec 1939, G. B. Hobbs, HHH; (13) roadside ditch in Riceboro, 5j♀, 7 Sep 1938, HHH; (14) Goshen Swamp Creek 2 mi SE of Flemington on US Hwy 82, 1j♀, 27 May 1969, ETH, HHH. *Long County*: (15) Goose Run Creek 7.7 mi NW of McIntosh Co line on St Rte 99, 1♂II, 1♀, 2j♂, 4j♀, 28 May 1969, ETH, HHH; (16) flood plain E of Beards Creek, 3.2 mi E of Glennville on St Rte 144, 1♀, 27 May 1969, ETH, HHH; (17) 1.5 mi NW of St Rte 99 and Goose Run Creek, 2♂II, 1♀, 1j♂, 31 Jan 1971, GKW, TR; (18) Goose Run Creek 7.8 mi SE of Ludowici on St Rte 99, 1♂II, 1♀, 2j♂, 2j♀, 31 Jan 1971, GKW, TR; 3♂II, 1♀, 1j♂, 6 Feb 1971, GKW; 3♂II, 3♀, 3j♂, 3j♀, 16 Mar 1971, GKW; 8♂II, 4♀, 18 Dec 1971, GKW. *McIntosh County*: (19) burrows in roadside ditch 10 mi S of Riceboro on US Hwy 17, 1j♂, 1j♀, 7 Sep 1938, HHH; (20) roadside ditch 4.9 mi SE of Eulonia, 1♂II, 1♀, 28 May 1969, ETH, HHH; (21) roadside ditch 3.2 mi NW of Darien on St Rte 251, 1j♂, 2j♀, 28 May 1969, ETH, HHH; (22) Sapelo Island, 2♀, 3j♂, 3j♀, 23 Jun 1964, W. L. Richards; 2♂II, 4♀, 7j♂, 7j♀, 3 Sep 1964, WLR, RWH; 3♀, Aug 1965, T. Linton; 3♂II, 1♀, 2j♂, 1j♀, 10 May 1970, RWH. *Tattnall County*: (23) Watermelon Creek at St Rte 144, 1♂II, 27 May 1969, ETH, HHH; (24) trib to Watermelon Creek about 3 mi W of Glenville on St Rte 144, 1♂II, 27 May 1969, ETH, HHH.

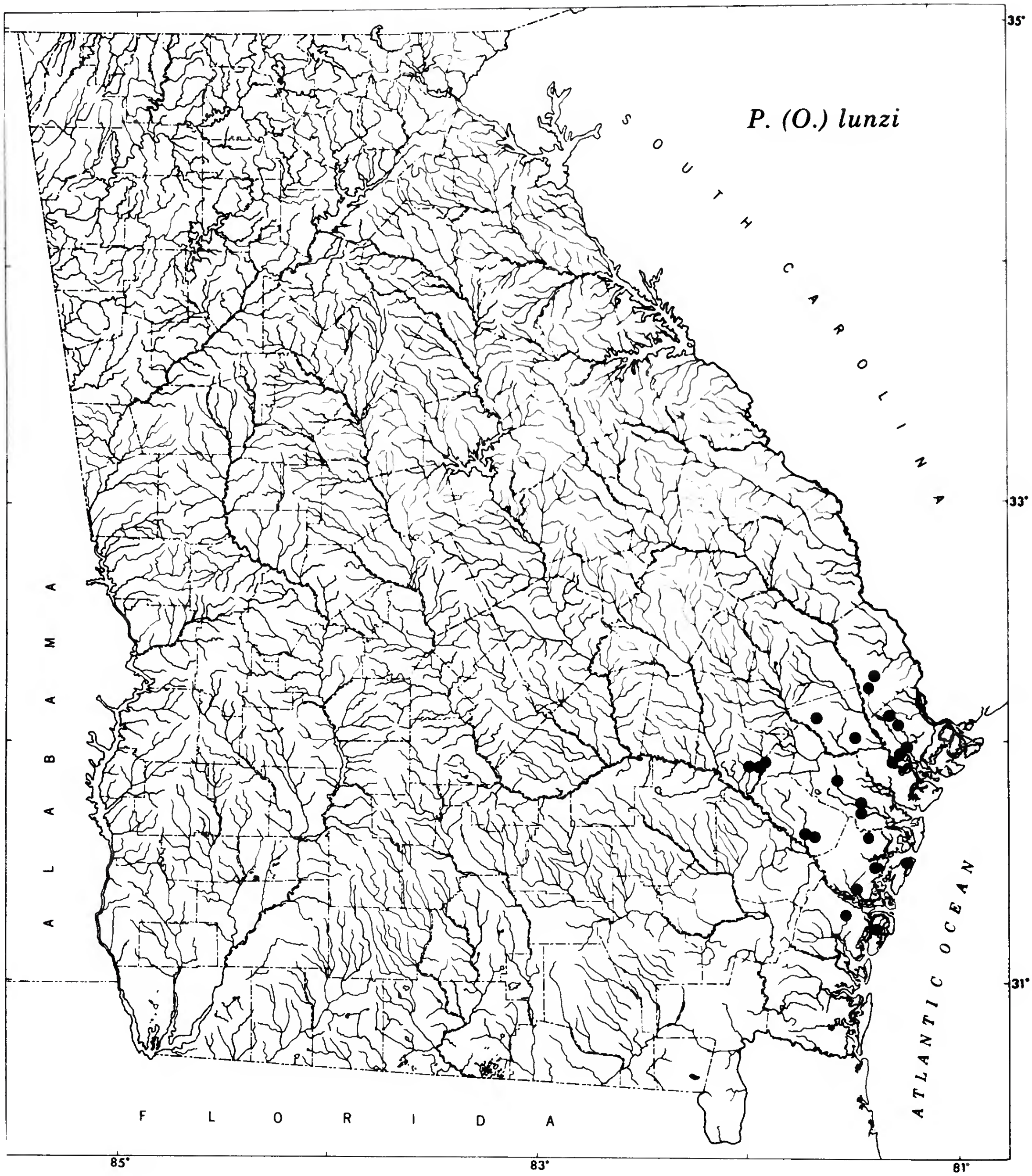


FIGURE 167.—Distribution of *Procambarus (O.) lunzi* in Georgia.

VARIATIONS.—Except for the shape of the rostrum and the proportionate width of the areola, there are few conspicuous variations in this crayfish, and none of them seems to be characteristic in a limited part of the range of the species. The rostrum (Figure 168) varies considerably. In general, those individuals in which it is long and slender and bears marginal spines live in bodies of water that are less likely to become dry. Those animals in which the rostrum is shorter, with strongly tapering margins devoid of marginal spine or tubercles (Figure 168*c*,*d*), have been found in burrows or in bodies of water that fluctuate considerably, the latter depending directly on rainfall for recharge. In dry seasons the water disappears in such habitats and the crayfish are forced to seek water or at least high humidity below the surface of the ground.

That the ranges of variation noted in the ratio of the length to the width of the areola and that of the length of the areola to the total length of the carapace do not appear to be invariably correlated with the type of habitat occupied by the crayfish seems evident in comparing the following limited data obtained from adult specimens collected in four localities.

The ratio of areola length (AL) to areola width (AW) is expressed directly, while that of the areola length to carapace length (CL) is a percentage. Averages are in parentheses following the ranges for the ratios.

Habitat	*Number of specimens*	*AL/AW*		*AL/CL × 100*	
River	2	8.0-13.0	(10.5)	34.1	(34.1)
Creek	6	8.1-10.1	(8.7)	31.2-32.4	(31.7)
Ditch	4	7.8-9.4	(8.6)	33.5-34.2	(33.8)
Pond and ditch	4	6.3-8.0	(7.2)	31.6-33.1	(32.1)

Obviously no conclusions on possible adaptations to the environment can be drawn from these limited data. I should have predicted, however, that the individuals living in streams would have had shorter and broader areolae than do those collected in ponds and ditches. Surprisingly enough, those from the river have the longest and narrowest areolae, those from the creek the shortest and next to the narrowest, and the broadest areolae occur in specimens inhabiting the pond and ditch.

Variations in the annulus ventralis are rather marked but none can be associated with local or regional populations. The features cited in the "Diagnosis" are about all that are uniform among the adults. Likewise, the sternum immediately anterior to the annulus may or may not bear prominences even in specimens from a single locality, and the prominences, if present, are variable in size, ranging from mere vestiges to ones that are perhaps even slightly larger than those illustrated.

SIZE.—The largest specimen from Georgia is a second form male, having a carapace length of 37.0 (postorbital carapace length 28.0) mm. Corresponding lengths of the smallest and largest first form males are 26.2 (21.0) mm and 30.3 (23.3) mm. The only ovigerous female available (see "Life History Notes"), collected in the type-locality, has corresponding lengths of 26.6 (21.2) mm.

LIFE HISTORY NOTES.—First form males have been collected in Georgia during April, May, November, and December and in South Carolina in January, February, May, June, August, and December. The single known ovigerous female

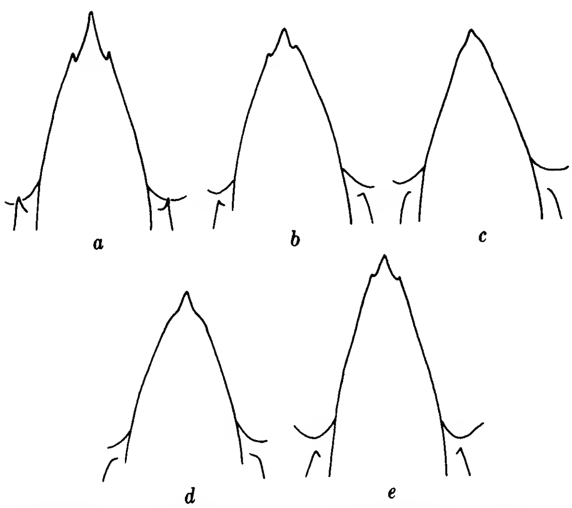


FIGURE 168.—*Procambarus (O.) lunzi*, variations in rostrum in Georgia: *a-d*, Chatham Co; *e*, Bryan Co.

was dug from a simple burrow on 31 August 1941. This specimen (see "Size") carried a complement of 84 eggs, having diameters of 1.5 to 1.6 mm.

Seasonal Data (Georgia and South Carolina)

Sex/stage	*J*	*F*	*M*	*A*	*M*	*J*	*J*	*A*	*S*	*O*	*N*	*D*
♂I	1	1		2	4	1		3			1	2
♂II	19	3	6	1	17			5	2		1	13
♀	19	1	16	8	23	3		8	4		2	21
♂j	25	1	12	6	27	3	1	8	8			11
♀j	16		8	5	34	3		16	8	5		7
♀ ovig								1				

ECOLOGICAL NOTES.—Accompanying the original description of this crayfish was a note that the holotype and allotype "were found in a single burrow about two feet deep, in sandy clay soil," and that "this species appears to be a flatwoods inhabitant" (Hobbs, 1940b:7). Later (1958a:80), in commenting on the ecological distribution of the *seminolae* Subgroup, of which this species was considered a member, he wrote:

> The members of this subgroup frequent streams (usually the very sluggish areas), ponds, lakes, swamps, and roadside ditches. Too, they are found both in permanent and temporary bodies of water provided the watertable recedes not more than a few feet below the surface. They frequently dig simple, straight or gently slanting burrows, but seldom are the chimneys well formed.

Except for the fact that there are no records of the occurrence of this crayfish in lakes, all of these remarks are applicable to what is known about its habitat distribution in Georgia. On the basis of the limited data available, there is no evidence that the quantity of vegetation growing in the water determines the presence or absence of the crayfish, for it has been found in vegetation-choked segments of streams as often as in temporary pools virtually devoid of all macrophytes. In such habitats, frequently, during the day, perhaps as the water level begins to drop, the pools are populated by large numbers of juveniles. The adults, however, are found only in burrows, the openings of some of which are within the pools. Several of the burrows that have been excavated contain pairs—a first form male and a female—and the only known ovigerous female was found in a burrow.

In most of the habitats in which the species has been found in Georgia, the water level fluctuates, even in the streams. On 20 April 1977, Savage Creek at State Route 119 in Bryan County, which usually flows with a sluggish current, had been reduced to a series of disconnected pools, and in them *P. (O.) lunzi* occurred in much larger numbers than did the other species (*P. (H.) pygmaeus*, *P. (O.) litosternum*, and *P. (S.) troglodytes*) that had been found there previously. Neither of the latter two were found on this date.

GEORGIA CRAYFISH ASSOCIATES.—*Procambarus (O.) lunzi* has been collected in the same locality with the following species (the numbers of times they have been found together are noted in parentheses): *Procambarus (H.) advena* (1), *P. (H.) pygmaeus* (4), *P. (L.) barbatus* (8), *P. (O.) enoplosternum* (1), *P. (O.) epicyrtus* (1), *P. (O). litosternum* (1), *P. (O.) seminolae* (1), and *P. (S.) troglodytes* (9).

Procambarus (Ortmannicus) seminolae Hobbs

FIGURES 14*b*, 136*f*, 138*k*, 169–172, 254

Cambarus pubescens.—Hobbs, 1937:154.—Kilby, 1945:84.

Procambarus seminolae Hobbs, 1942b:13, 15, 20, 21, 31, 45, 78, 106, 113, 124, 129, 130, 142–146*, figs. 166–170, 335–346; 1958a:73*, 79, 80*, 83, 85, 86, 88, fig. 11; 1958b:160, 167; 1959:889*; 1962:285*, fig. 36; 1966b:70; 1968b:K-11*, fig. 25 l.—Hoff, 1944:345*, 349*, 356*.—Hart, 1959:201*, 203.—Anonymous, 1967b, tab. 3*.—Hobbs III, 1969: 41.—Cooper, 1969:203–205, fig. 1.—Hart and Hart, 1974: (21, 22, 30, 87, 90)*.—Franz, 1977a:93.—Burgess and Franz, 1978:167.—Wharton, 1978:220*.

Procambarus pubescens.—Penn, 1950b:647, 650.

Procambarus (Ortmannicus) seminolae.—Hobbs, 1972a:9; 1972b:63*, 152, 154*, figs. 21c, 26e, 49e; 1974b:60*, fig. 232.

Procambaris seminolae.—Wharton, 1978:46* [erroneous spelling].

These references are believed to constitute a complete bibliography for the species. Citations to Georgia are noted by asterisks.

SUMMARY OF LITERATURE.—The first reference to this crayfish was that of Hobbs (1937), who misidentified it as *Cambarus pubescens* Faxon (the description of the latter species was based on a second form male and a female). Not until the following year, when I obtained a first form male of Faxon's species, was I certain that the specimens from Florida had been misidentified. In the meantime, Kilby, in the course of his study of the feeding habits of two Florida frogs, asked me to identify specimens of this crayfish. His study was not published until 1945, and unfortunately my erroneous determination was not known to him. Kilby's record of *Rana pipiens sphenocephala* feeding upon this crayfish was repeated by Penn; however, the latter followed Hobbs (1942a) in using the combination *Procambarus pubescens*. Accompanying the original description of *Procambarus (O.) seminolae* (Hobbs, 1942b:145) were records of its occurrence in Appling, Ben Hill, Brooks, Camden, Clinch, Colquitt, Cook, Dooly, Echols, Glynn, Lowndes, and Wayne counties in Georgia, as well as in seven of the more northeastern counties in Florida. These records, together with life history, ecological, and geographical data, constitute most of our knowledge of the species. Hoff (1944), in describing new entocytherid ostracods, reported the occurrence of two previously undescribed species, *Entocythere elliptica* and *E. hobbsi*, associated with this crayfish in Clinch and Colquitt counties, respectively. Hobbs (1958a), discussing the evolutionary history of the *pictus* Group of the genus *Procambarus*, pointed out the affinities of this crayfish with its congeners. New records of its occurrence in the Suwannee River basin were reported by Anonymous (1967b and 1973c), and Hart and Hart (1974) noted its serving as host to one or more of five entocytherids in Atkinson, Brantley, Clinch, Coffee, Crisp, Jeff Davis, and Worth counties. Cooper (1969), in comparing *P. (O.) seminolae* with one of its troglobitic relatives, *P. (O.) lucifugus alachua* (Hobbs, 1940a:402), found that the latter has longer, slenderer chelae and a larger number of aesthetascs on the flagellum of the antennule. Franz (1977a) suggested the possibility that the striped swamp snake *Regina alleni* might well utilize this crayfish as a food item where the range of the snake extends beyond those of *Procambarus (Leconticambarus) alleni* and *P. (O.) fallax*. The remaining references are to keys, brief discussions of relationships, statements of the range of the species, and/or include excerpts of data from earlier contributions.

DIAGNOSIS.—Rostrum with or without marginal spines or tubercles, lacking median carina. Carapace with or with only vestiges of 1 pair of small cervical spines or tubercles. Areola 3.8 to 7.6 (average 5.2) times as long as broad and constituting 26.3 to 32.3 (average 29.7) percent of entire length of carapace (36.4 to 41.9, average 39.1, percent of postorbital carapace length). Antennal peduncle almost always with spine (often adnate) or tubercle on ischium. Lateral half of ventral surface of ischium of third maxilliped lacking conspicuous mat of long plumose setae, although moderately conspicuous pilosity sometimes present on proximal half. Basis of cheliped without mesial spine. Mesial surface of palm of chela of male with mesialmost row of tubercles consisting of 6 to 12 (usually 7 or 8). Male with hooks on ischia of third and fourth pereiopods, in first form male that on third simple and overreaching basioischial articulation and that on fourth usually bituberculate and not reaching articulation but opposed by prominent caudodistally disposed protuberance on distal end of corresponding basis. First pleopods asymmetrical and reaching coxae of third pereiopods (one or more terminal elements of right pleopod often reaching caudal surface of coxa of second pereiopod), distal part of appendage straight and lacking hump on cephalic surface; subapical setae flanking mesial, cephalic, and lateral base of cephalic process; mesial and cephalic processes subspiculiform, former directed distally and caudolaterally, curving around distomesial surface of tumescent part of shaft; cephalic process straight and directed distally, frequently overreaching (rarely falling short of level of tip of central projection) other terminal elements; caudal process absent; caudal knob not clearly delimited from tumescent end of shaft; and corneous central projection consisting of long, narrow, acute, curved blade, with tip directed more caudally than distally. Female with sternum cephalic to

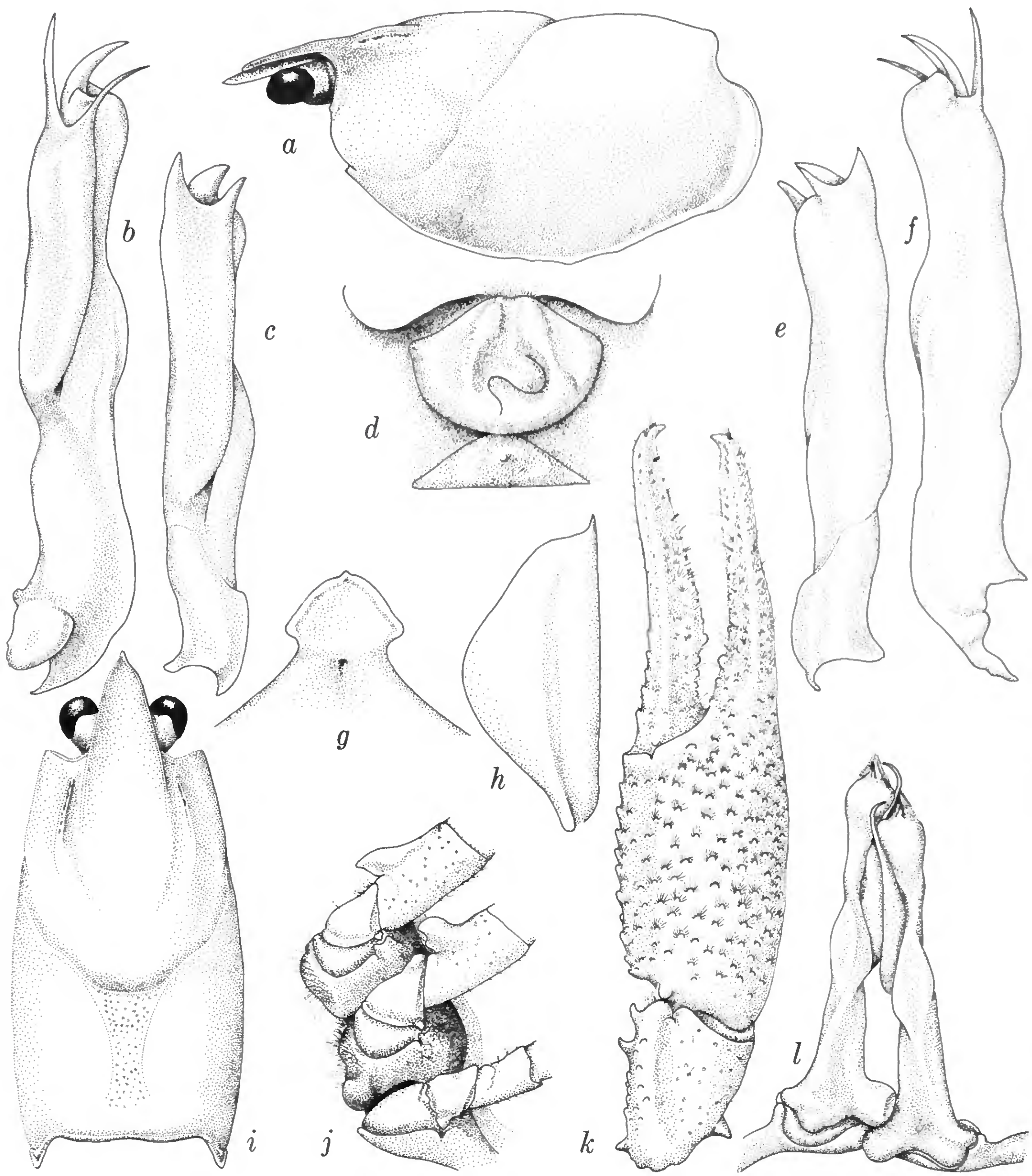


FIGURE 169.—*Procambarus (Ortmannicus) seminolae* from 4 mi S of US Hwy 441 on Hwy 221, Jeff Davis Co (all from first form male except *c*, *e*, from second form male, and *d*, from female): *a*, lateral view of carapace; *b*, *c*, mesial view of first pleopod; *d*, annulus ventralis; *e*, *f*, lateral view of first pleopod; *g*, epistome; *h*, antennal scale; *i*, dorsal view of carapace; *j*, proximal podomeres of third, fourth, and fifth pereiopods; *k*, dorsal view of distal podomeres of cheliped; *l*, caudal view of first pleopods.

annulus ventralis usually unadorned; rarely with 1 to 3 small tubercles on each side, but none projecting over anteroventral surface of annulus; annulus ventralis subovate in outline, greatest width in transverse plane; ventral surface with high lateral walls flanking broad median, often caudally flared, depression; sinus originating in depression near median line slightly anterior to midlength of annulus, and, after coursing caudolaterally across median line and making hairpin turn, continuing across median line before turning back to it and ending short distance anterior to posterior margin of annulus; tongue directed either dextrally or sinistrally. Postannular sclerite at least two-thirds as wide as annulus and either arched ventrally or with median subconical protuberance; first pleopod present.

COLOR NOTES (Figure 136*f*).—Carapace predominately dark brown, fading ventrally to pinkish or grayish tan and bearing broad dorsomedian orange tan stripe extending posteriorly from acumen almost to caudal margin of carapace; rostral margins reddish brown; antennal, anterior part of mandibular, and ventral hepatic regions with cream spots separated by limited dark brown area. Branchiostegites with 2 pairs of black spots dorsolaterally: 1 at level of posterior extremity of cervical groove and other just anterior to junction of caudal ridge and caudal flange; latter pair usually joined by reticulate, very dark transverse band along anterior side of caudal ridge (band sometimes broken by median longitudinal stripe, and sometimes hardly discernible); ventrolateral part of branchiostegites with irregular cream tan splotches. Abdomen with median dorsal dark brown stripe narrowing caudally to base of telson; stripe flanked by paired, narrower pinkish brown ones, and these in turn by darker reddish brown ones extending along bases of pleura; latter pinkish brown, with centrally located pinkish cream spot on each, spots diminishing in size on succeeding segments caudally. Telson with reddish brown, paired cephalolateral spots, transverse band near midlength, and broad band along margin expanding over most of caudal section; uropods with reddish brown keels and broad bands distally. Antennular and antennal peduncles dark grayish tan with reddish markings, flagella reddish brown. Dorsal surface of cheliped distal to ischium olive brown, becoming suffused with orange on propodus and dactyl and studded with very dark brown to black tubercles; ventral surface of more distal podomeres mostly orange. Remaining pereiopods grayish olive to brown and mottled with reddish brown; distal parts of merus and carpus darker than remainder of appendages. Ventral surface of body cream to orange cream.

TYPES.—Holotype, allotype, and "morphotype," USNM 81286 (♂I, ♀, ♂II); paratypes, MCZ, ANSP, USNM.

TYPE-LOCALITY.—Roadside excavation about 9 miles northeast of Gainesville on State Route 24, Alachua County, Florida.

RANGE.—Except for a few localities in Bryan, Montgomery, and Toombs counties, Georgia, this crayfish ranges from the Ocmulgee-Altamaha River southward in the Suwannee, Satilla, and Saint Marys basins to Marion County and lower Saint Johns Basin in Florida. In Georgia, it has been found in tributaries on the lower Ocmulgee, Oconee, Altamaha, and Flint watersheds, and it appears to occur throughout the Satilla, Saint Marys, and Suwannee drainage systems. While occupying virtually all of the Barrier Island Sequence, Okefenokee Basin, and Bacon Terraces districts, it ranges through that part of the Tifton Upland drained by the Suwannee River, the southern part of the Vidalia Upland, and small segments of the Fall Line Hills and Dougherty Plain districts. The occurrence of this crayfish in Bryan County is surprising, and almost certainly the species was introduced there in an area well within the range of its close morphological and ecological ally *P. (O.) lunzi*.

SPECIMENS EXAMINED.—I have examined a total of 1859 specimens, of which 272 were collected in Florida and 1587 in Georgia from the following counties (Figure 170) (the numbers of localities in each are included in parentheses and the only localities detailed here are those along the northern and northwestern extremities of the range): Appling (6), Atkinson (6), Bacon (3), Ben Hill (6), Berrien (3), Brantley (3), Brooks (4), Bryan (1, roadside ditch 5.2 mi W of US Hwy 280 on St Rte 119), Camden (3), Charlton (6), Clinch (13), Coffee (12), Colquitt (6), Cook (3), Crisp (1, drainage ditch 0.9 mi N of Turner Co line on US Hwy 41),

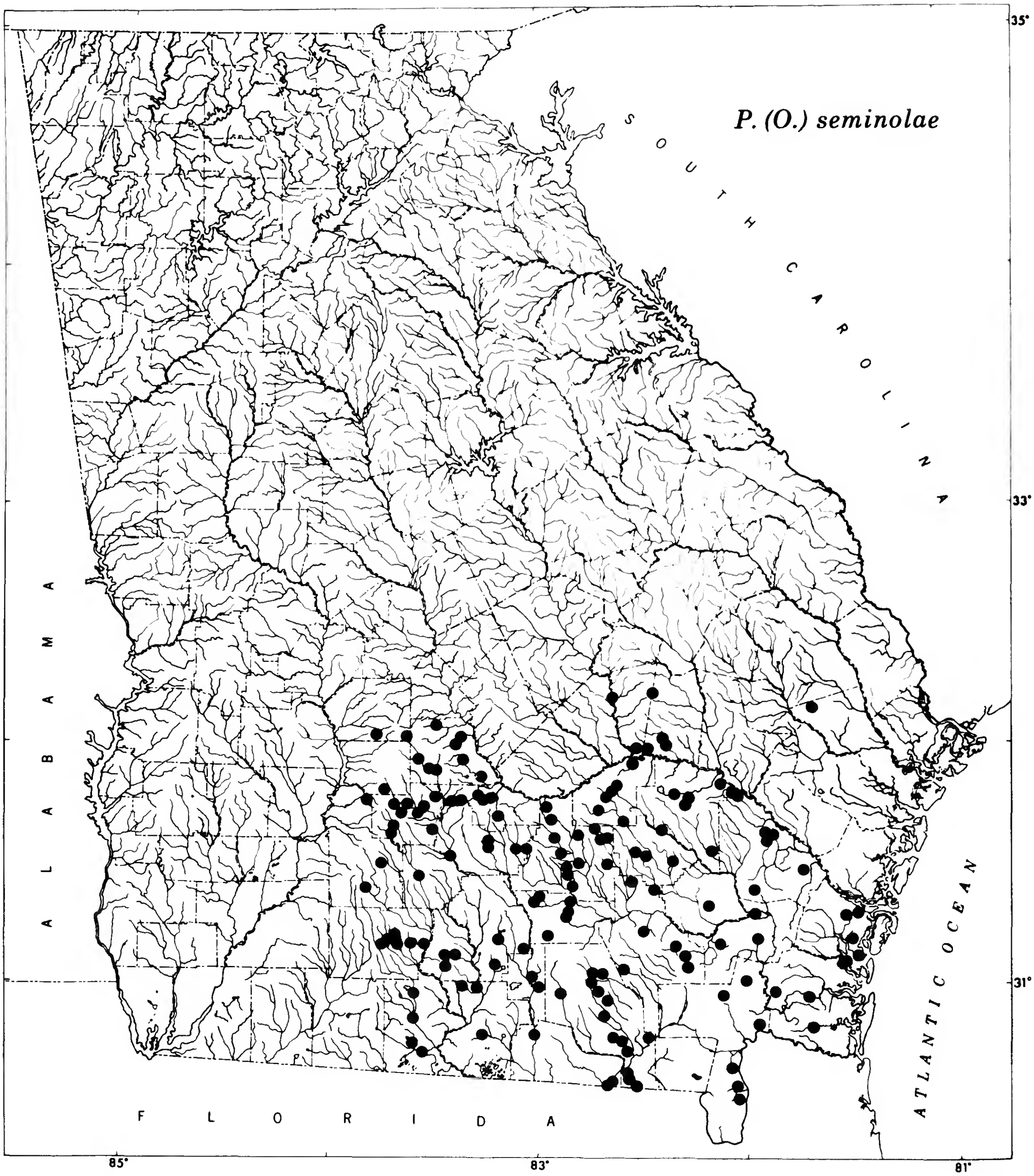


FIGURE 170.—Distribution of *Procambarus (O.) seminolae* in Georgia.

Dooly (2, roadside ditch 2.8 mi N of Crisp Co line on US Hwy 41, and ditch 0.6 mi NW of Wilcox Co line on St Rte 215), Echols (3), Glynn (5), Irwin (4), Jeff Davis (7), Lanier (2), Lowndes (3), Montgomery (3, temporary pool off Oconee River at US Hwy 280), Pierce (1), Tift (3), Toombs (4, Alligator Creek 1.0 mi E of Montgomery Co line on St Rte 130), Turner (9), Ware (7), Wayne (7), Wilcox (8), and Worth (3).

VARIATIONS.—Despite the marked variations that have been observed in members of this species, there is no evidence that any are restricted to a limited part of its range. As in most of the tertiary burrowing crayfishes, the rostrum exhibits a tremendous amount of variation (Figure 171), both in the degree of convergence in the margins and in the ornamentation of the apical region. In some specimens there are well-defined acute marginal spines, delimiting the base of a subspiculiform acumen; in others the marginal spines are represented by low tubercles and the acumen is short with a rounded tip; the extreme suppression of apical features occurs in specimens from burrows in beds of temporary bodies of water; in these crayfish the margins of the rostrum

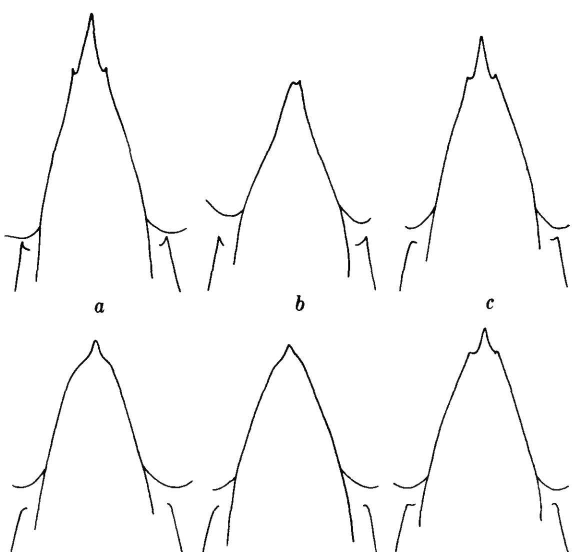


FIGURE 171.—*Procambarus (O.) seminolae*, variations in rostrum: *a*, *b*, Turner Co; *c*, Toombs Co; *d*, *e*, Jeff Davis Co; *f*, Charlton Co.

converge uninterrupted to the tip. The length is also variable, and there is considerable evidence that in at least some individuals the shortening is associated with the burrowing habit of the specimen—those living in temporary bodies of water frequently having shorter rostra, lacking well-developed spines or tubercles. The areola also varies rather strikingly in both relative length and width, but much of the apparent difference in length is a reflection of the much more variable rostral length. Many of the narrower (more than 5.9 times as long as broad) areolae are in the larger individuals, suggesting that the areola may decrease in width with age, but some of the broadest areolae occur among the larger specimens: the broadest areola observed occurs in a second form male, having a carapace length of 38.7 (postorbital carapace length 28.2) mm, and the narrowest (one-half as wide as the broadest) in a first form male, with corresponding lengths of 42.8 (31.6) mm. The cervical spine, which is often well developed in some of the stream-dwelling members of the species, is frequently greatly reduced in size. In some individuals inhabiting temporary ponds or pools, the tuberculate remnant of the spine is scarcely, if at all, larger than other tubercles adjacent to it. The hook on the ischium of the fourth pereiopod of the male is usually rather obviously weakly bituberculate, but in an occasional individual the hook has a broad, truncate distal extremity and rarely appears to be tapering from the base to a rounded tip. In the first pleopod of the first form male, the cephalic process may fall short of (Figure 172*b*,*c*) or overreach (Figure 172*a*,*d*,*e*,*f*) the level of the distal extremity of the central projection. The latter is occasionally much reduced in size (Figure 172*e*), sometimes, at least, probably resulting from regeneration following injury. Furthermore, the dextral pleopod may or may not reach the level of the caudal margin of the coxa of the second pereiopod. In the female, the annulus ventralis always exhibits a broad, median longitudinal trough, flanked by high lateral walls, but the trough may be of nearly uniform width or may be considerably broader posteriorly (thus being somewhat ovoid in shape), and occasionally

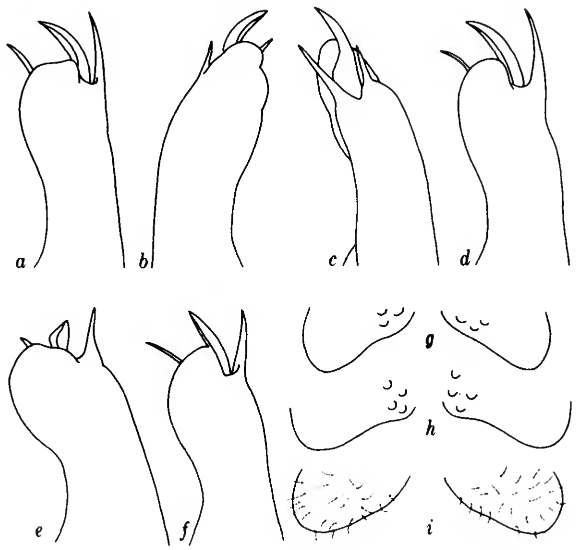


FIGURE 172.—*Procambarus (O.) seminolae*, variations (*a*, *d–f*, lateral view of distal part of left first pleopod of first form male; *b*, lateral view of distal part of right first pleopod of first form male; *c*, mesial view of same; *g–i*, sternum immediately cephalic to annulus ventralis): *a*, typical appendage from Wilcox Co; *b*, *c*, regenerated or abnormal appendage from Wilcox Co; *d*, *e*, typical and regenerated appendages from Ware Co; *f*, typical appendage from Charlton Co; *g*, from Jeff Davis Co; *h*, *i*, from Ware Co.

it may appear to be subcircular. The flanking walls may be comparatively smooth, irregular, or even rarely multituberculate. The sternum immediately anterior to the annulus is most often smooth; occasionally it is studded with short setae (Figure 172*i*) or bears one or more tubercles on each side (Figure 172*g*,*h*). The postannular sclerite, although usually broadly arched, occasionally has a median subconical prominence.

SIZE.—The largest specimen available is a female, with a carapace length of 44.0 (postorbital carapace length 33.8) mm. Corresponding lengths of the smallest and largest first form males are 22.2 (17.2) mm and 42.8 (31.6) mm; those of the smallest ovigerous female, 20.9 (15.6) mm.

LIFE HISTORY NOTES.—In Georgia first form males have been found during every month of the year except February and August, and there are records of their occurring in northern Florida during these two months. Thus, breeding males are probably present in Georgia throughout the year. Ovigerous females and those carrying young have been found there only during September and October. In northern Florida, one ovigerous female was also found in November. In view of the fact that more than 150 adult females were collected (many from burrows) from March through June and none was found carrying eggs or young, one must suppose that ovulation is confined to late summer and early fall. Pairs, consisting of a first form male and female, have been dug from burrows during the spring, summer, and fall, and all of the females carrying eggs or young were taken from burrows.

Listed here are five of the ovigerous females and the numbers and diameters of the eggs carried by them:

Carapace and postorbital carapace lengths (mm)	*Number of eggs*	*Diameter of eggs (mm)*
20.9 (15.6)	146	1.4–1.5
21.5 (15.8)	132	1.4–1.5
22.1 (16.5)	135	1.4–1.5
24.1 (18.0)	93	1.5
25.4 (19.6)	220	1.5–1.6

The two females carrying young had corresponding lengths of 26.0 (20.1) mm and 30.9 (21.9) mm and bore 172 and 188 young, respectively.

Seasonal Data (Georgia and Florida)

Sex/stage	*J*	*F*	*M*	*A*	*M*	*J*	*J*	*A*	*S*	*O*	*N*	*D*	*?*
♂I	1	2	12	23	10	23	3	1	10	16	7	1	1
♂II	6	10	17	79	11	71	4	4	33	72	26	8	2
♀	5	15	28	107	8	93	7	3	40	68	53	17	2
♂j	3		21	123	7	32	4	27	96	105	29	15	1
♀j	8	1	17	120	12	29	1	22	126	105	38	34	1
♀ ovig									3	3	1		
♀ with young									2	1			

ECOLOGICAL NOTES.—This crayfish has a rather broad ecological tolerance as might be suspected, both by its range and by the list of crayfish associates. The latter corroborates the assertion in that such species as *P. (Pe.) spiculifer* are restricted to lotic, well-oxygenated habitats, whereas to have been collected so frequently with *P. (H.) talpoides*, it must have been dug from burrows. Indeed, it has been found in virtually every type of habitat exploited by other crayfishes that occur within its range. The following account of the ecological distribution of *P. (O.) seminolae* in Florida is in concurrence with my observations of its distribution in Georgia.

It has been collected from clear, swift streams, stagnant pools, roadside ditches, flatwoods ponds, and burrows. Even the types of soils in which the burrowing specimens were taken were markedly different.

P. seminolae is most common in the flatwoods, where it inhabits both temporary ponds and ditches. During and after a rainy season it is abundant in the small flatwoods ponds. In a dry season numerous burrows are scattered over the bottom of the dried up ponds and crowded around the roots of trees or stumps which are found in the shallow basins. They often have an opening at the surface of the ground and another at the bottom of the ditch (the latter flooded after rains), but the burrow itself is always relatively simple. Although many of these burrows extend to a depth of two or three feet, it often happens particularly in dry seasons that the water table falls below this depth. At such times *P. seminolae* is able to maintain itself in the moist bottom of the burrow for considerable periods. In the flatwoods ditches burrows are also numerous. The crayfish appear to inhabit the burrows even in seasons of abundant rainfall and leave them only at night. Even then they do not wander far from the mouth of the burrow and at the slightest disturbance scurry back to their holes.

In creeks *P. seminolae* is often abundant; especially is this true for the flatwoods streams of northeastern Florida where members of this species conceal themselves in vegetation or leaf drift. They were taken in small numbers from sand-bottom creeks and small rivers (Hobbs, 1942b:145–146).

Whereas most of the burrows inhabited by members of this species are indeed simple, consisting of a single passageway extending nearly vertically or gently sloping, occasionally they are more complex, bifurcating somewhere along their length. At least some such burrows appear to have resulted from double occupancy, with an ovigerous female occurring in one arm and a first form male in the other. In such burrows containing a lone female, I suspect that a male had occupied one of the galleries, having been trapped there by dry weather but had departed during or following the advent of rain. Like all crayfishes with which I am familiar, that burrow along or in beds of fluctuating temporary pools, this crayfish may plug its chimney as well as the upper part of the exit gallery from below, thus allowing deepening of the tunnel without having to come to the surface.

Georgia Crayfish Associates.—*Procambarus (O.) seminolae* has been collected in the same locality with the following species (the number of times they were found together is noted in parentheses): *Faxonella clypeata* (6), *Procambarus (H.) advena* (2), *P. (H.) caritus* (6), *P. (H.) pygmaeus* (21), *P. (H.) talpoides* (26), *P. (L.) barbatus* (1), *P. (L.) pubischelae deficiens* (12), *P. (L.) p. pubischelae* (25), *P. (O.) a. acutus* (1), *P. (O.) enoplosternum* (2), *P. (O.) fallax* (6), *P. (O.) lunzi* (1), *P. (Pe.) spiculifer* (8), *P. (S.) howellae* (3), and *P. (S.) paeninsulanus* (4).

Subgenus *Pennides*

Subgenus *Cambarus*.—Ortmann, 1905a:97 [in part; not Erichson, 1846:97].

Subgenus *Ortmannicus* Fowler, 1912:341 [in part].

Subgenus *Ortmanmanicus*.—Hobbs, 1942a:342 [in part; erroneous spelling].

Subgenus *Pennides* Hobbs, 1972a:10 [type-species, *Procambarus natchitochae* Penn, 1953:5].

Diagnosis.—Body and eyes pigmented, latter well developed. Rostrum with marginal spines, occasionally (*P. (Pe.) lylei* Fitzpatrick and Hobbs (1971:95) and *P. versutus*) with median carina. Carapace with 2 or more cervical spines. Areola 3 to 5 times as long as broad and constituting 25 to 29 percent of entire length of carapace. Ventral surface of ischium of third maxilliped not obscured by dense mat of long plumose setae. Mesial surface of palm of chela never bearded. First 3 pairs of pereiopods without conspicuous brush of setae extending from basis to merus. Simple hooks on ischia of third and fourth pereiopods. Coxa of fourth pereiopod with bulbous or subangular caudomesial boss. First pleopods reaching coxae of third pereiopods, asymmetrical, contiguous or overlapping basally, with or without broad, somewhat laterally situated, proximomedian lobe,

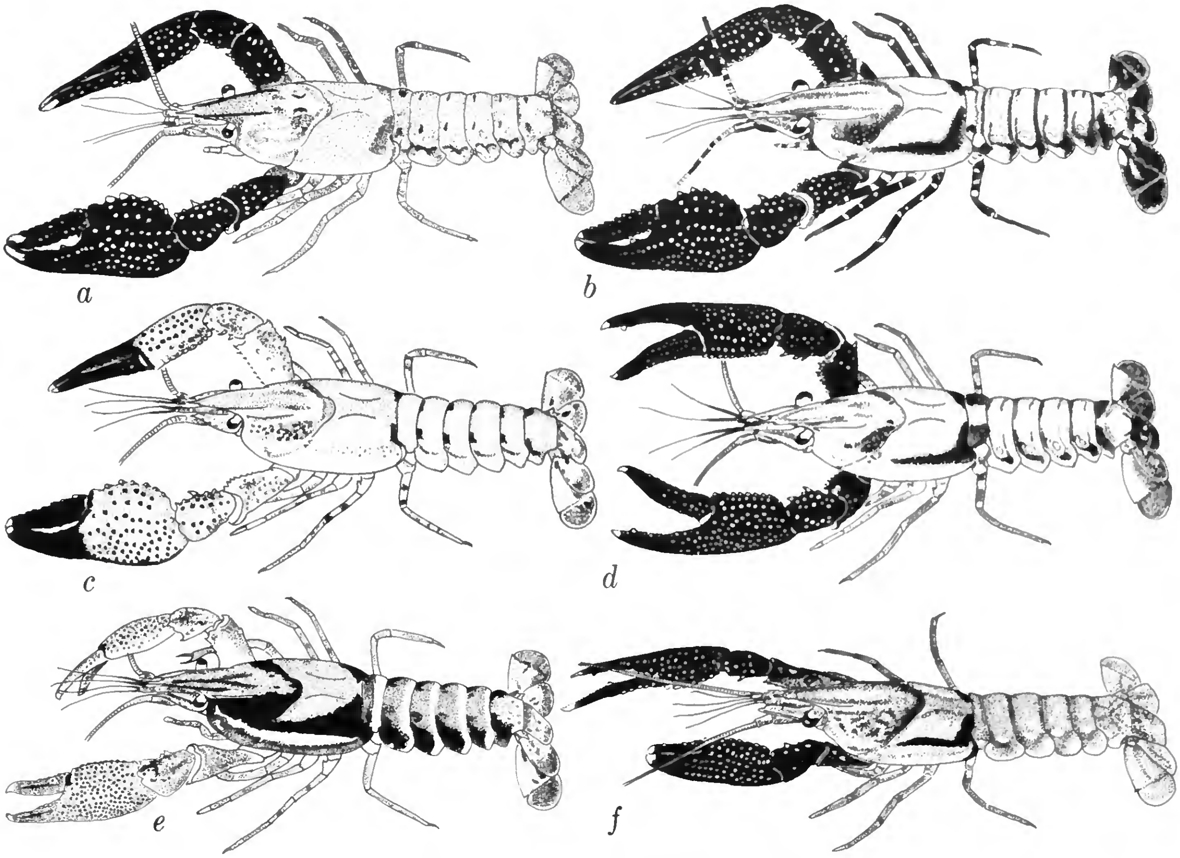


FIGURE 173.—Color patterns of Georgia representatives of subgenus *Pennides: a, Procambarus (Pe.) spiculifer* from Barber Creek 1.3 mi NE of Monroe on US Hwy 78, Oconee Co; *b*, same from Satilla River at US Hwy 441, Coffee Co; *c, P. (Pe.) raneyi* from North Fork of Broad River 4.0 mi SW of Lavonia on St Rte 59, Franklin Co; *d, P. (Pe.) petersi* from Rocky Comfort Creek 1.7 mi N of Gibson on Rte S2126, Glascock Co; *e, P. (Pe.) versutus* from tributary of Patsaliga Creek 1.4 mi S of St Rte 10 on Rte 77, Crenshaw Co, Alabama; *f, P. (Pe.) gibbus* from type-locality.

without proximomesial spur; seldom with shoulder on cephalic surface; subapical setae present, concealing much of central projection in lateral aspect. Terminal elements of first pleopod with caudally to distally directed, slender, usually acute mesial process; mesially to cephalolaterally situated cephalic process (absent in *P. gibbus, P. raneyi, P. spiculifer,* and occasionally in *P. (Pe.) ouachitae* Penn (1956:109)); caudal element variable, typically with caudal knob and process but either sometimes reduced or absent; and central projection subdentiform to almost bladelike. Mesial ramus of uropod with distomedian spine never extending markedly beyond margin of ramus, usually not reaching margin.

RANGE.—From the Edisto River basin in South Carolina to the Red and Trinity drainage systems in Arkansas and Texas. One disjunct species in La Media Luna, San Luis Potosí, Mexico.

RANGE IN GEORGIA.—Throughout most of the state except in tributaries of the Tennessee River (including the Little Tennessee and Hiwassee basins).

GEORGIA SPECIES.—*Procambarus (Pe.) gibbus, P.*

(Pe.) petersi, P. (Pe.) raneyi, P. (Pe.) spiculifer, and *P. (Pe.) versutus.*

HABITAT.—All of the members of the subgenus *Pennides* are inhabitants of streams, and, while most of the 17 species assigned to it are largely restricted to the coastal plain, several are represented in the piedmont and one (*P. spiculifer*) has invaded the Ridge and Valley Province in Georgia. To my knowledge, there are no records of the occurrence of members of this subgenus in lentic habitats. Whereas they occupy shallow burrows within the stream bed or in the banks, except during droughts, the mouths of their lairs are always under water.

REMARKS.—As is true of several species groups of the genus, on the basis of our present knowledge, the females and second form males are difficult or virtually impossible to identify. The color patterns in living or recently preserved specimens of *P. raneyi* (pale chelae with black tubercles) and *P. versutus* (pale longitudinal stripe on carapace) render them readily recognizable, and the presence of a mesial spine on the basis of the cheliped is diagnostic for all members of *P. versutus.* Preserved specimens of *P. petersi* and *P. raneyi* are separable from those of *P. gibbus* and *P. spiculifer* on the basis of the first pleopod in the second form male and by the ornamentation of the sternum immediately anterior to the annulus ventralis in the female. Distinguishing the individuals in each of the two pairs is more difficult; usually the terminal part of the first pleopod will serve to recognize the males, but I have been unable to find any character that is reliable for separating the females of *P. gibbus* from those of *P. spiculifer* or those of *P. petersi* from *P. raneyi.* Fortunately the latter two appear to be allopatric, but the range of *P. spiculifer* surrounds that of *P. gibbus.* Strangely, however, the males of the two have not been collected together, thus presumably neither have the females. *Procambarus spiculifer* and *P. raneyi* occur syntopically in the upper Ocmulgee Basin, and, while the former has not been collected with *P. versutus* in Georgia, the ranges of the two overlap and they have been taken in the same seine haul in Alabama.

Key to Georgia Members of Subgenus *Pennides*

1. Basis of cheliped with spine on mesial surface; rostrum with median carina .... ***versutus***
   Basis of cheliped lacking spine on mesial surface; rostrum without median carina 2
2. First pleopod of first form male with well-developed caudal knob; apex of central projection directed caudodistally; sternum cephalic to annulus ventralis weakly tuberculate and never extending far over much of cephalomedian part of annulus 3
   First pleopod of first form male with caudal knob greatly reduced or absent; apex of central projection directed caudally; sternum cephalic to annulus ventralis strongly tuberculate and extending over at least one-fourth of cephalomedian part of annulus 4
3. First pleopod of first form male with caudodistal extremity of shaft angular or subangular .... ***gibbus***
   First pleopod of first form male with caudodistal part of shaft gently sloping .... ***spiculifer***
4. First pleopod of first form male with caudal process digitiform and central projection broad basally in transverse plane; chela pale with dark tubercles .... ***raneyi***
   First pleopod of first form male with caudal process subtriangular and

central projection not conspicuously broad basally in transverse plane; chela dark with cream-tipped tubercles .... ***petersi***

Procambarus (Pennides) gibbus Hobbs

FIGURES 12*e*, 173*f*, 174, 175, 183*a*, 255

Procambarus gibbus Hobbs, 1969b:337-343, 345-347, figs. 12-23.—Bouchard, 1972:87.

Procambarus (Pennides) gibbus.—Hobbs, 1972a:10; 1972b:70, 150, 154, fig. 55d; 1974b:62, fig. 275.

The above is believed to be a complete bibliography for the species, and, inasmuch as this crayfish is endemic to the state, all references apply to Georgia.

SUMMARY OF LITERATURE.—No information has been added to our knowledge of this crayfish subsequent to its description (Hobbs, 1969b). Originally placed in the "Spiculifer Group" of the genus, it, along with the other members of the group, was assigned to the subgenus *Pennides* by Hobbs (1972a).

DIAGNOSIS.—Rostrum with marginal spines and lacking median carina. Carapace with 2 pairs of cervical spines. Areola 2.8 to 3.5 times as long as broad and constituting 23.8 to 27.8 percent of entire length of carapace (34.0 to 37.3 percent of postorbital carapace length). Antennal peduncle with spine on ischium. Ventral surface of basis and ischium of third maxilliped not densely bearded. Basis of cheliped without spine. Mesial surface of palm of chela bearing prominent row of 5 or 6 tubercles. Male with simple hook on ischium of third pereiopod and weakly bituberculate one on that of fourth. First pleopods asymmetrical and reaching coxae of third pereiopods, cephalic surface without shoulder; subapical setae abundant, many arising from distolateral surface of appendage; mesial process slender and directed caudodistally at angle of approximately 30 degrees to shaft of appendage; cephalic process absent; central projection beaklike, corneous, not extending distally beyond mesial process, but cephalic base situated far proximal to level of base of caudal process, and directed distally even though cephalic margin convex; caudal element consisting of simple, small bladelike corneous process closely applied to caudal margin of central projection, mesial adventitious ridge and caudal knob poorly delimited from much swollen caudolateral end of shaft, although somewhat fingerlike at lateral base of caudal process. Female with sternum cephalic to annulus ventralis not multituberculate, never with more than single pair of lobiform prominences extending caudally and obscuring very little part of annulus; cephalic half of latter with median longitudinal trough and with subplane triangular midcaudal depressed area incised by straight or obliquely directed sinus; first pleopod present. (Modified from Hobbs, 1969b:337.)

COLOR NOTES (Figure 173x).—Dorsum of carapace pale tan, with margins of rostrum and postorbital ridges dark brown. Cephalodorsal areas dark brown, changing to reddish brown in caudal hepatic and gastric areas; ventral hepatic region with pair of dark brown oblique bars on cream tan background. Branchiostegites with usual saddle: horns and caudoventral portion of saddle almost black; bar, very narrow dorsally, connecting broader dorsolateral portions by thin line on extreme caudodorsal margin; area below horns pale tan, fading to cream. Abdominal terga tan to olive, with caudal margins black and each with pair of transverse dorsolateral black bars; first 5 abdominal pleura with longitudinal black stripe at base and narrow border along margins, each with scarlet spot above stripe, and with cream area between stripe and margin. Sixth tergum with caudally emarginate scarlet band cephalically and entire band caudally. Telson bearing pair of black spots in cephalolateral corners of caudal section, otherwise tan to dark brown. Lateral ramus of uropod blackish brown mesially and distally; mesial ramus mostly blackish brown but with light spot proximomesial to midlength. Antennules and antennae dark brown. Chela brownish black, with white to cream-tipped tubercles; tips of fingers scarlet; carpus and distal part of merus blackish tan

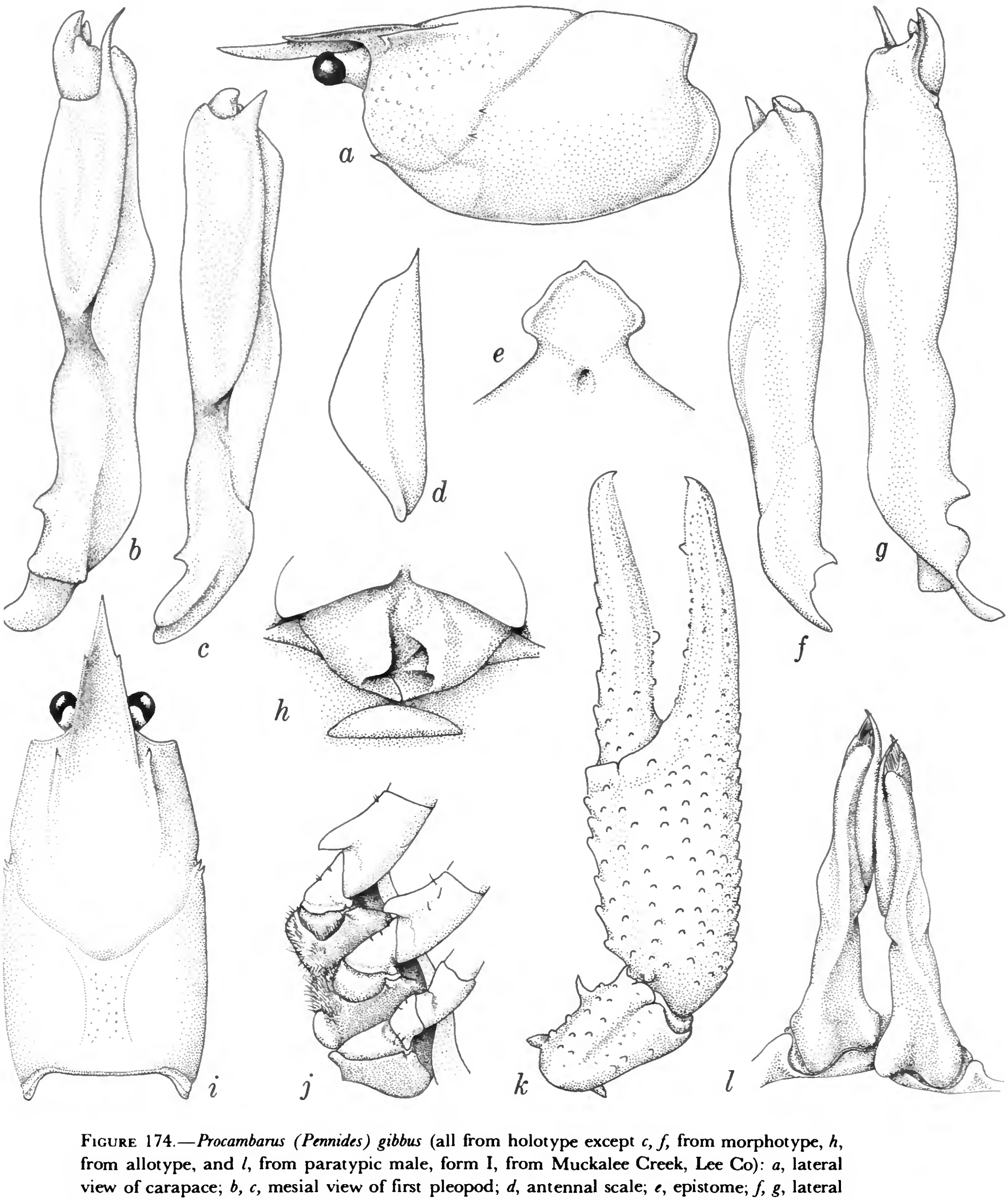


FIGURE 174.—*Procambarus (Pennides) gibbus* (all from holotype except *c, f,* from morphotype, *h,* from allotype, and *l,* from paratypic male, form I, from Muckalee Creek, Lee Co): *a,* lateral view of carapace; *b, c,* mesial view of first pleopod; *d,* antennal scale; *e,* epistome; *f, g,* lateral view of first pleopod; *h,* annulus ventralis; *i,* dorsal view of carapace; *j,* proximal podomeres of third, fourth, and fifth pereiopods; *k,* dorsal view of distal podomeres of cheliped; *l,* caudal view of first pleopods.

dorsally, latter fading proximally through greenish tan to cream tan, with ischium and coxa mostly cream. Remaining pereiopods greenish, with brownish markings above, paler below, fading proximally to cream tan. (Modified from Hobbs, 1969b:341–342.)

TYPES.—Holotype, allotype, and morphotype, USNM 129804, 129803, 129805 (♂I, ♀, ♂II); paratypes, USNM.

TYPE-LOCALITY.—Tributary to Muckalee Creek (Flint River basin), 3.2 miles north of Americus on U.S. Highway 19, Sumter County, Georgia.

RANGE.—Endemic in the Dougherty Plain and Fall Line Hills districts of the Coastal Plain Province of Georgia, where it is confined to the Flint River watershed between Crawford and Baker counties.

GEORGIA SPECIMENS EXAMINED.—I have examined 210 specimens from the following localities. *Baker County*: (1) Coolewahee Creek 7.2 airmi N of Newton on Co Rd, 1♂II, 28 Jan 1972, J. W. Ramsey, collector. *Crawford County*: (2) trib to Flint River 1.5 mi E of Taylor Co line on St Rte 128, 9♂II, 13♀, 1j♂, 6j♀, 17 Apr 1968, G. B. Hobbs, HHH; 4♂II, 1♀, 11j♂, 10j♀, 25 Sep 1972, E. T. Hall, Jr., W. D. Kennedy, HHH. *Lee County*: (3) trib to Muckalee Creek about 7 mi E of Leesburg, 2♂I, 3♂II, 2♀, 4j♂, 1j♀, 11 Aug 1932, E. B. Williamson; (4) trib to Muckalee Creek about 7 mi S of Leesburg, 1♂I, 1♂II, 4♀, 4j♂, 1j♀, 11 Aug 1932, EBW; (5) "Lee County," 1♂I, 1♀, 11 Aug 1932, EBW; (6) spring near Leesburg, 2♂II, 1♀, 1j♂, 29 Nov 1952, P. Heath; (7) Muckalee Creek 6 mi SW of Sumter Co line, 1♀, 15 Apr 1968, GBH, HHH; (8) Muckaloochee Creek in Smithville, 1♂II, 3♀, 12j♂, 14j♀, 14 Apr 1968, GBH, HHH. *Marion County*: (9) Muckalee Creek 2.5 airmi SE of Buena Vista, 1♂II, 2♀, 8j♂, 6j♀, 22 Nov 1976, M. W. Walker, K. W. Martin; (10) trib to Muckalee Creek 3.5 mi SE of Buena Vista, 1♂II, 3♀, 2j♂, 1j♀, 23 Nov 1976, MWW, KWM. *Schley County*: (11) trib to Muckalee Creek 3.8 mi SW of Ellaville on St Rte 153, 1♂II, 2♀, 2j♂, 15 Apr 1968, GBH, HHH. *Sumter County*: (12) type-locality, 1♂I, 2♂II, 4♀, 11j♂, 25j♀, 15 Apr 1968, GBH, HHH; 5♂II, 7♀, 4j♂, 2j♀, 26 Mar 1952, E. C. Raney; (13) trib to Muckalee Creek 5 airmi ESE of Friendship on Co Rd, 1♂II, 1♀, 1j♂, 1j♀, 14 Apr 1972, D. D. Martin, F. L. Martin.

VARIATIONS.—

Among the few variations noted, none of which are associated with a restricted portion of the range, are occasional cephalolateral tubercles on the epistome, telson with one or two spines in caudolateral corner of cephalic section, inner margin of palm of chela with five or six tubercles, upper distal surface of merus of cheliped with two or three spines, ischium of cheliped with two to four spines, and hooks on ischia of fourth pereiopods in first form male simple or weakly bituberculate (Hobbs, 1969b:342–343).

SIZE.—The largest specimen available is a second form male, having a carapace length of 48.7 (postorbital carapace length 34.0) mm. Corresponding lengths of the smallest and largest first form males are 29.8 (21.4) mm and 37.0 (26.3) mm, respectively, and those of the largest female, 41.4 (27.8) mm.

LIFE HISTORY NOTES.—First form males have been collected in April and August; no ovigerous females nor those carrying young have been found. The variations in size of juvenile specimens collected on 25 September 1973 suggest a prolonged hatching period during the late spring and early summer months.

Seasonal Data

Sex/stage	*J*	*F*	*M*	*A*	*M*	*J*	*J*	*A*	*S*	*O*	*N*	*D*
♂I				1				4				
♂II	1		5	14				4	4		4	
♀			7	24				7	1		5	
♂j			4	28				8	11		10	
♀j			2	46				2	10		8	

ECOLOGICAL NOTES.—There are few ecological data available for this crayfish; however, the few observations I have made in collecting it lead me to believe that its habits do not differ in any obvious way from those of its closest ally, *P. (Pe.) spiculifer*.

GEORGIA CRAYFISH ASSOCIATES.—Collected in one or more localities with *P. (Pe.) gibbus* were the following (the number of times they were found together is noted in parentheses): *Cambarus (D.) latimanus* (2), *C. (L.) diogenes diogenes* (3), *Faxonella clypeata* (2), and *Procambarus (S.) paeninsulanus* (2).

Procambarus (Pennides) petersi, new species

FIGURES 12*b*, 173*d*, 176, 177, 183*b*, 256

Procambarus spiculifer.—Hart and Hart, 1974:21.

The single reference to this crayfish is based on my tentative identification of the host of the

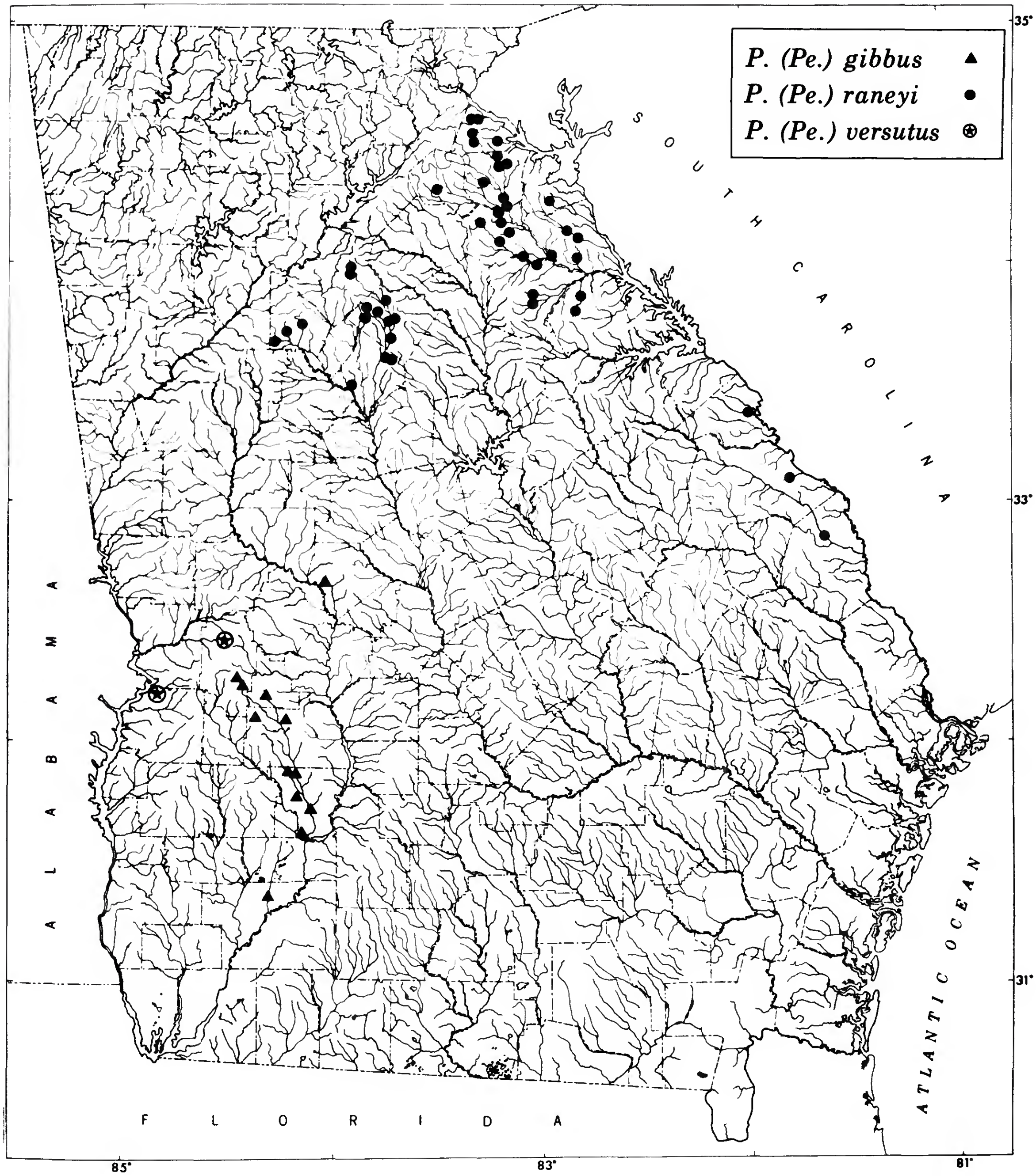


FIGURE 175.—Distribution of *Procambarus (Pe.) gibbus*, *P. (Pe.) raneyi*, and *P. (Pe.) versutus* in Georgia.

entocytheroid ostracod *Ankylocythere ancyla*, which was collected in Burke County, Georgia (see "Georgia Specimens Examined" below).

DIAGNOSIS.—Rostrum with marginal spines and lacking median carina. Carapace with 2 pairs of cervical spines. Areola 2.5 to 3.9 times as long as broad and constituting 22.8 to 26.8 percent of entire length of carapace (35.3 to 38.8 percent of postorbital carapace length). Antennal peduncle with spine on ischium. Ventral surface of basis and ischium of third maxilliped not densely bearded. Basis of cheliped without spine. Mesial surface of palm of chela bearing prominent row of 6 to 9 tubercles. Male with hooks on ischia of third and fourth pereiopods. First pleopods asymmetrical and reaching coxae of third pereiopods, cephalic surface without prominent shoulder; subapical setae sparse and lacking on distolateral surface of appendage; mesial process slender and curved caudodistally at angle of approximately 80 degrees to shaft of appendage; cephalic process small but clearly defined and situated at cephalolateral base of central projection; latter extending distally (not caudodistally) distinctly beyond mesial process; caudal element consisting of small caudal knob lateral to base of corneous, subtriangular caudal process. Female with cephalomedian part of annulus ventralis concealed beneath multi-tuberculate sternum, tubercles of sternum meeting or overlapping along median line; cephalic portion of annulus bearing pair of caudally diverging ridges emerging from beneath tuberculate sternum cephalic to it; sinus originating slightly sinistral to median line between ridges and extending in sinuous curve to caudal margin of annulus; postannular sclerite broader than long, arched cephalically, and flattened caudally; first pleopods present.

HOLOTYPIC MALE, FORM I.—Body (Figure 176*c,h*) subovate, compressed laterally. Abdomen narrower than thorax (19.9 and 23.6 mm). Width of carapace slightly less than height at caudodorsal margin of cervical groove. Areola 2.8 times as long as wide, with 6 to 8 punctations across narrowest part. Cephalic section of carapace almost 3 times as long as areola; length of latter 25.2 percent of entire length of carapace (36.2 percent of postorbital carapace length). Rostrum with dorsal surface punctate, subplane cephalically and concave caudally; margins slightly thickened, convex basally but gently converging anteriorly to well-defined marginal spines at base of long acumen, latter reaching beyond peduncle of antennule. Subrostral ridges moderately well developed but evident in dorsal aspect only along caudodorsal margin of orbit. Postorbital ridges prominent, grooved dorsolaterally and bearing prominent curved spines cephalically. Suborbital angle small but distinct. Branchiostegal spine strong. Carapace punctate dorsally and granulotuberculate laterally with well-defined tubercles on hepatic and cephaloventral branchiostegal regions; 2 strong cervical spines present on each side of carapace; gastric area with prominent pair of oval elevations caudomesial to caudal extremities of postorbital ridges. Abdomen slightly longer than carapace (51.3 and 49.7 mm). Cephalic section of telson with 2 spines in each caudolateral corner. Uropods with 2 well-developed spines on basal podomere; mesial ramus with distinct spine on lateral margin and another premarginal one on median ridge; lateral ramus with usual row of small spines immediately proximal to transverse suture and larger spine at lateral extremity of suture. Cephalic lobe of epistome (Figure 176*g*) subcordiform with cephalomedian prominence and strong spine on cephalosinistral border; margin thickened, ventral surface slightly convex; main body with prominent median fovea and arched epistomal zygoma. Antennule of usual form, with prominent spine arising from near midlength of ventral surface. Antenna extending caudally to midlength of telson, with very strong lateral spine on basis and ventral one on ischium of peduncle; antennal scale (Figure 176*k*) about 2.7 times as long as broad, greatest width proximal to midlength, and broadest part of lamellar area distinctly wider than thickened lateral portion, latter terminating in strong corneous-tipped spine.

Third maxilliped with ventral surface of ischium not conspicuously setose, only those setae

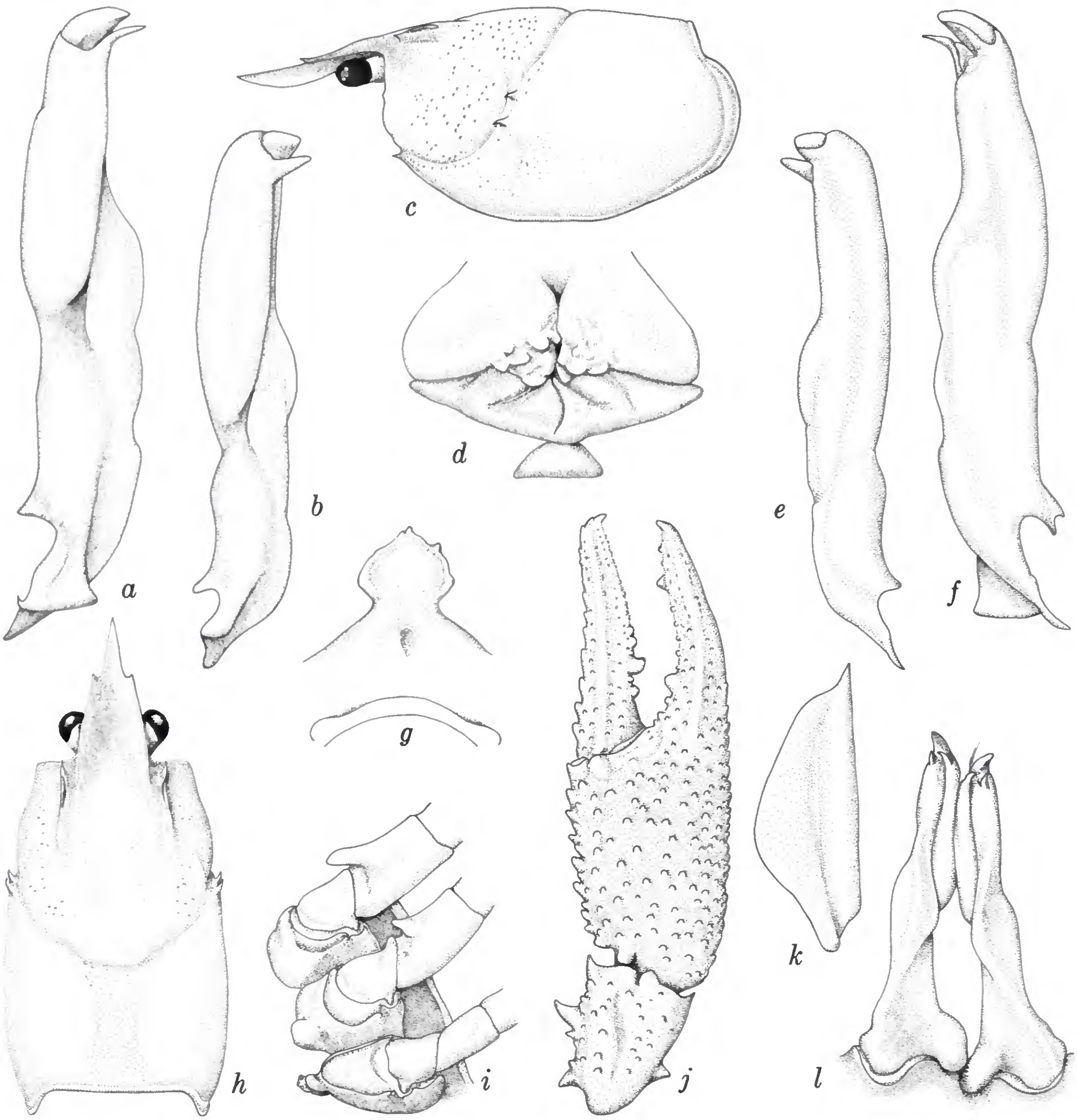


FIGURE 176.—*Procambarus (Pennides) petersi* (*a*, *f*, from topotypic male, form I; *c*, *g–l*, from holotype; *b*, *e*, from morphotype; *d* from allotype): *a*, *b*, mesial view of first pleopod; *c*, lateral view of carapace; *d*, annulus ventralis; *e*, *f*, lateral view of first pleopod; *g*, epistome; *h*, dorsal view of carapace; *i*, proximal podomeres of third, fourth, and fifth pereiopods; *j*, dorsal view of distal podomeres of cheliped; *k*, antennal scale; *l*, caudal view of first pleopods.

bordering crista dentata long, all plumose setae very small.

Right chela (Figure 176*j*) about 3 times as long as broad, subovate in cross section, rather strongly depressed. Mesial surface of palm with row of 9 (left with 10) tubercles subtended dorsally by sublinear series of 7 and ventrally by row of 5; entire palm studded with prominent tubercles. Fixed finger with distinct, rounded median longitudinal elevation dorsally and ventrally, flanked by tubercles along proximal half of finger and setiferous punctations distally; lateral margin of finger with row of tubercles along proximal half and setiferous punctations along distal half; opposable margin with row of 16 tubercles extending from base almost to corneous tip of finger (fourth from base conspicuously larger than others), second more ventral row of 8 tubercles (fourth from base also noticeably larger than others) along distal two-fifths of finger, and row of minute denticles extending from proximalmost large tubercle to base of corneous tip of finger. Dorsal and ventral surfaces of dactyl similar to those of fixed finger; mesial surface with row of tubercles reaching almost to corneous tip of finger, more distal ones with acute tips; opposable surface with row of 17 tubercles (third from base largest), second more ventral row of 5 (first largest), and minute denticles as on fixed finger.

Carpus of right cheliped longer than broad (15.2 and 10.1 mm), tuberculate, with weakest tubercles ventrally and laterally; dorsal surface with well-defined oblique furrow; mesial surface with row of 3 spikelike tubercles, middle one largest; ventrodistal margin with 2 very prominent spiniform tubercles, 1 at base of lateral condyle and other on mesial angle.

Merus of right cheliped more tuberculate distally than proximally; mesial and lateral surfaces sparsely tuberculate; dorsal surface with 2 very prominent spiniform tubercles subdistally, ventral with lateral row of 7 and mesial row of 12 spikelike tubercles (5 and 11 on left cheliped), with additional smaller ones flanking rows, latter converging distally; and distolateral margin with prominent spiniform tubercle. Ischium with mesial row of 3 tubercles (4 on left), 2 of which spikelike.

Hooks on ischia of third and fourth pereiopods (Figure 176*i*), both simple and extending proximally beyond basioischial articulation. Hook on fourth pereiopod opposed by weak tubercle on corresponding basis; coxa of fourth with prominent rounded, vertically disposed caudomesial boss; that on fifth smaller and compressed in longitudinal plane of body.

Sternum between third, fourth, and fifth pereiopods moderately deep and bearing fringe of plumose setae on ventrolateral margins.

First pleopod (Figure 176*a,f,l*) as described in "Diagnosis."

ALLOTYPIC FEMALE.—Differing from holotype, other than in secondary sexual characters, as follows: areola 3 times as long as wide, with 7 punctations across narrowest part; telson with 3 spines in left caudolateral corner; epistome with strong cephalolateral spine on right instead of left side; chela proportionately much shorter (Figure 183*b*; see "Measurements"), with 7 or 8 tubercles along mesial margin of palm, 11 tubercles in dorsal row on opposable margin of fixed finger and 2 in ventral one; dactyl with only single row of 14 tubercles on opposable margin; ventral surface of carpus of cheliped with spine flanking that on distolateral articular condyle and 2 proximal to more distomesial spine; ventral surface of merus of cheliped with lateral row of 3 spikelike tubercles and mesial one of 12; mesial margin of ischium of cheliped with 4 or 5 tubercles (see "Measurements"). Annulus ventralis (Figure 176*d*) as described in "Diagnosis." First pleopod reaching midlength of annulus.

MORPHOTYPIC MALE, FORM II.—Differing from holotype in following respects: epistome with much reduced cephalolateral projections but with small, preapical, cephalomedian tubercle; right chela regenerated but left with mesial margin of palm bearing row of 8 tubercles; opposable margin of fixed finger with upper row of 15 tubercles (fifth from base largest) and lower of 2; opposable margin of dactyl with single row of 14; carpus as in allotype; ischium with 4 tubercles; only 1 of which spikelike. Hooks on ischia of third and fourth pereiopods reduced to small tubercles. First pleopod (Figure 176*b,e*) with no corneous elements: cephalic process obsolete; mesial process less acute than in holotype; central projection directed caudally at approximately 90 degrees; caudal element so reduced as to be hardly discernible and with almost no evidence of caudal process. (See "Measurements.")

COLOR NOTES (Figure 173*d*).—Ground color of carapace and abdomen olive tan. Rostrum dark olive, with narrow olive cream margins and dark area extending onto gastric region (between pale green postorbital ridges) caudally to level of cephalic margins of paired reddish brown mandibular adductor regions. Hepatic area dark brown dorsally, with large pale greenish blue spot delimited cephalically and ventrally by broad cream area abutting linear black cephalic margin of carapace. Branchiostegites with dark greenish brown saddle, consisting of sharply defined lateral horns and caudal transverse bar, latter bearing cephalomedian notch. Terga of first 5 segments with paired dark brown rectangular markings and ventrolateral parts bearing U-shaped dark marking, with scarlet spot between upper section of arms of U and light tan splotches above and below. Pleura uniformly pale tan except for short triangular extension from U-shaped markings dorsally at midlength. Telson, uropods, antennules, and antennae greenish brown, mottled with darker brown; flagella of latter two dark basally, fading to reddish tan distally. Cheliped reddish brown dorsally (lighter ventrally) from base of merus to proximal end of fingers, latter almost black with scarlet tips; all tubercles cream, at least distally; remaining pereiopods distinctly banded from ischium distally, pale bands at articulations and near midlength of merus and propodus. Ventral surface, pleopods, and ventral parts of second through fifth pereiopods cream to bluish cream.

TYPES.—The holotypic male, form I, allotypic female, and morphotypic male, form II, are deposited in the National Museum of Natural History (Smithsonian Institution), numbers 144960, 144961, 144962, respectively. Paratypes consisting of 2♂I, 5♂II, 24♀, 13j♂, and 7j♀ are deposited in the same institution, and 1♂I, 1♂II, and 1♀ in the Rijksmuseum van Natuurlijke Historie, Leiden, Holland.

Measurements (mm)

	Holotype	*Allotype*	*Morphotype*
Carapace			
Height	22.7	20.1	21.0
Width	23.6	20.0	20.0
Entire length	49.7	42.6	45.3
Postorbital length	34.5	29.2	30.8
Areola			
Width	4.5	3.9	3.9
Length	12.5	10.7	11.8
Rostrum			
Width	8.0	7.0	7.3
Length	17.5	15.6	16.8
Chela			
Length of mesial margin of palm	17.5	9.0	9.2
Width of palm	15.5	9.5	7.8
Length of lateral margin	44.7	15.2	25.4
Length of dactyl	23.9	14.0	14.5
Abdomen			
Width	20.0	19.9	18.5
Length	52.2	45.1	46.5

TYPE-LOCALITY.—Rocky Comfort Creek (tributary to the Ogeechee River), 1.7 miles north of Gibson, Glascock County, Georgia, on Route S2126 and 0.4 miles east on Chalker Smith Road. At this locality, the clear stream is some 10 to 15 meters wide and flows with a moderate current over a sandy bottom, with scattered rocks and debris. Shading the marginal areas of the stream are *Salix* sp., *Platanus occidentalis*, *Betula* sp., *Liquidambar styraciflua*, *Alnus rugosa*, and *Quercus* sp. Sharing the stream with this crayfish were *Cambarus (D.) latimanus* and *Procambarus (O.) pubescens.*

RANGE.—A Georgia endemic, this crayfish ranges in the Piedmont and Coastal Plain provinces from the headwaters almost to the tidewater segment of the Ogeechee River basin, but only in a few localities have more than several specimens been collected.

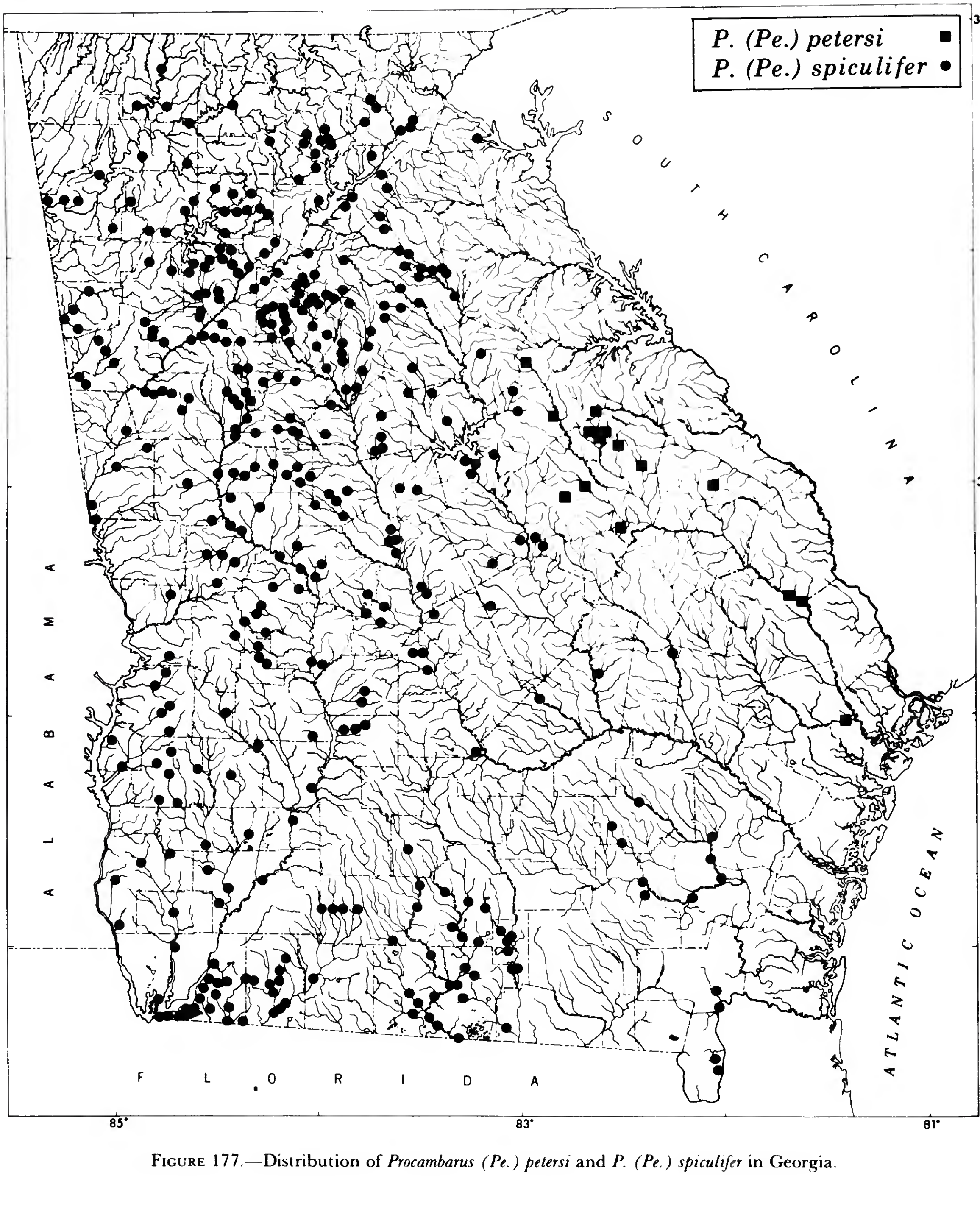


Figure 177.—Distribution of *Procambarus (Pe.) petersi* and *P. (Pe.) spiculifer* in Georgia.

GEORGIA SPECIMENS EXAMINED.—I have examined a total of 91 specimens from the following localities (those lots constituting the type series are noted by asterisks). *Bryan County:* (1) Canoochee River 4.5 mi W of Ways (= Richmond Hill) on St Rte 63, 2 juvenile specimens that have decayed, 18 Oct 1939, HHH, collector. (This record should be confirmed.) *Bulloch County:* (2) Ogeechee River at Williams Landing, 1j♂, 23 Oct 1968, E. T. Hall, Jr.; (3) Ogeechee River at St Rte 24, 1♀, 18 Apr 1977, C. E. Carter, C. W. Hart, Jr., J. E. Pugh, HHH. *Burke County:* (4) Rosemary Creek about 7 mi SW of Waynesboro (Hart and Hart, 1974: 21), 1j♂, 1j♀, 29 Aug 1941, E. H. Blount, Jr., HHH; 1j♂, 1j♀, 1943, EHB, HHH. *Glascock County:* *(5) type-locality, 3♂I, 2♂II, 7♀, 1j♂, 2j♀, 15 Jun 1972, D. J. Peters, JEP, HHH; *(6) Rocky Comfort Creek 1.1 mi E of Gibson on St Rte 80, 1♀, 15 Jun 1972, DJP, JEP, HHH; (7) Deep Creek 2.7 mi E of Mitchell on St Rte 102, 3j♂, 2j♀, 27 Apr 1966, ETH, HHH; *(8) Deep Creek 4.1 mi SE of Gibson on St Rte 80, 1♀, 15 Jun 1972, DJP, JEP, HHH; (9) Joe's Creek 6.3 mi SE of Warren Co line on St Rte 102, 1♀, 2j♂, 1j♀, 1 Oct 1972, G. B. Hobbs, HHH. *Hancock County:* (10) Fulsome Creek 1.4 mi S of Mayfield on St Rte 248, 1♀, 2j♂, 3j♀, 4 Oct 1977, T. A. English, Jr., HHH. *Jefferson County:* (11) Big Creek 6 mi S of Wrens, 1♂II, 2♀, 2j♂, 24 Mar 1950, E. C. Raney; *(12) Duhart Creek 6.5 mi W of Wrens on St Rte 88, 5♀, 5j♂, 1j♀, 15 Jun 1972, DJP, JEP, HHH; *(13) Salter Branch 1.4 mi W of Bartow on St Rte 242, 1♂II, 3♀, 1j♀, 16 Jun 1972, DJP, JEP, HHH. *Taliaferro County:* * (14) North Fork of Ogeechee River 3.6 mi E of Greene Co line on US Hwy 278 and 1.5 mi S on Co Rd, 1♂I, 3♂II, 3♀, 2j♂, 14 Jun 1972, DJP, JEP, HHH; (15) South Fork of Ogeechee River at St Rte 22, 1♂II, 3 Apr 1978, R. J. Dubois, DJP, JEP, HHH. *Warren County:* (16) creek 1.3 mi N of Glascock Co line on St Rte 80, 1j♂, 27 Apr 1966, ETH, HHH. *Washington County:* (17) Williamson Swamp Creek 4.1 mi W of Jefferson Co line on St Rte 88, 1♂II, 6♀, 5j♂, 3j♀, 15 Jun 1972, DJP, JEP, HHH; (18) Hill Creek 5 mi E of Sandersville on St Rte 24, 3j♂, 1j♀, 21 Jul 1971, B. A. Caldwell, M. W. Walker.

VARIATIONS.—None of the differences noted among the specimens available have been associated with a restricted part of the range, and, among those characters that distinguish it from its relatives, none seems worthy of note.

SIZE.—The largest specimen available is a first form male, with a carapace length of 53.2 (postorbital carapace length 35.8) mm. The smallest first form male has corresponding lengths of 45.3 and 30.9 mm.

LIFE HISTORY NOTES.—Almost nothing is known of the life history of this crayfish. The four first form males were collected in June. No ovigerous females or ones carrying young have been found.

Seasonal Data

Sex/stage	*J*	*F*	*M*	*A*	*M*	*J*	*J*	*A*	*S*	*O*	*N*	*D*	*?*
♂I						4							
♂II			1	1		7							
♀			2	1		26				2			
♂j			2	4		13	3	1		5			1
♀j				2		7	1	1		4			1

+ 2j (sex and date not recorded).

ECOLOGICAL NOTES.—There is every reason to believe that this crayfish is an ecological equivalent of its relatives, *Procambarus (Pe.) raneyi* and *P. (Pe.) spiculifer.* (See "Ecological Notes" in the sections devoted to these crayfishes.)

RELATIONSHIPS.—*Procambarus (Pe.) petersi* has its closest affinities with *P. (Pe.) raneyi* and *P. (Pe.) echinatus* Hobbs (1956a:117) and is more distantly related to *P. (Pe.) gibbus* and *P. (Pe.) spiculifer.* These five species form such a closely knit group that after preservation only the males are readily identifiable, and young second form males occasionally cannot be assigned a specific name with certainty. *Procambarus petersi* and *P. echinatus* differ from the others in possessing a cephalic process on the first pleopod. Whereas in the latter species this process is long (its tip is evident when the appendage is viewed mesially), in *P. petersi* it is short and is not evident in mesial aspect of the pleopod.

GEORGIA CRAYFISH ASSOCIATES.—Collected with this crayfish were the following (the number of times they were found together is noted in parentheses): *Cambarus (D.) latimanus* (9), *C. (D.) reflexus* (1), *Faxonella clypeata* (1), *Procambarus (O.) enoplosternum* (1), *P. (O.) pubescens* (8), and *P. (S.) troglodytes* (2).

ETYMOLOGY.—This crayfish is named in honor of my friend and fellow student of entocytherid ostracods, Daniel J. Peters, who has assisted me on many field excursions during the course of my study of the crayfishes of Georgia.

Procambarus (Pennides) raneyi Hobbs

FIGURES 12*c*, 173*c*, 175, 178, 183*c*, 257

Procambarus raneyi Hobbs, 1953b:412–416*, figs. 1–13; 1956a: 117; 1959:885*; 1962:281*, 283, fig. 14; 1968b:K-10*, fig.

21h; 1969b:345*-347, fig. 37.—Penn, 1956:119.—Anonymous, 1969b:(29, 30, 32, 35, 36)*; 1975a:(142, 143, 146, 149)*.—Fitzpatrick and Hobbs, 1971:95*. —Bouchard, 1972:87.—Hart and Hart, 1974:(21, 61, 79, 88, 134)*.—Wharton, 1978:46*, 220*.

Procambarus rayeni.—Anonymous, 1967c, tab. 3* [erroneous spelling].

Procambarus (Pennides) raneyi.—Hobbs, 1972a:10; 1972b:70*, 152*, 154*, fig. 55g; 1974b:63* fig. 277.—Hobbs III, Thorp, and Anderson, 1976:3, 8, 9, 11, 41*-42, figs. 18, 23.

The above is believed to be a complete bibliography for the species. References to Georgia are indicated by asterisks.

Summary of Literature.—Accompanying the description of this crayfish (Hobbs, 1953b:415-416) was a list of eight localities in De Kalb, Elbert, Madison, Oglethorpe, and Stephens counties, Georgia, and four in Abbeville County, South Carolina. Keys for its identification appeared in Hobbs (1959, 1962, 1969b, and 1972b), and a discussion of its relationship to the other members of the *spiculifer* Group (= subgenus *Pennides*) was presented by the same author (1962). Anonymous (1969b) added five new localities in Newton and Walton counties, Georgia, and four additional ones in Franklin, Madison, and Oglethorpe counties were cited by Anonymous (1975a). Fitzpatrick and Hobbs (1971) noted the syntopic occurrence of this crayfish with *P. (Pe.) spiculifer* in Big Flat Creek, a tributary to the Alcovy River in Walton County, Georgia. Two additional localities were cited by Hart and Hart (1974) in Banks and Madison counties, Georgia, where this crayfish served as host to *Ankylocythere ancyla*, *Dactylocythere leptophylax*, *Donnaldsoncythere hiwasseensis* (= *Dn. donnaldsonensis*), *Entocythere elliptica*, and *Uncinocythere simondsi*.

A single locality in Richmond County, Georgia, was cited by Anonymous (1967c). Hobbs III, Thorp, and Anderson (1976), in reporting the occurrence of this crayfish in the Savannah River Plant area in Aiken County, South Carolina, presented a treatment similar to that included here and added several new locality records in Aiken and Barnwell counties, South Carolina.

Diagnosis.—Rostrum with marginal spines and lacking median carina. Carapace with 2 pairs of cervical spines. Areola 2.5 to 4.3 times as long as broad and constituting 25.7 to 30.2 percent of entire length of carapace (36.1 to 41.5 percent of postorbital carapace length). Antennal peduncle with spine on ischium. Ventral surface of basis and ischium of third maxilliped not densely bearded. Basis of cheliped without mesial spine. Mesial surface of palm of chela bearing prominent row of 6 to 9 tubercles. Male with simple hooks on ischia of third and fourth pereiopods and conspicuous bosses on coxae of fourth and fifth pereiopods. First pleopods asymmetrical and reaching coxae of third pereiopods, cephalic surface without prominent shoulder; subapical setae abundant, some arising from distolateral surface of appendage; mesial process slender and directed caudodistally at angle of approximately 80 degrees to shaft of appendage; cephalic process rudimentary or absent; central projection not extending distally beyond mesial process and its cephalic base situated no farther proximally than level of base of caudal process; caudal element consisting of small, compressed, but somewhat digitiform, caudal process; caudal knob absent. Female with cephalomedian part of annulus ventralis concealed beneath tubercles projecting caudally from multituberculate sternum, some tubercles meeting or overlapping along median line; cephalomedian portion of annulus bearing pair of ridges somewhat flanking sinus; first pleopods present.

Color Notes (Figure 173*c*).—Ground color of carapace and abdomen light olive tan, with dark tan to brown markings. Dorsal surface of rostrum and dorsomesial postorbital areas greenish tan. Hepatic and both median and posterior gastric areas mottled with brown. Branchiostegites with paired, transverse, subrectangular, brown bars on caudodorsal margin, and horns of saddle well developed or represented by sparsely arranged, small brown spots not contiguous with bars. Marginal spines on rostrum, postorbital, and cervical spines cream. Abdomen with cephalic 5 terga bearing paired, dark brown rectangular spots dorsolaterally, those on sixth extending laterally onto

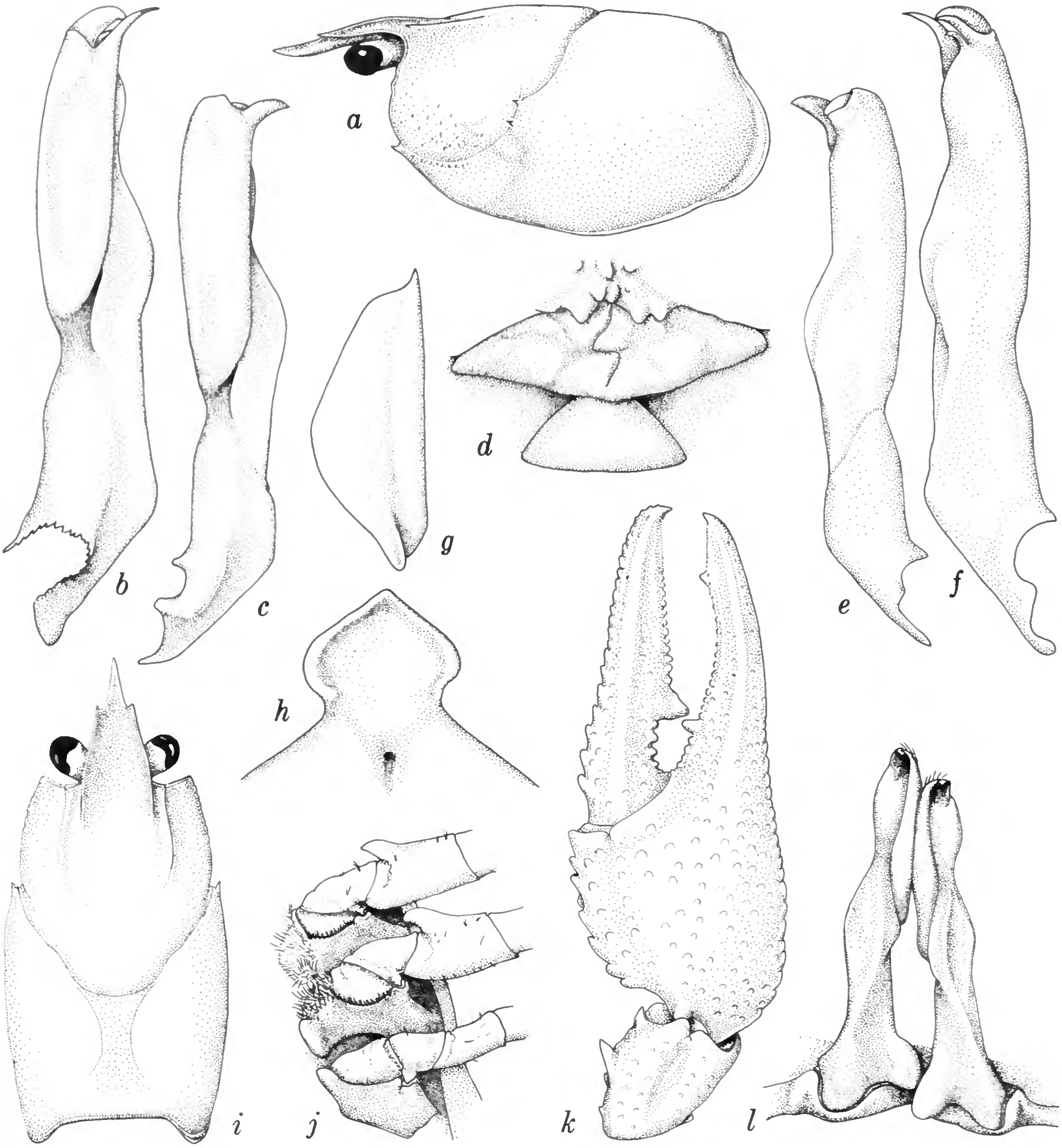


FIGURE 178.—*Procambarus (Pennides) raneyi* (all from holotype except *c*, *e*, from morphotype, *d*, from allotype, and *l*, from paratopotypic male, form I): *a*, lateral view of carapace; *b*, *c*, mesial view of first pleopod; *d*, annulus ventralis; *e*, *f*, lateral view of first pleopod; *g*, antennal scale; *h*, epistome; *i*, dorsal view of carapace; *j*, proximal podomeres of third, fourth, and fifth pereiopods; *k*, dorsal view of distal podomeres of cheliped; *l*, caudal view of first pleopods.

pleura. Pleura of second through fifth segments with bluish brown line at base and vertical band along caudal margin; pleuron of second segment also with cephalic vertical bar. Telson with cephalic region bearing dark transverse band and cephalomedian and cephalolateral brown spots; caudal region mottled dark brown. Uropods mottled, but basal podomere, proximal portion of mesial ramus, lateral margin of lateral ramus, and distal parts of both rami mostly dark brown. Antennule and antenna with mottled peduncles and flagella, latter dark brown basally and fading distally to reddish tan. Antennal scale mottled laterally and along lateral portion of lamellar area. Distal part of merus and carpus of cheliped olive tan, mottled with dark brown, and bearing white-tipped tubercles; dorsal surface of palmar area of propodus yellowish tan and studded with dark brown tubercles, those along mesial margin of palm with white or cream tips; fingers of chela dark brown dorsally and ventrally with lighter tubercles, those on mesial margin of dactyl cream tipped, and tips of both fingers red. Remaining pereiopods mottled olive on cream distal to midlength of merus. Ventral surface of body and bases of appendages bluish cream or cream.

TYPES.—Holotype, allotype, and morphotype, USNM 95124, 95125, 95126 (♂I, ♀, ♂II); paratypes, MCZ, TU, USNM.

TYPE-LOCALITY.—South Fork of the Broad River, 1 mile south of Carlton on the Oglethorpe-Madison county line, Georgia.

RANGE.—The range of *P. (Pe.) raneyi* is discontinuous. It has been collected in the Savannah River drainage system from Oconee to Aiken counties, South Carolina, and from Stephens to Screven counties, Georgia; and, in the upper Ocmulgee drainage system, in De Kalb, Gwinnett, Newton, and Walton counties, Georgia.

SPECIMENS EXAMINED.—I have examined a total of 367 specimens—64 from South Carolina, and 303 from 46 localities in the following counties in Georgia (Figure 175): Banks (1 locality), Burke (1), De Kalb (3), Elbert (4), Franklin (6), Gwinnett (2), Hart (1), Madison (6), Newton (3), Oglethorpe (3), Richmond (1), Screven (1), Stephens (5), Walton (7), and Wilkes (2).

VARIATIONS.—I have discovered no variations that are restricted either to local populations or to those frequenting the two major drainage basins; nor have any variations been encountered that make difficult separating adult male members of this species from their near relatives.

SIZE.—The largest specimen available is a first form male, having a carapace length of 55.1 (postorbital carapace length, 40.3) mm. The length of the largest female is 50.5 (35.5) mm, respectively, of the smallest first form male, 37.1 (26.7) mm, and of the smallest ovigerous female, 42.5 (29.1) mm.

LIFE HISTORY NOTES.—First form males have been collected from March to June and September to November. Only two ovigerous females have been collected, one in Abbeville County, South Carolina, on 22 April 1967 (carapace length 42.6, postorbital carapace length 30.6 mm, carrying 422 eggs 1.9 to 2.2 mm in diameter), and the other in Oconee County, South Carolina, on 24 April 1967 (corresponding lengths of 42.5 and 29.1 mm, carrying 282 eggs of same diameter). Juveniles of approximately the same size have been found in spring, summer, and fall.

Seasonal Data (Georgia and South Carolina)

Sex/stage	*J*	*F*	*M*	*A*	*M*	*J*	*J*	*A*	*S*	*O*	*N*	*D*
♂I			6	6	2	5			3	2	1	
♂II	1		1	23	7	12	5	2	2	2	8	
♀			8	28	3	19	3	4	10	4	3	
♂j	4			26	7	16		6	4	10	3	
♀j	2		2	28	7	27		6	12	11	24	
♀ ovig				2								

ECOLOGICAL NOTES.—This species, like all other members of the subgenus *Pennides*, is confined to lotic habitats. Although occasionally it is encountered in small brooks, it is more typically an inhabitant of rivers and larger creeks, where individuals congregate in debris and in rock-littered areas in which there is a moderate current and the rocks are sufficiently large and stable to afford cover. Whether the streams are clear or silt laden seems to have little influence on the size of the populations inhabiting them. On several occasions, individuals have been dug from simple burrows in the hard clay bed of the stream. While this crayfish has never been observed in the act of excavating a burrow, there is no reason to believe that it occupies the lair that has been constructed by a crayfish belonging to another species with which it is associated. Never has a specimen been obtained or observed in a burrow the mouth of which was situated above the water level of the stream. That the occupation of burrows within the stream bed is a characteristic of the species seems likely in view of the fact that only two ovigerous females and no female carrying young have, to my knowledge, been observed. It is probable that most females secrete themselves in burrows prior to laying their eggs and do not venture into open water until after the young have become independent.

GEORGIA CRAYFISH ASSOCIATES.—Collected with this crayfish were the following (the number of times they have been collected together is noted in parentheses): *Cambarus (C.) bartonii* (5), *C. (D.) latimanus* (35), *C. (D.) reflexus*, (1), *C. (L.) acanthura* (1), *Procambarus (O.) pubescens* (6), *P. (Pe.) spiculifer* (4), and *P. (S.) troglodytes* (1).

Procambarus (Pennides) spiculifer (LeConte)

FIGURES 12*d*, 173*a,b*, 177, 179, 180, 183*d*, 258

Astacus spiculifer LeConte, 1856:401*.—Hagen, 1870:9*, 10.—Hobbs, 1972a:2.

Cambarus spiculifer.—Hagen, 1870:28, 31, 33, 34, 48-50*, 52, 97, 100, 106, 107, pl. I: figs. 59-62, pl. III: fig. 147.—Faxon, 1884:138*; 1885a:8, 12, 17-19, 30, 31, 33*-34, 158*, 167*, 173*, pl. II: fig. 5; 1885b:358*; 1914:412*.—Underwood, 1886:373*.—Hay, 1899b:959*, 962.—Ortmann, 1902:277.—Harris, 1903a:(58, 130, 138, 143, 144, 152)*.—Creaser, 1934:4.—Hobbs, 1937:154; 1942c:56, 57, figs. 15, 16.—Carr, 1940:44.

Cambarus (Cambarus) spiculifer.—Ortmann, 1905a:101, 128*.

Cambarus (Ortmannicus) spiculifer.—Fowler, 1912:341 [by implication].—Lyle, 1937:61* [in part]; 1938:76.

Cambaru spiculifer.—Goodnight, 1941:70, 72, 73 [lapsus calami].

Procambarus spiculifer.—Hobbs, 1942a:340; 1942b:6, 8, 9, 13-15, 20, 21, 32, 66, 91, 93, 103, 106, 113, 116, 118, 119-125*, 127, 128, 145, 152, 153, 155, 162, 166, 170-172, figs. 131-135; 1945a, fig. 9; 1945b:254; 1951:272, 275; 1952a:212; 1952b:172*; 1953a:173; 1953b:412, 415, 416*; 1956c:117; 1959:884*, fig. 31.24; 1962:273, 279, 281*, 283, fig. 15; 1963:8; 1966b:70; 1968a:272*; 1968b:K-11*, fig. 21i, 1,m; 1969b:345*-347, fig. 38; 1972a:2.—Penn, 1946:29; 1950b:647*; 1953:1; 1956:119.—Williams, 1954:822.—Hobbs and Hart, 1959:148*, 151, 159-165*, 167, 168, 170, 171, 174, 184-187, fig. 23.—Hart, 1959:195, 198*, 201*, 203, 204*.—Anonymous, 1967a, tabs. 3*, 6; 1967b, tab. 3*; 1967d, tab. 3; 1967e, tabs. 3*, 6*; 1967f, tab. 3*; 1967g, tab. 3*; 1967h, tab. 3*; 1967i, tab. 3*; 1969a:C-26*; 1969b:33*, 35*, 38*; 1969c:(61, 63-66, 68, 73, 74, 76-80, 85)*; 1970a, photo on cover; 1970b:(174, 191, 192, 196, 198, 219, 220, 223, 225)*; 1971:(154, 155, 168, 170, 171, 178, 179, 181, 184, 188, 190, 192, 195, 201)*; 1972a:64*; 1972b:(10, 12-14)*; 1972d:(79, 81, 82, 85, 86, 88, 90-92, 94, 99, 101)*; 1972f:(171, 173-179, 181, 186, 187, 190-192, 196, 197, 208)*; 1973a:(39, 41, 43, 47, 51, 52, 54, 55, 57, 59)*; 1973c:(54, 56, 58, 60, 62, 65, 67, 71, 73, 78, 80, 83)*; 1973d:44*; 1975b:213*.—Taylor, 1967:742.—Black, 1968:5, 8, 9.—Hobbs III, 1969:45, 62.—Boyce, 1969:1, 66-69, 73-75, 77, 83, 85, 88-90, 92, 93, 95-101.—Chace and Hobbs, 1969:23.—Sullivan and Heard, 1969:304*, 307.—Hobbs and Hall, 1969:286*; 1974:199*, 202, 204, 206*.—Hart and Hart, 1971:107*.—Fitzpatrick and Hobbs, 1971:95.—Bouchard, 1972:87.—Holt, 1973b:93, 94.—Caine, 1974a:490; 1974b:2, 5, 7, 8, 14-16, 19, 20, 22, 25, 26, 28-30, 33, 34, 36-38, 45, 47-49, 51-53, 56, 58, 59, 66, 67, 69, figs. 1a, 4a, 5a.—Hart and Hart, 1974:21*, 27, 31-33*, 44*, 61*, 73*, 87, 88*, 90*, 96*, 128, 129*, 131*, 134*, 136*, 141*.—Wharton, 1978:(36, 37, 46, 220)*.

Procambarus (Pennides) spiculifer.—Hobbs, 1972a:10; 1972b:70*, 152*, 154*, fig. 55e; 1974b:64*, fig. 274.—Hobbs and Hall, 1972:159*.—Villalobos and Hobbs, 1974:9.—Bouchard, 1976c:14.

?*Procambarus* sp.—Anonymous, 1975b:90, 213.

Crayfish.—Anonymous, 1975b:267.

The above is believed to be a nearly, if not entirely, complete bibliography of the species. References to Georgia are indicated by asterisks.

SUMMARY OF LITERATURE PERTAINING TO GEORGIA.—The first localities cited for this crayfish were recorded by Hagen (1870:49), and his description (in Latin) was considerably more complete than was that of LeConte (1856). Faxon (1885a) reported it from localities in the Chattahoochee, Etowah, and Ocmulgee drainage systems, gave measurements, and compared it with several related species. Almost nothing was added to our knowledge of it until Hobbs (1942b), having elevated Ortmann's subgenus *Procambarus* to generic rank (1942a), presented a revised diagnosis of the species, remarked on variations occurring in Florida populations, and included a rather detailed account of its geographical and ecological distribution (pp. 122-125). Its presence in Georgia was noted in the following counties: Baker, Baldwin, Brooks, Bryan, Clarke, Cobb, Colquitt, Decatur, Dougherty, Early, Fulton, Grady, Greene, Hall, Houston, Jones, Lowndes, Mitchell, Oconee, and Sumter. He erroneously recorded it from "Roswell County," which does not exist: Roswell is in Fulton County. Carr (1940) noted that *P. spiculifer* is preyed upon by *Amphiuma tridactylum.* Hobbs and Hart (1959:159) depicted its range in the Apalachicola Basin to include Clay County in addition to those cited by Hobbs (1942b). They also recorded notes on color and on the ecology and life history of the species. Most important in contributing to our knowledge of the range of the species in the state are the stream surveys published anonymously. Numerous locality records included on Figure 177 were cited in them. Most, if not all, of the identifications included in these reports were made or verified by me. Also, the records of this species presented by the Harts (1974) in their entocytherid studies are based largely on collections and host determinations made by me. Taylor (1967) investigated the detection of sound pulses in this crayfish. Sullivan and Heard (1969), in describing the progenetic trematode *Macroderoides progeneticus*, cited *P. spiculifer* as the host of the cercaria. The unpublished thesis of Boyce (1969) contains valuable information on aspects of the ecology of this crayfish as well as on those of *Cambarus (D.) latimanus* in the Yellow River, a headwater tributary of the Ocmulgee River. Caine's (1974b) study of *P. spiculifer* in Florida adds much to our knowledge of its adaptations to an epigean lotic habitat. Hobbs and Hall (1974) summarized observations on its reactions to ash deposits as well as on its tolerance to low oxygen tensions and to high pH values.

DIAGNOSIS.—Rostrum with marginal spines and lacking median carina. Carapace with 2 (very rarely 1) pairs of cervical spines. Areola 2.4 to 4.2 times as long as broad, constituting 24.2 to 29.3 percent of entire length of carapace (35.2 to 41.9 percent of postorbital carapace length). Antennal peduncle usually with spine on ischium. Ventral surface of basis and ischium of third maxilliped not densely bearded. Basis of cheliped without spine. Mesial surface of palm of chela bearing prominent row of 6 to 8 tubercles. Male with hooks on ischia of third and fourth pereiopods. First pleopods asymmetrical and reaching coxae of third pereiopods, cephalic surface without prominent shoulder; subapical setae abundant, many arising from distolateral surface of appendage; mesial process slender and directed caudodistally at angle of approximately 30 degrees to shaft of appendage; cephalic process absent; central projection beaklike, corneous, not extending distally beyond mesial process, but cephalic base situated far proximal to level of base of caudal process; caudal element consisting of (1) caudal process, small corneous blade at caudolateral base of central projection, (2) caudal knob, noncorneous lobe at lateral base of caudal process, and (3) adventitious process, heavy corneous lobe at caudomesial base of central projection. Female with sternum cephalic to annulus ventralis never with more than single pair of lobiform prominences extending caudally and obscuring small segments of annulus; cephalic half of annulus with median longitudinal trough, leading to centrally located depressed area, flanked by paired transverse ridges, anterior slopes of latter gentle, posterior ones much steeper; sinus originating on side of central depression, and, following tilted S-shaped course, ending on caudal wall of annulus; tongue situated in anterior concavity of S-shaped curve, postannular sclerite no less than two-thirds as broad as annulus and about one-half as long; first pleopod present.

MALE, FORM I (The following descriptions are based on specimens from tributaries of the Oconee River in the vicinity of Athens, Clarke County, Georgia).—Body (Figure 179*a,h*) subovate, compressed laterally. Abdomen narrower than thorax (17.1 and 19.2 mm). Width of carapace slightly less than height at caudodorsal margin of cervical groove. Areola 3.3 times as long as wide, with 6 to 8 punctations across narrowest part. Cephalic section of carapace about 2.7 times as long as areola; length of latter 27.6 percent of entire length of carapace (38.2 percent of postorbital carapace length). Rostrum concave and sparsely punctate dorsally; margins slightly thick-

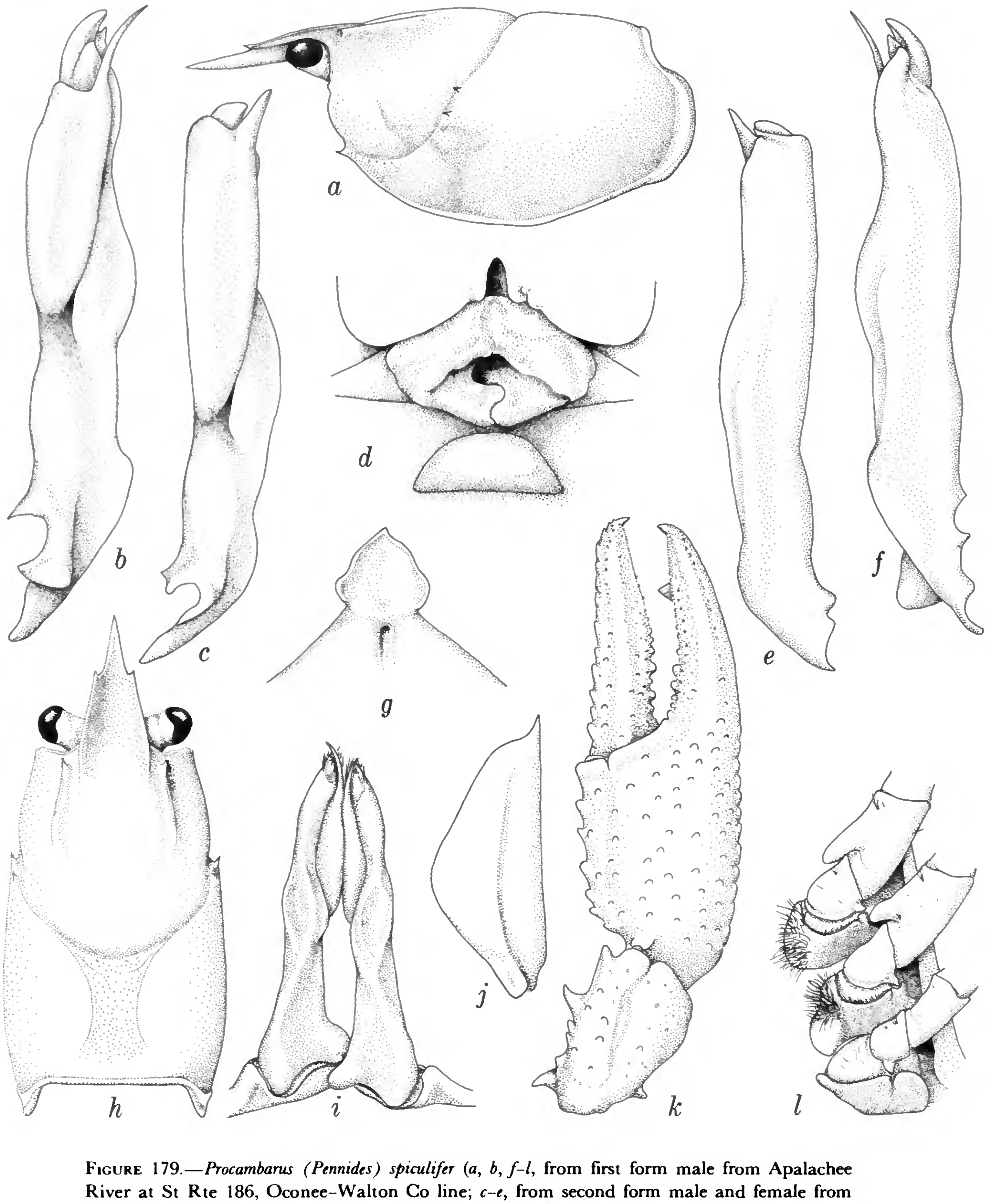


FIGURE 179.—*Procambarus (Pennides) spiculifer* (*a, b, f–l*, from first form male from Apalachee River at St Rte 186, Oconee-Walton Co line; *c–e*, from second form male and female from tributaries of Oconee River in Athens, Clarke Co): *a*, lateral view of carapace; *b, c*, mesial view of first pleopod; *d*, annulus ventralis; *e, f*, lateral view of first pleopod; *g*, epistome; *h*, dorsal view of carapace; *i*, caudal view of first pleopods; *j*, antennal scale; *k*, dorsal view of distal podomeres of cheliped; *l*, proximal podomeres of third, fourth, and fifth pereiopods.

ened, convex basally, and gently converging anteriorly to marginal spines at base of long acumen; latter almost reaching distal end of antennular peduncle. Subrostral ridges rather weak and evident in dorsal view only along basal fourth of rostrum. Postorbital ridges well developed, grooved dorsolaterally, bearing prominent spine cephalically, and forming broad laterally convex arc on dorsolateral part of gastric region. Suborbital angle small but subacute. Branchiostegal spine strong. Carapace punctate dorsally and granulate laterally, with few tubercles in hepatic region and stronger ones flanking cervical groove in mandibular and anteroventral branchiostegal region; 2 strong cervical spines on each side of carapace. Abdomen slightly longer than carapace (43.5 and 41.4 mm); pleura of third through sixth segments truncate ventrally and subangular posteroventrally. Cephalic section of telson with 2 spines in each caudolateral corner. Proximal podomere of uropod with 2 spines; mesial ramus with well-developed distolateral and distomedian spines, latter situated on level slightly proximal to former; lateral ramus with usual row of small fixed spines flanking proximal side of transverse suture and larger lateral spine; prominent movable spine present between 2 lateral fixed ones. Cephalic lobe of epistome (Figure 179*g*) subtriangular, lacking spines cephalolaterally; margins slightly thickened and elevated ventrally, ventral surface slightly convex; main body with conspicuous elongate median fovea and arched epistomal zygoma. Antennule with strong spine slightly proximal to midlength of ventral surface of basal podomere. Antenna broken but extending caudally at least to midlength of abdomen, with strong spine distolaterally on basis and ventrally on ischium; antennal scale (Figure 179*j*) about 2.5 times as long as broad, greatest width proximal to midlength, and broadest part of lamellar area wider than thickened lateral area, latter terminating in strong corneous-tipped spine.

Third maxilliped with ventral surface of ischium not conspicuously setose; long, rather stiff setae restricted to 2 rows of clusters lateral to crista dentata; short plumose setae scattered over ventrolateral half of podomere and forming submarginal row laterally.

Right chela (Figure 179*k*) about 2.8 times as long as broad, subovate in cross section, and somewhat depressed; mesial surface of palm with row of 6 tubercles, flanked dorsolaterally by sublinear series of 5 and ventrally by single (left with 2) tubercle opposite sixth from base in mesial series; almost entire palm studded with prominent tubercles, latter few or absent on mesial and distolateral parts of ventral surface. Fixed finger with low, rounded median longitudinal ridge dorsally and ventrally, dorsal one flanked along proximal third by squamous tubercles and more distally by punctations; opposable margin with row of 15 (17 on left) tubercles (fifth from base slightly larger than fourth and more distal ones, latter decreasing in size distally); distal fourth of finger with more ventral row of tubercles consisting of massive one followed distally by 4 (2 on left) very small ones; single row of minute denticles, interrupted by tubercles, extending from fourth tubercle from base to distal fourth of finger, where merging with band of denticles, situated between tubercular rows, reaching base of corneous tip of finger; lateral surface of finger with row of tubercles along proximal two-fifths diminishing in size distally, and giving way to row of setiferous punctations along distal three-fifths. Dorsal and ventral surfaces of dactyl similar to those of fixed finger; mesial surface with row of tubercles (for most part diminishing in size distally) almost reaching corneous tip of finger, distal 4 with subacute corneous tips; opposable margin with single row of 15 (20 on left) tubercles, second and fourth from base larger than others which, in general, decreasing in size distally; minute denticles arranged similarly to those on fixed finger.

Carpus of right cheliped longer than broad (12.8 and 7.8 mm), tuberculate, sparsely so in lateral half; dorsal surface with oblique furrow; mesial surface with row of 4 tubercles, third from base largest, and distal 2 spikelike; ventrodistal margin with 2 large tubercles, 1 at base of lateral condyle and other on mesial angle; 2 smaller tubercles situated proximal to, and forming ventromesial row with, large mesial marginal tubercle.

Merus of right cheliped tuberculate dorsally, with distal 2 preapical tubercles large and acute; mesial and lateral surfaces punctate, and ventral surface with lateral row of 5 tubercles and mesial one of 12 (left member with 7 and 11, respectively), several of which spikelike; few additional small tubercles flanking rows and 1 large acute one at base of distal ventrolateral articular knob. Ischium with row of 4 tubercles mesially and 1 minute one laterally (latter lacking on left podomere).

Hooks on ischia of third and fourth pereiopods (Figure 179*l*), both simple and extending proximally over distal part of corresponding basis, neither opposed by tubercle on latter. Coxa of fourth pereiopod with prominent, vertically disposed caudomesial boss; that on fifth smaller and compressed in longitudinal plane of body.

Sternum between third, fourth, and fifth pereiopods moderately deep and bearing sparse fringe of setae on ventrolateral margins.

First pleopod (Figure 179*b,f,i*) as described in "Diagnosis."

FEMALE.—Differing from first form male, other than in secondary sexual characters, in following respects: acumen reaching distal end of antennular peduncle; mesial row of tubercles on palm of chela flanked dorsolaterally by row of 4; opposable margin of fixed finger of chela with dorsal and ventral rows of tubercles consisting of 12 and 2, respectively; ventral surface of merus of cheliped with lateral and mesial rows of 4 and 11, and mesial surface of ischium with 3 tubercles. (See "Measurements.") Annulus ventralis (Figure 179*d*) as described in "Diagnosis."

MALE, FORM II.—Differing from first form male, other than in secondary sexual characteristics, in only few minor aspects of cheliped: only 2 tubercles in dorsolateral row, flanking series on mesial margin of palm; opposable surfaces of both fingers of chela with single row of 13 tubercles, and only most proximal member of opposable ventral row on fixed finger present; ventrolateral row of tubercles on merus of cheliped consisting of 6. (See "Measurements.") Hooks on ischia of third and fourth pereiopods greatly reduced, neither reaching basioischial articulation; bosses on coxae of fourth and fifth pereiopods also reduced in size but clearly defined. First pleopod (Figure 179*c,e*) markedly similar to that of first form male but with only slight trace of caudal process; remaining terminal elements shortene and inflated, none corneous.

COLOR NOTES (Figure 173*a,b*).—It is probable that in all populations of this crayfish two color phases exist in the basic pattern: tan with markings in various shades of brown, and bluish green with greenish or bluish black to black markings. The tan and brown phase of the pattern typical of the Oconee River watershed is described here.

Carapace mostly pale tan with rostral margins, cephalolateral and caudal margins of carapace, and postorbital ridges dark brown; hepatic area slightly darker than branchiostegite. Mandibular adductor region marked by conspicuous reticulate dark brown patches, and paired dorsal longitudinal stripes extending from rostrum almost to cervical groove, stripes becoming almost black before merging with caudomesial margins of reticulate patches. Areola straw brown, darker along branchiocardiac grooves. Primitive dark saddle of thoracic area represented by paired lateral segments of bar, separated by span slightly less than width of areola, and very small cephalic extremities of horns (sometimes absent) situated immediately dorsal to cervical spines (Figure 173*a*). Abdomen with caudal margins of terga bearing narrow dark brown band and cephalolateral surface of each with conspicuous almost black spot: that on first largest, those on succeeding segments smaller, subequal in size, and transversely linear. Scarlet spot present laterally above base of pleura of second through fifth segments, sixth with more elaborate scarlet markings. Pleura with very narrow dark brown cephalic margin, cephalic half cream and caudal half straw brown, each pleuron separated from respective tergum by broadly V-shaped brown to blackish mark. Cephalic section of telson with subtriangular dark reddish brown area, apex directed caudally, and caudolateral angles and entire caudal section dark brown. Proximal podomere of uropod pale tan, with dark brown cephalolateral margin; mesial ramus mostly dark; lateral ramus with lateral margin, mesial part of proximal section, and all of distal section dark brown; remainder of ramus pale tan. Antennular and antennal peduncle mottled, darker laterally and distally; flagella dark brown; antennal scale with lateral margin dark straw brown, lamella mostly pale tan but with brown markings adjacent to thickened lateral part. Cheliped with dorsal portions of merus through palmar area of propodus dark reddish brown with cream-colored tubercles, both fingers black, with distal sixth to tenth scarlet. Remaining pereiopods banded, with ischium and merus darker than other podomeres, all fading ventrally.

Individuals in Flint River at Flat Shoals on Meriwether-Pike county line consistently exhibiting bluish ground color but otherwise similar to those from Oconee and Ocmulgee (Altamaha) basins.

Coloration in populations frequenting Coosa, lower Flint, and Tallapoosa river basins differing from that in Oconee drainage system chiefly in development of saddle on carapace: horns complete, extending from caudal margin of carapace to cervical groove, and bar broken by gap distinctly narrower than areola. Populations frequenting Satilla and Saint Marys watersheds also exhibiting complete horns of saddle, and gap in horizontal bar even narrower than that in individuals inhabiting lower Flint and Tallapoosa basins.

TYPES.—Syntypes, ANSP 316 (♂II), MCZ 172 (2♂I, 4♀, 2j♂, 3j♀), MCZ 3376 (♂I), USNM 4962 (specimen decayed), MHNP (♂I, ♀).

TYPE-LOCALITY.—"Georgia superiore" (LeConte, 1856:401); restricted by Faxon (1914:412) to Athens, Clarke County, Georgia.

RANGE.—From the Altamaha River basin in Georgia, southward to the Saint Marys and Suwannee basins in Florida, northwestward to and including most of the Alabama River basin in Georgia (Coosa and Tallapoosa drainages), and throughout southern and eastern Alabama and the Florida panhandle. In Georgia it has been collected in all of the major drainage basins except the Ogeechee, Chattooga, and tributaries of the Tennessee River. In the Savannah Basin it has been found in only one locality, Little Eastanollee Creek at Yow Hill Road, north of Avalon, Stephens County, where it was collected with *P. (Pe.) raneyi*.

Measurements (mm)

	Male, form I	*Female*	*Male, form II*
Carapace			
Height	19.3	19.4	19.5
Width	19.2	19.5	19.6
Entire length	41.4	42.6	43.2
Postorbital length	29.6	30.4	32.0
Areola			
Width	3.4	4.6	4.0
Length	11.3	11.5	12.3
Rostrum			
Width	6.6	6.8	7.6
Length	13.2	14.5	13.0
Chela			missing
Length of mesial margin of palm	13.4	10.0	-
Width of palm	13.3	9.3	-
Length of lateral margin	37.1	28.3	-
Length of dactyl	19.6	15.3	-
Abdomen			
Width	17.1	18.9	17.4
Length	43.5	42.2	46.7

GEORGIA SPECIMENS EXAMINED.—I have examined no fewer than 2824 specimens from some 375 localities (Figure 177) in the majority of the counties of the state drained by the Altamaha, Satilla, Saint Marys, Suwannee, Ochlockonee, Flint, Chattahoochee, Tallapoosa, and Coosa rivers.

VARIATIONS.—The ranges of variation in most of the nonsecondary sexual characters in four of the five members of the Georgia representatives of the subgenus *Pennides* overlap to such an extent that species recognition rests almost solely on secondary sexual features. Despite the fact that *P. (Pe.) spiculifer* is so distinctive that the first form male would be unlikely to be confused with that of any other species, the same cannot be said of the second form male and female. Usually the central projection of the second form male is not bent nearly so strongly caudally as that in *P. (Pe.) raneyi* and *P. (Pe.) petersi*, but occasionally there is little difference between the pleopods of the three. It is also difficult to separate the young males of *P. (Pe.) spiculifer* from those of *P. (Pe.) gibbus* for there is considerable variation in the development of the caudodistal portion of the shaft of the first pleopod in the latter; generally, after some differentiation is observed in the terminal portion of the pleopod, its prominence in *P. (Pe.) gibbus* increases with successive molts until the male reaches the first form, at which time its subangular form is clearly distinct from the sloping caudodistal extremity of the shaft in *P. (Pe.) spiculifer*.

The variations in the annulus ventralis and the sternum immediately cephalic to it are so markedly similar in some individuals of *P. (Pe.) spiculifer* and *P. (Pe.) gibbus* that, without the associated males, I am unable to distinguish between the female members of the two species.

Among the conspicuous variations that seem not to be restricted to a limited portion of the range are differences in the hooks on the ischia of the third and fourth pairs of pereiopods in the first form male. In many specimens, the hooks on both pereiopods are simple, with slightly flattened and gently bent distal extremities. In others, the distal ends of the hooks on the fourth pereiopods are weakly or distinctly bituberculate, and in an occasional specimen the hooks on the third pereiopods are feebly bituberculate. The orbit in some individuals (many from the Suwannee drainage system) is less concave caudally than in the majority of available specimens. Some of the variations observed in proportional lengths of sections of the carapace seem to be associated with injury. With the long, even though strong, rostral acumen, often the distalmost portion is broken, and unfortunately there are no data to indicate its rate or degree of regeneration. Surprisingly, however, the range of variation of the ratio of the areola length to carapace length, which includes the rostrum, is narrower than that of the areola length to postorbital carapace length.

The average length of the rostrum, while not markedly different in the several watersheds, is apparently longer in specimens from the Satilla, Saint Marys, and Suwannee drainage systems, comprising 29.9 to 35.5 (average 32.0) percent of the total length of the carapace. Because an accurate length of the rostrum (measured classically from its apex to the cephalic end of the postorbital ridges, exclusive of the apical tubercle or spine of the latter) is somewhat subjective, the length employed here is that from the apex of the acumen to the caudal margin of the orbit. The corresponding percentage range in the other river systems in the state is from 23.4 to 33.6 (average 28.6) percent: Chattahoochee 25.6 to 33.2 (28.1); Coosa 23.4 to 29.2 (27.1); Flint 25.8 to 33.2 (29.0); Ochlockonee 27.3 to 33.0 (29.9); Ocmulgee 26.4 to 31.4 (28.2); and Oconee 26.0 to 33.6 (29.1).

The areola length as expressed by the ratio of its length to that of the postorbital carapace length times 100 ranges from 34.4 in the Flint and Chattahoochee basins to 41.6 in the Satilla Basin, the greatest range of variation occurring in the Flint (34.4 to 40.3) but with no indication of a cline occurring within the river system. Only in the Satilla does the length of the areola sometimes exceed 40.5 percent of the postorbital carapace length, but even there it drops to 37.5 percent. In all other drainage basins, the range of variation occurs within that cited for the Flint.

The typical form of *P. (Pe.) spiculifer* is, of course, that found in the Oconee Basin, and the first pleopod of the male from this river system (Figure 180*a*) is characterized by a slightly curved mesial process that extends a short distance distal to the tip of the central projection, which is also moderately curved caudodistally; the caudal process is variable in size but comparatively large; the adventitious process is conspicuously long. The pleopod that typifies individuals from the Ocmulgee (Figure 180*b*) and Flint (Figure 180*f*) drainages shows few consistent variations differing from the Oconee type, although frequently

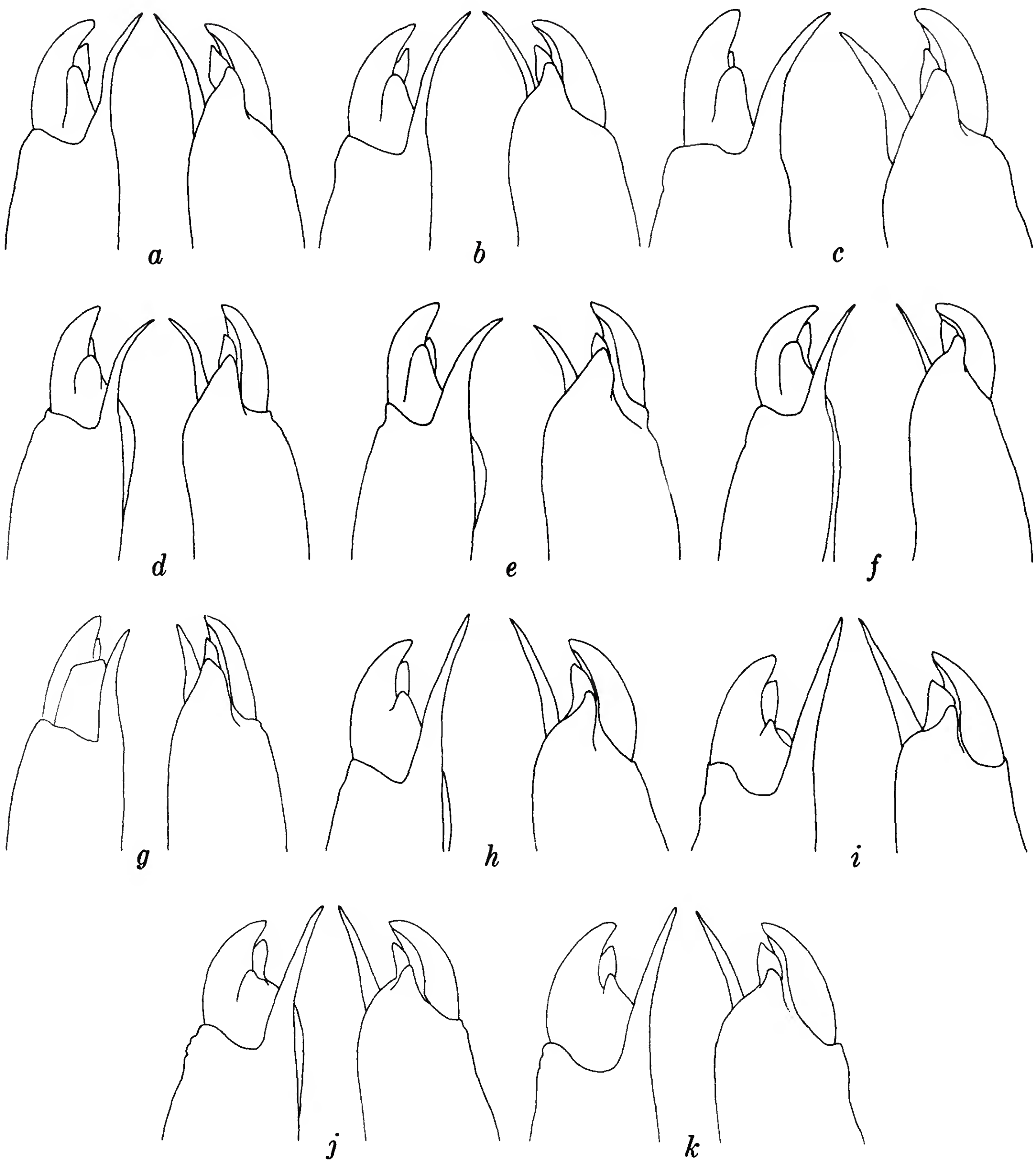


FIGURE 180.—*Procambarus (Pe.) spiculifer*, variations in mesial and lateral views of distal part of first pleopod of first form male: *a*, upper Oconee Basin, Greene Co; *b*, lower Ocmulgee Basin, Bleckley Co; *c*, middle Satilla Basin, Bacon Co; *d*, Suwannee Basin, Cook Co; *e*, Ochlockonee Basin, Grady Co; *f*, lower middle Flint Basin, Lee Co; *g*, lower Chattahoochee Basin, Early Co; *h*, upper middle Chattahoochee Basin, Coweta Co; *i*, upper Chattahoochee Basin, Habersham Co; *j*, Tallapoosa Basin, Haralson Co; *k*, Coosa Basin, Gilmer Co.

the central projection is more strongly recurved.

The most distinctive pleopod type is that of specimens from the upper Chattahoochee (Figure 180*i*), in which the adventitious process is much less conspicuous than that in the Oconee type, and the proportionately shorter central projection results in the mesial process extending distally much beyond the tip of the projection. In the lower Chattahoochee (Figure 180*g*), the pleopod resembles the Oconee type much more closely than do pleopods from specimens in either the upper or middle segments (Figure 180*h*) of the Chattahoochee. Strongly resembling the pleopod of specimens from the upper Chattahoochee are those of populations from the Coosa (Figure 180*k*) and Tallapoosa (Figure 180*j*) basins, both in the small adventitious process and short central projection. The pleopods that typify individuals from the Suwannee (Figure 180*d*) and Satilla (Figure 180*c*) drainage systems resemble the Oconee type more closely than those typical of the Chattahoochee, Coosa, or Tallapoosa.

The much more variable annulus ventralis and sternum immediately cephalic to it show some degree of consistency in certain portions of the range. The basic form of the annulus ventralis consists of a subelliptical, transversely arched (ventrally) sclerite, with a shallow cephalomedian depression and a broad inverted U- or V-shaped ventromedian excavation in the caudal half or two-thirds. The excavation bears the sinuous sinus and often obscure fossa. In the Oconee, Ocmulgee, and Ochlockonee drainages, the caudal margin of the annulus usually bears a distinct median prominence projecting caudally; elsewhere this prominence has not been observed to be so well developed. In some specimens from the lower Chattahoochee, the cephalomedian depression is lacking and the subtriangular excavation extends far cephalically, forming a cavernous space beneath the arched cephalic and cephalolateral portions of the annulus. The depth of the hollowed space increases, at least in part, with the size of the animal, but only in the lower Chattahoochee, Suwannee, and Satilla drainage systems do the concavities become so extreme, and in the latter two systems the cephalomedian depression is also maintained. In the Suwannee, Satilla, and Saint Marys basins, a pair of knoblike bosses flank the median line of the annulus cephalically, appearing to articulate with the sternal lobes. The sternum that consistently overhangs to some degree the cephalic margin of the annulus is decidedly variable but usually bears one to three pairs of caudal lobes or tubercles. The largest pair is usually swollen, resulting in an intervening trench of varying width extending for a short distance cephalically from the caudal margin. Some of the narrowest occur in specimens in the Suwannee, Coosa, Satilla, and lower portions of the Flint and Chattahoochee basins.

A population consisting of small individuals exists in the Flint River approximately 3.5 miles northwest of Molina on the Pike-Meriwether county line. From this locality, four first form males and two females are available, of which the largest specimen is a female, with a carapace length of 33.0 (postorbital carapace length 24.2) mm. The corresponding lengths of the largest and smallest males are 29.2 (21.7) mm and 28.7 (20.3) mm.

SIZE.—The largest specimen available is a first form male, with a carapace length of 70.4 (postorbital carapace length 49.8) mm. The corresponding lengths of the smallest first form male are 28.7 (20.3) mm, and those of the smallest female carrying eggs or young, 33.2 (23.3) mm.

LIFE HISTORY NOTES.—Probably because of the secretive habits of the ovigerous females and of those carrying young, there are few data available on the life history of this crayfish. No collections of this species containing first form males have been made in Georgia during the month of January, but first form males have been found in each of the other months, and in Florida they have been obtained in January. One ovigerous female was collected in April, three in May, and an additional three in August. An eighth was collected in "the spring." No females carrying young have been obtained. Boyce (1969:83) found ovarian egg counts of 455 and 375 "partially mature eggs" in two specimens collected during the winter. He believed that the hatching of the eggs occurs primarily in the fall (p. 94).

A tabulation of the number of eggs carried by seven of the ovigerous females from Georgia follows. There was evidence of loss of a number of eggs from the first and third specimens.

Carapace and postorbital carapace lengths (mm)	*Number of eggs*	*Diameter of eggs (mm)*
33.2 (23.3)	72	1.6–1.8
34.7 (24.9)	189	1.9–2.0
35.4 (24.5)	22	1.6–1.9
36.9 (26.3)	305	1.6–1.8
37.5 (27.0)	346	1.9–2.0
41.3 (29.5)	363	1.7–1.8
43.8 (32.0)	331	1.6–1.8

Seasonal Data

Sex/stage	*J*	*F*	*M*	*A*	*M*	*J*	*J*	*A**	*S*	*O*	*N*	*D*	*?*
♂I		1	8	13	6	19	5	18	14	18	5	1	3
♂II	14	3	39	82	33	43	20	92	76	28	16	2	12
♀	16	3	39	87	46	49	22	71	78	56	8	4	12
♂j	25	1	51	171	44	59	64	111	187	120	45	4	
♀j	21		37	175	46	38	41	116	204	123	44	1	
♀ ovig				1	3			3					1

* + 26 juveniles.

Ecological Notes.—Like other members of the subgenus *Pennides*, this crayfish is restricted to lotic waters, but whether the stream is a small brook or a sizable river, it exploits such habitats available to it. It does not shun swift water, and indeed, in the larger streams, the largest populations have been encountered in riffle areas (perhaps an artifact of availability) in which the rocks have not been partially buried by shifting sand. While this crayfish has not been taken in the cascading brooks in the northern part of the state, it occurs in the larger swift streams directly receiving the cool waters from such brooks. Perhaps surprisingly, *P. (Pe.) spiculifer* seems equally successful in springfed streams, those in which organic acids and pigments render the water coffee colored, and in those supporting a heavy load of silt; in the latter, however, populations are absent in areas bearing appreciable silt deposits.

This crayfish occurs rarely, or is absent, in sectors of streams flowing over a bare sand or bed-rock bottom; within limits, the greater the quantity of submergent plants, moderate to large-sized rocks, or tree litter (excluding deep leaf drifts, which tend to become anaerobic), the larger the size of the population.

Whether by choice or necessity, *P. (Pe.) spiculifer* constructs burrows in the stream bed, most often in the submerged portions of the banks. Such burrows are simple, often unbranched, tunnels that lead horizontally or slope gently downward for a distance of 20 to 140 centimeters. Along undercut banks of streams, frequently both young and adults spend the daylight hours in mats of roots and entrapped debris.

At night, this crayfish frequently wanders into open water, crawling about the stream bed, or, in areas with luxuriant growths of *Vallisneria*, individuals may climb up the matted leaves to near the surface of the water, quickly retreating when disturbed by light or commotion nearby.

To my knowledge, there are no records of the occurrence of this crayfish in any of the impounded areas of any stream in the state. Undoubtedly its absence in these lakes is at least indirectly due to the destruction of the lotic habitat, permitting the accumulation of quantities of silt on the lake beds that not only envelop their hiding places beneath rocks and in debris but also fill any burrow that might be constructed. This together with oxygen depletion in benthic areas, particularly in those impoundments receiving organic enrichment, render a once congenial river habitat for this crayfish a totally intolerable one.

Georgia Crayfish Associates.—*Procambarus (Pe.) spiculifer* has been collected with the following crayfishes (the number of times they have been found together is noted in parentheses): *Cambarus (C.) bartonii* (9), *C. (C.) howardi* (4), *C. (D.) englishi* (4), *C. (D.) halli* (8), *C. (D.) latimanus* (127), *C. (D.) striatus* (16), *C. (H.) coosawattae* (2), *C. (H.) fasciatus* (7), *C. (H.) speciosus* (1), *C. (J.) conasaugaensis* (2), *C. (L.) acanthura* (6), *C. (L.) d. diogenes* (14), *C. (P.) coosae* (14), *Fallicambarus (C.) hedgpethi* (1), *Faxonella clypeata* (7), *Orconectes erichsonianus* (1), *O. spinosus* (7), *Procambarus (H.) pyg-*

maeus (4), *P. (H.) talpoides* (1), *P. (O.) enoplosternum* (6), *P. (O.) fallax* (1), *P. (O.) lophotus* (1), *P. (O.) pubescens* (2), *P. (O.) seminolae* (8), *P. (Pe.) raneyi* (4), *P. (S.) howellae* (10), and *P. (S.) paeninsulanus* (21).

Procambarus (Pennides) versutus (Hagen)

FIGURES 12*f*, 173*e*, 175, 181, 183*e*, 259

Cambarus versutus Hagen, 1870:28, 31, 34, 51-52, 97, 101, 106, 107, pl. I: figs. 55-58, pl. III: fig. 150.—Faxon, 1884:138; 1885a:8, 17-19, 31, 33-34, 158, 167, 168, 173; 1885b:358; 1890:619; 1898:646; 1914:367, 412.—Underwood, 1886: 373.—Lönnberg, 1895:4.—Hay, 1899b:959, 962.—Ortmann, 1902:277.—Harris, 1903a:58, 131, 138, 144, 151, 152.—Creaser, 1936:125.—Goodnight, 1941:72, 73.—(?)Penn, 1941:8.—Hobbs, 1942b:8, 9; 1972a:2.—Hoff, 1944:349.

Cambarus (Cambarus) versutus.—Ortmann, 1905a:101, 128.

Cambarus (Ortmannicus) versutus.—Fowler, 1912:341 [by implication].—Creaser, 1934:4 [by implication].—(?)Lyle, 1937:31, 37, 61-63; 1938:76.

Procambarus versutus.—Hobbs, 1942b:13-15, 20, 21, 32, 92, 95, 103, 109, 118-121, 123, 126-129, 166, figs. 136-140; 1951: 272, 275; 1952a:218; 1953a:173, 178; 1953b:412, fig. 13; 1956a:117; 1959:884*; 1962:273, 281, 283, 286, fig. 18; 1968b:K-11*, fig. 21g; 1969b:344, fig. 34; 1976, fig. 1c,j,k.—Penn, 1946:29; 1953:1.—Villalobos, 1959:312.—Hobbs and Hart, 1959:148, 151, 159, 160, 165, 167, 169, figs. 9, 22.—Black, 1968:5.—Hobbs III, 1969:22, 41, 42, 55, tab. 3.—Fitzpatrick and Hobbs, 1971:95.—Holt, 1973b:99.—Hart and Hart, 1974:21, 30, 61, 87, 131, 134.—Bouchard, 1976a:577.

Procambarus (Pennides) versutus.—Hobbs, 1972a:10; 1972b:67, 152*, 154*, fig. 54a; 1974b:64, fig. 267.—Fitzpatrick, 1976:57.—Bouchard, 1976c:14.

The above is believed to be a complete bibliography for the species. References to Georgia are indicated by asterisks.

SUMMARY OF LITERATURE.—Hagen (1870) described this crayfish on the basis of two lots of specimens, one from Spring Hill, Mobile County, Alabama, and the other from 10 miles east of Mobile, presumably in Baldwin County. Faxon (1884) reported its occurrence in the neighborhood of Mobile and at Cape Barrancas, Florida. In his revision of the Astacidae, Faxon (1885a) assigned it to his Group I, and, in 1890, 1898, and 1914, cited five new localities in Alabama: Escambia River at Flomaton, at Pollard (both in Escambia County), Greenville (Butler County), Calera (Shelby County), and Auburn (Lee County). In 1914, he cited the type-locality as Spring Hill, the first locality listed by Hagen. Although Ortmann correctly recognized the relationships of the crayfishes in assigning it to his subgenus *Cambarus*, he overlooked the fact that the type-species of the genus *Cambarus* (*Astacus Bartonii* Fabricius) had been selected by Faxon (1898:644). As pointed out by Fowler (1912), the name *Cambarus* had to replace Ortmann's *Bartonius*, thus leaving the group that Ortmann had assigned to his subgenus *Cambarus* without a name, and Fowler proposed *Ortmannicus* as a substitute.

No new data were offered subsequently until Lyle (1937, 1938) and Penn (1941) reported the occurrence of this species in Mississippi and Louisiana, respectively. There is every reason to believe that both records were based on erroneous identifications. Hobbs (1942a), in elevating Ortmann's subgenera to generic rank, transferred this crayfish to the genus *Procambarus* and, in his study of the crayfishes of Florida (1942b), he presented an account of its presence in Florida and cited two new county records (Conecuh and Elmore) in Alabama. In 1953 (b), he presented a spot map including all of the localities known for the species at the time. The first record of its occurrence in Georgia was noted by Hobbs (1959), and, although no locality was cited, the record was based on the only three specimens known from the State at that time. In their summary of the crayfishes of the lower Apalachicola River basin, Hobbs and Hart (1959) utilized the same data presented by Hobbs (1942b). Other references cited contain a few additional locality records, lists of crayfish associates, and statements concerning its affinities with other species.

DIAGNOSIS.—Rostrum with marginal spines and median carina. Carapace with 2 pairs of cervical spines. Areola 2.1 to 2.7 times as long as broad and constituting 23.8 to 27.7 percent of entire length of carapace (35.0 to 39.3 percent of postorbital carapace length). Antennal peduncle with spine on ischium. Ventral surface of basis and ischium of third maxilliped not densely bearded. Basis of cheliped with ventromesial

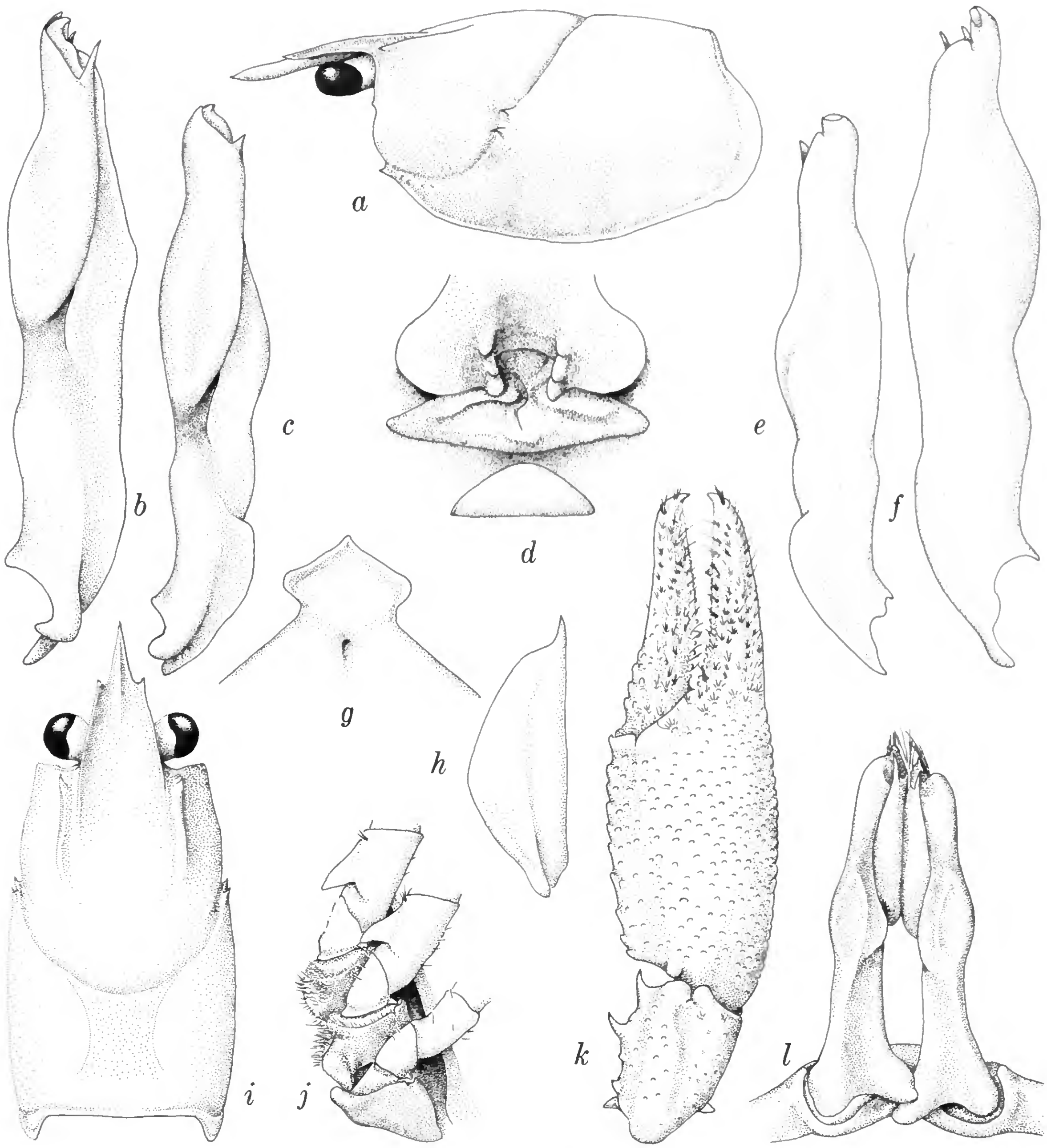


FIGURE 181.—*Procambarus (Pennides) versutus* (*d*, from female from Fort Benning, Muscogee Co, Georgia; *c*, *e*, from second form male, all others from first form male from tributary to Uchee Creek 3.1 mi E of Marvyn on US Hwy 80, Russell Co, Alabama): *a*, lateral view of carapace; *b*, *c*, mesial view of first pleopod; *d*, annulus ventralis; *e*, *f*, lateral view of first pleopod; *g*, epistome; *h*, antennal scale; *i*, dorsal view of carapace; *j*, proximal podomeres of third, fourth, and fifth pereiopods; *k*, dorsal view of distal podomeres of cheliped; *l*, caudal view of first pleopods.

spine. Mesial surface of palm of chela bearing crowded, irregularly arranged or sublinear rows of 9 or 10 tubercles. Male with hooks on ischia of third and fourth pereiopods. First pleopods asymmetrical, suddenly contracted distally, and reaching coxae of third pereiopods; cephalic surface with moderate shoulder; subapical setae abundant, many arising from distolateral surface of appendage; mesial process slender, extending caudodistally at angle of approximately 30 degrees to shaft of appendage; cephalic process also slender, similarly disposed, and situated on lateral side of central projection; central projection somewhat beaklike, corneous, exceeded distally only by cephalic process, its cephalic base situated distinctly distal to base of caudal process; caudal element consisting of (1) short, corneous, subacute caudal process, (2) prominent caudal knob, noncorneous lobe lateral to base of caudal process, and (3) adventitious process in form of caudomesial ridge somewhat rudimentary. Female with sternum cephalic to annulus ventralis bearing paired tuberculate projections extending far over ventral surface of cephalic part of annulus; first pleopod present.

COLOR NOTES (Figure 173*e*; based on population of Conecuh County, Alabama, Escambia River drainage).—Basic color of carapace tan to brown, with black and cream markings. Rostrum with black margins, and black median line extending from carina caudally, dividing at base of rostrum, with branches diverging over cephalic part of gastric area; orbital, antennal, and much of hepatic area black and continuing in narrow band, flanking cervical groove in posterior gastric region; cream-colored stripe extending from posterior parts of antennal and mandibular areas caudally just below cervical spines and continuing over branchiostegite almost to caudal flange; stripe flanked dorsally on branchiostegite by large right-triangular black mark, apex of triangle continuous with black marking in hepatic region and broad base lying on caudal margin of carapace, posterior acute apices of triangle almost reaching median line of carapace. (Black triangle representing horn and part of bar of saddle in postulated primitive color pattern (see Hobbs, 1958a: 74).) Tergum of first abdominal segment cream posteriorly, with reduced pleura almost white; succeeding segments tan to brown dorsally, with similar black markings arranged serially on ventrolateral part of each tergum and expanding onto cephalic part of pleuron, latter with broad cream tan band along oblique caudal margin continuous with that along posterior margin of tergum. Telson and uropods with prominent dark, often black splotches, those at base and on posterior part of telson and on uropods most conspicuous. Antennule and antenna dark brown to almost black, and antennal scale with black line on lateral margin. Cheliped cream from base through half of merus, latter with dark patch dorsally just distal to midlength and olive to tan with black markings distally; carpus and chela tan with black tubercles dorsally, fingers tipped with scarlet. Dorsal surface of remaining pereiopods mostly olive tan from merus distally, fading to cream ventrally and proximally; sternal areas cream to pinkish cream.

TYPES.—Syntypes, MCZ 190 (3♂II, ♀), USNM 4963 (♂I), MHNP (2 specimens), AMS (lost.)

TYPE-LOCALITY.—Spring Hill, Mobile County, Alabama (see Faxon, 1914:412).

RANGE.—From the Mobile River drainage (as far north as Choctaw, Tuscaloosa, Blount, and Tallapoosa counties) in Alabama eastward to the Chattahoochee-Apalachicola drainage in Alabama, Florida, and Georgia.

GEORGIA SPECIMENS EXAMINED.—Only five specimens from two localities are available from Georgia. *Marion County:* (1) Pine Knot Creek 11.4 airmi NNW of Buena Vista on St Rte 355, 1♂I, 1♀, 29 Apr 1978, Keith Floyd and Win Seyle, collectors. *Muscogee County:* (2) Fort Benning, 2♀, 1j♂, Jan 1951, Joseph Pollock.

VARIATIONS—Although this crayfish demonstrates considerable variation in certain features throughout its range, the Georgia specimens differ little from the syntypic first form male in the Smithsonian except as follows: a median carina is present on the rostrum; there is a lateral shoulder-like prominence at the base of the more spiniform caudal process of the pleopod of the first form male; the cephalic process extends slightly distal to the central projection; the ratio of the areola to the length of the carapace is perhaps slightly greater, but there are too few specimens available to be certain as to whether or not this is a consistent feature of the populations in the Georgia localities. The specimens from Marion County did not reach me until after this study had gone to press.

SIZE.—The largest specimen of the species available is a first form male, with a carapace length of 39.2 (postorbital carapace length, 27.4) mm. Corresponding lengths of the smallest first form male are 16.3 (11.5) mm, and those of the smallest female carrying eggs or young are 17.1 (12.3) mm.

LIFE HISTORY NOTES.—(Based on specimens from Alabama and Florida). First form males have been collected during every month of the year (pers. comm., J. F. Fitzpatrick, Jr.). Females with eggs were found in April and June, and a single female carrying young was collected in April.

ECOLOGICAL NOTES.—*Procambarus (Pe.) versutus*, like other members of the subgenus *Pennides*, is apparently confined to lotic habitats, occurring most abundantly in debris in moderately swift areas of streams. In most localities within its range where there are beds of *Orontium aquaticum*, this crayfish may be found in numbers. It also frequents sand-bottomed streams in areas where not only is there very little litter over the stream bed but also there is an absence of aquatic plants. In such habitats, the size of the population can be appreciated only after dark, when the crayfish move from their diurnal retreats into the open stream bed.

> Apparently once established in a stream, *versutus* penetrates farther into the headwaters than does *spiculifer*. This species is abundant in the headwaters of Little Sweetwater Creek, Liberty County [Florida], while in the lower reaches of the same stream *spiculifer* seems to be the sole crayfish inhabitant (Hobbs, 1942b:128).

It has also been found in springs and occurs abundantly adjacent to channels in vegetation-choked areas of clear to coffee-colored streams. Nothing is known of the habitat from which it was collected in Georgia. I failed to find it in several tributaries of the Chattahoochee River in habitats similar to ones from which I had obtained it in Alabama.

GEORGIA CRAYFISH ASSOCIATE.—Collected with this crayfish in the stream at Fort Benning was *Cambarus (D.) latimanus*.

REMARKS.—As pointed out in the brief discussion of "Variations," the crayfish occurring in tributaries of the Chattahoochee River in Lee and Russell counties, Alabama, exhibit several characters that distinguish them from specimens from the vicinity of the type-locality, and at least some of these differences have been noted in collections in the intervening area, both in Alabama and Florida. Until a study has been made of the species throughout its range, I am tentatively assigning the three specimens from Georgia to Hagen's species.

Subgenus *Scapulicambarus*

Subgenus *Cambarus*.—Ortmann, 1905a:97 [in part; not Erichson, 1846:97].

Subgenus *Ortmannicus* Fowler, 1912:341 [in part].

Subgenus *Ortmanmanicus*.—Hobbs, 1942a:342 [in part; erroneous spelling].

Subgenus *Scapulicambarus* Hobbs, 1972a:11 [type-species: *Cambarus clarkii paeninsulanus* Faxon, 1914:369].

DIAGNOSIS.—Body and eyes pigmented, latter well developed. Rostrum with or without margin spines or tubercles, rarely with weak median carina. Carapace with or without 1 cervical spine or tubercle. Areola obliterated or as wide as 6.5 times as long as broad, and constituting 22 to 38 percent of entire length of carapace. Ventral surface of ischium of third maxillipeds rarely with more than proximal half obscured by long plumose setae. Mesial surface of palm of chela never bearded. First three pairs of pereiopods without conspicuous brush of setae extending from basis to merus. Simple hooks on ischia of third and fourth pereiopods. Coxa of fourth pereiopod with bulbous caudomesial boss. First pleopods reaching coxae of third pereiopods, symmetrical or asymmetrical, contiguous basally, with broad, short proximomedian lobe, without proximomesial spur; prominent shoulder on cephalic sur-

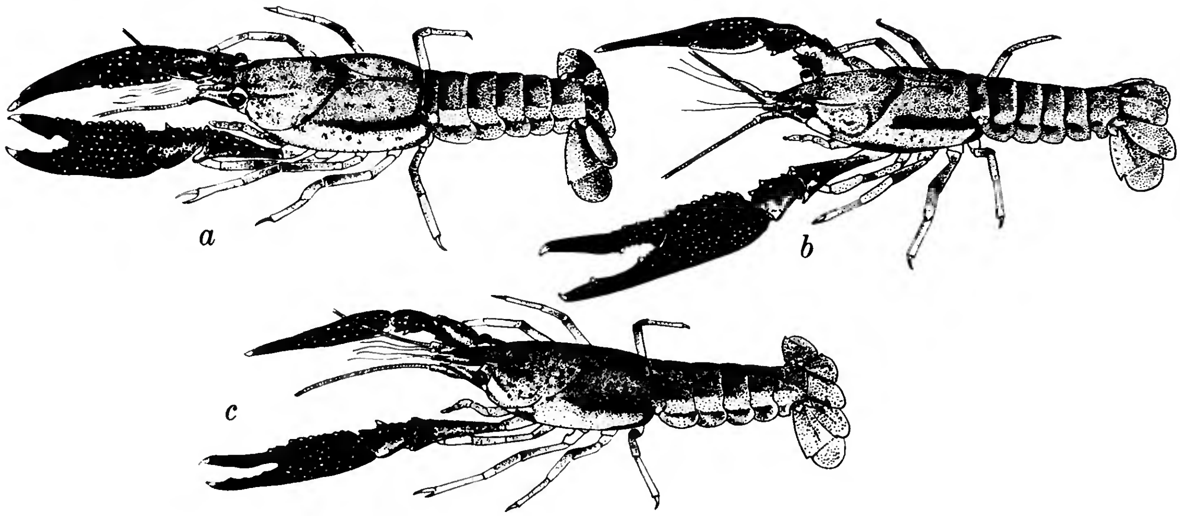


FIGURE 182.—Color patterns of Georgia representatives of subgenus *Scapulicambarus*: *a, Procambarus (S.) troglodytes* from 0.6 mi W of St Rte 24 on Rte S9720, Screven Co; *b, P. (S.) howellae* from Alligator Creek 7.2 mi E of Telfair Co line on U S Hwy 280, Wheeler Co; *c, P. (S.) paeninsulanus* from 2.0 mi S of Folkston on St Rte 121, Charlton Co.

face of left pleopod, that on right either reduced or folded caudomesially, lying against mesial face of mesial lamella, thus making shoulders asymmetrical; subapical setae usually rather sparse but occasionally abundant. Terminal elements of first pleopod consisting of caudodistally directed (and sometimes mesially or laterally deflected), acute mesial process; cephalically situated acute or lamelliform process; caudolateral subspatulate caudal process (distinct caudal knob usually absent); and small to prominent central projection. Mesial ramus of uropod with distomedian spine situated far proximal to, and never extending beyond, margin of ramus.

RANGE.—From the Pee Dee watershed in South Carolina westward in most of the coastal plain (as far north as southern Illinois) to Texas and southward to San Luis Potosí, Mexico. Introductions of *P. (S.) clarkii* are widespread, including Virginia, South Carolina, peninsular Florida, northern Alabama, Nevada, California, Idaho, and Baja California in continental North America. Other introductions include Hawaii, Japan, Spain, Costa Rica, Sudan, Kenya, and Uganda. (See Huner, 1978.)

RANGE IN GEORGIA.—Most of the Coastal Plain Province of the state.

GEORGIA SPECIES.—*Procambarus (S.) howellae, P. (S.) paeninsulanus*, and *P. (S.) troglodytes*.

HABITAT.—With the possible exception of *P. (S.) strenthi*, all six members of the subgenus frequent a wide range of habitat types within the Coastal Plain and lower Piedmont provinces. Whereas they do not shun any type of temporary or permanent major aquatic habitat within their ranges, they appear to be most successful in fluctuating lentic waters, which frequently they share with a number of secondary burrowers (most belonging to the subgenera *Leconticambarus* and *Ortmannicus*) and small-sized species belonging to the genera *Cambarellus, Faxonella*, and *Procambarus* (subgenera *Capillicambarus* and *Hagenides*). In their utilization of streams and burrows in flatwoods, the members of the subgenus *Scapulicambarus*, including the three Georgia representatives, become associated with members of virtually every crayfish species occurring within their respective ranges.

REMARKS.—The recognition of the close affinities of at least some members of the genus was evident as early as 1885 when Faxon (1885a:28) suggested that "... I am inclined to suspect that further explorations will break down the specific distinctions between *C. troglodytes* and *C. Clarkii*." Later, Hobbs (1942b:105) stated: "There is some indication that there may be intergrades *troglodytes* × *paeninsulanus* in the region just south of the Altamaha River in Georgia, but the evidence is too meager to be convincing." In light of our present knowledge of variation and ranges of these crayfishes, there is little likelihood that *P. (S.) troglodytes* (restricted to eastern Georgia and South Carolina) and its closest ally, *P. (S.) clarkii* (ranging from Alabama westward into Mexico), participate in the same gene pool. Opportunity to do so, if such is possible, has been made feasible by the recent introduction of the latter into South Carolina within the range of *P. (S.) troglodytes*. Even though the ranges of the three Georgia members of the subgenus are contiguous and may well be found to overlap, the only evidence of intergradation that appears possible at the moment occurs in specimens from Sumter, Lee, and Dougherty counties (Flint River basin) that seem to exhibit a mixture of characters of *P. (S.) howellae* and *P. (S.) paeninsulanus*. Until series of adult members of both sexes from this area become available, no adequate assessment of whether or not the two are interbreeding there can be made.

On the basis of their morphology, certainly *P. (S.) howellae* and *P. (S.) paeninsulanus* are more closely related than either is to *P. (S.) troglodytes*, and the latter, in turn, shares more in common with *P. (S.) clarkii* than with any other species.

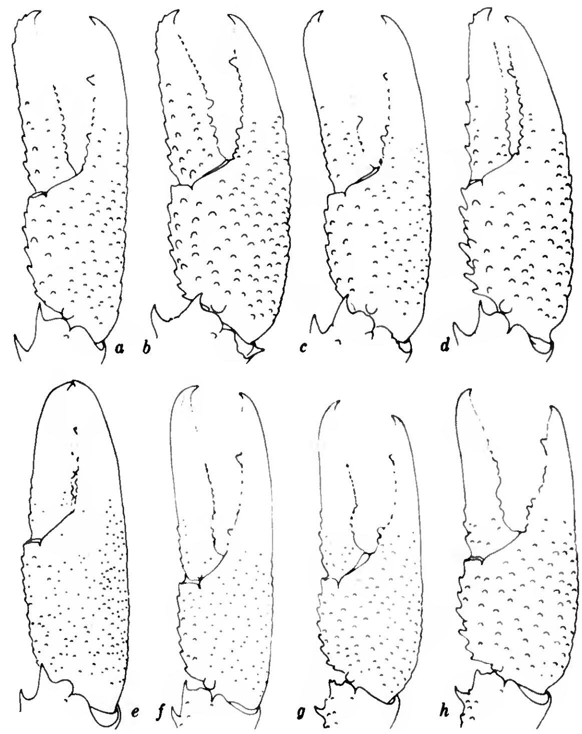


FIGURE 183.—Dorsal view of distal podomeres of chelipeds of female members of subgenera *Pennides* and *Scapulicambarus*: *a*, *Procambarus (Pe.) gibbus* from type-locality; *b*, *P. (Pe.) petersi* from type-locality; *c*, *P. (Pe.) raneyi* from Franklin Co; *d*, *P. (Pe.) spiculifer* from Clarke Co; *e*, *P. (Pe.) versutus* from Muskogee Co; *f*, *P. (S.) howellae* from type-locality; *g*, *P. (S.) paeninsulanus* from Charlton Co; *h*, *P. (S.) troglodytes* from Liberty Co.

The color patterns of the three Georgia members of the subgenus are so markedly similar (Figure 182) that I have found no constant unique feature in any one of the three.

Key to Georgia Members of Subgenus *Scapulicambarus*

1. Cephalic process of first pleopod of first form male in form of broadly arched lamelliform lobe; annulus ventralis fully exposed ventrally, not partly hidden by lobes or tubercles projecting caudally from sternum anterior to annulus, and with anteromedian subcircular to oval elevation (ventrally) .... ***troglodytes***

Cephalic process of first pleopod of first form male consisting of compressed, often acute, projection directed caudally or caudodistally; annulus ventralis frequently partly obscured in ventral aspect by lobes or large tubercles projecting from sternum anterior to annulus but never with anteromedian subcircular to oval elevation (ventrally) 2

2. Distal part of first pleopod of first form male tapering in lateral aspect from level of shoulder on cephalic surface; annulus ventralis partly obscured in ventral aspect by usually prominent lobes or large tubercles projecting caudally from sternum over anteroventral surface of annulus .... ***howellae***

Distal part of first pleopod of first form male not tapering in lateral aspect from level of shoulder on cephalic surface, rather, caudal surface convex; annulus ventralis almost always fully exposed, rarely partly obscured in ventral aspect by single pair of prominences projecting caudally from sternum over anteroventral surface of annulus .... ***paeninsulanus***

Procambarus (Scapulicambarus) howellae Hobbs

FIGURES 16*b*, 182*b*, 183*f*, 184–188, 260

Procambarus howellae Hobbs, 1952b:167–173, figs. 1–14; 1959: 885; 1962:290, 291, fig. 63; 1968b:K-9, fig. 22e.—Villalobos, 1959:312.—Hart and Hart, 1974:22, 28, 30, 32, 33, 90, 131.

Procambarus (Scapulicambarus) howellae.—Hobbs, 1972a:12; 1972b:71, 151, 154, fig. 56a; 1974b:65, fig. 281; 1977a: 419.

These citations are believed to constitute a complete bibliography of the species. All of the references pertain to Georgia.

SUMMARY OF LITERATURE.—This crayfish was described by Hobbs (1952b), who reported it from lotic and lentic habitats in three localities, one each in Bibb, Emanuel, and Telfair counties, Georgia. Except for discussions of relationships to other crayfishes, its assignment to the subgenus *Scapulicambarus*, its inclusion in keys, and statements concerning its range, no noteworthy information appeared in the literature until 1974. Hart and Hart (1974) reported this Georgia endemic from Bibb, Bleckley, Dooly, Telfair, Twiggs, Wheeler, and Wilkinson counties, where it served as hosts to entocytherid ostracods. The most recent reference includes a statement concerning its relationship to a Mexican crayfish, *Procambarus (S.) strenthi.*

DIAGNOSIS.—Rostrum usually with marginal spines, tubercles, or angle at base of acumen and lacking median carina. Carapace with 1 pair of cervical spines or tubercles. Areola in adults 9 to 35.3 (as little as 7 in juveniles) times as long as broad and constituting 29.6 to 36.8 percent of entire length of carapace (39.9 to 47.7 percent of postorbital carapace length). Antennal peduncle with spine (rarely reduced to tubercle) on ischium. Ventral surface of basis and ischium of third maxilliped not covered with dense plumose setae. Basis of cheliped without mesial spine. Mesial surface of palm of chela bearing prominent row of 6 to 9 tubercles. Male with simple hooks on ischia of third and fourth pereiopods, that on fourth opposed by tubercle on corresponding basis and conspicuous caudomesial boss on coxae of fourth and fifth. First pleopods asymmetrical and reaching coxae of third pereiopods; cephalic surface of left member of pair with prominent (usually acute) angular shoulder (that on right member folded caudomesially in first form male) at base of distal third of shaft and in lateral view latter tapering distally; subapical setae rather sparse; mesial process slender, acute, and directed caudally to caudodistally, sometimes almost at right angle to shaft of appendage; cephalic process short, acute, and situated lateral to central projection; latter dentiform, with apex directed caudomesially; caudal element consist-

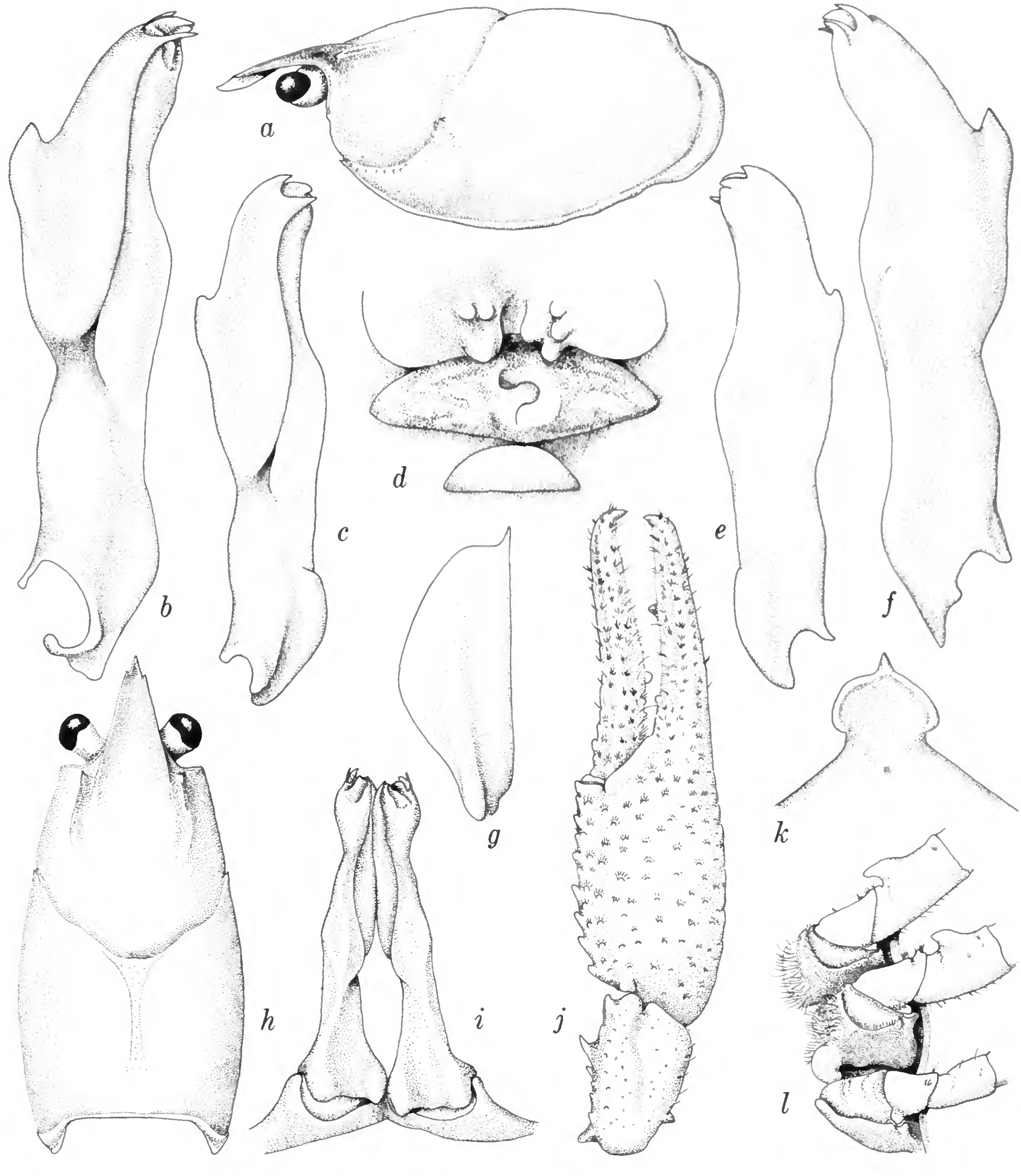


FIGURE 184.—*Procambarus (Scapulicambarus) howellae* (all from holotype except *c*, *e*, from morphotype, *d*, from allotype, and *i*, from first form male from Bleckley Co): *a*, lateral view of carapace; *b*, *c*, mesial view of first pleopod; *d*, annulus ventralis; *e*, *f*, lateral view of first pleopod; *g*, antennal scale; *h*, dorsal view of carapace; *i*, caudal view of first pleopods; *j*, dorsal view of distal podomeres of cheliped; *k*, epistome; *l*, proximal podomeres of third, fourth, and fifth pereiopods.

ing of caudal process closely applied to caudolateral surface of central projection and adventitious ridgelike prominence flanking caudal and mesial base of projection. Female with cephalomedian part of annulus ventralis partly concealed beneath paired projections from often multituberculate sternum immediately anterior to annulus; first pleopod present.

COLOR NOTES (Figure 182*b*).—Carapace dark reddish brown to brown dorsally, with scattered irregular darker spots; rostral margins, postorbital ridges, and pair of spots of gastric region black. Broad pinkish splotch extending caudoventrally from antennal region across mandibular area, narrow one flanking postorbital ridge, and third irregular one in ventral hepatic area; posterior hepatic and mandibular adductor regions dark brown; cervical groove black. Branchiostegite with black longitudinal stripe laterally, extending from level opposite base of abdominal pleura almost to cervical groove; posteriorly, stripe continuous with black area covering caudal flange and extending along ventral margin of branchiostegite; area between black stripe and dark ventral area pinkish cream with brown and small white irregular spots. Cephalic half of first abdominal tergum with transverse black bar bearing posteromedian notch, caudal half dark pinkish tan, and reduced pleuron bright pink. Remaining segments of abdomen with dorsal part of tergum bearing black band anteriorly, followed by broader dark brown one, and slightly paler narrower one along caudal margin; lateral part of terga with broad pinkish tan stripe interrupted by narrow black bands connecting anterodorsal band with irregular black to dark brown splotches on bases of corresponding pleura; remainder of pleura brick red. Telson reddish brown, with very narrow black band basally and paired lateral and median longitudinal dark brown stripes in cephalic section. Uropods also dark reddish brown, both rami slightly darker mesially than laterally. Antennular and antennal peduncles mostly tan to dark brown, but with black markings; flagella brown to olive tan. Third maxilliped pale olive tan, with orange markings on more distal articular membranes. Cheliped, from distal part of ischium to yellowish tips of fingers black to slightly diluted orange black dorsally; tubercles bright orange; ventral surface of distal podomeres also orange. Dorsal surface of other pereiopods olive tan on distal part of ischium, intensifying to olive brown at end of merus; carpus somewhat paler, and propodus and dactyl dilute pinkish orange (some individuals with entire pereiopods pinkish orange with brownish mottlings dorsally). Ventral region of cephalothorax pinkish to pale orange.

TYPES.—Holotype and allotype, USNM 93158 (♂I, ♀); morphotype, USNM 93159 (♂II); paratypes, MCZ, USNM.

TYPE-LOCALITY—Drainage ditch on campus of Wesleyan College, Rivoli, Bibb County, Georgia.

RANGE.—Endemic in Georgia, where widespread in the coastal plain of the Flint and Altamaha river basins, occurring most abundantly in the Fall Line Hills and Vidalia Upland districts.

GEORGIA SPECIMENS EXAMINED.—I have examined a total of 379 specimens from 54 localities (Figure 185) in the following counties in Georgia: Ben Hill (1), Bibb (1), Bleckley (2), Dodge (5), Dooly (2), Emanuel (1), Houston (1), Jeff Davis (1), Johnson (1), Laurens (3), Long (1), Macon (1), Marion (1), McIntosh (1), Montgomery (3), Pulaski (2), Schley (1), Screven (1), Sumter (1), Telfair (6), Toombs (1), Twiggs (1), Washington (2), Wheeler (4), Wilcox (7), and Wilkinson (3).

VARIATIONS.—Most conspicuous among the variations observed in this species is the rostrum (Figure 186) in which, although always possessing margins that are convergent to the base of the acumen, the degree of convergence is highly variable, and the usual marginal spines may be reduced to small tubercles or to obtuse angles that become abraded in late intermolt stages. The areola ranges in width from less than 9 times as long as broad (in most juveniles with a carapace length of less than 25 mm) to as much as 35.3 times in a first form male from Pulaski County, having a carapace length of 40.3 mm. The ratios of the length of the areola to that of the entire length of the carapace range in adults from 30.7 to 36.8 (average 33.1) percent, that of the length of the areola to the postorbital carapace length 39.9 to 47.7 (average 43.7) percent. There appears

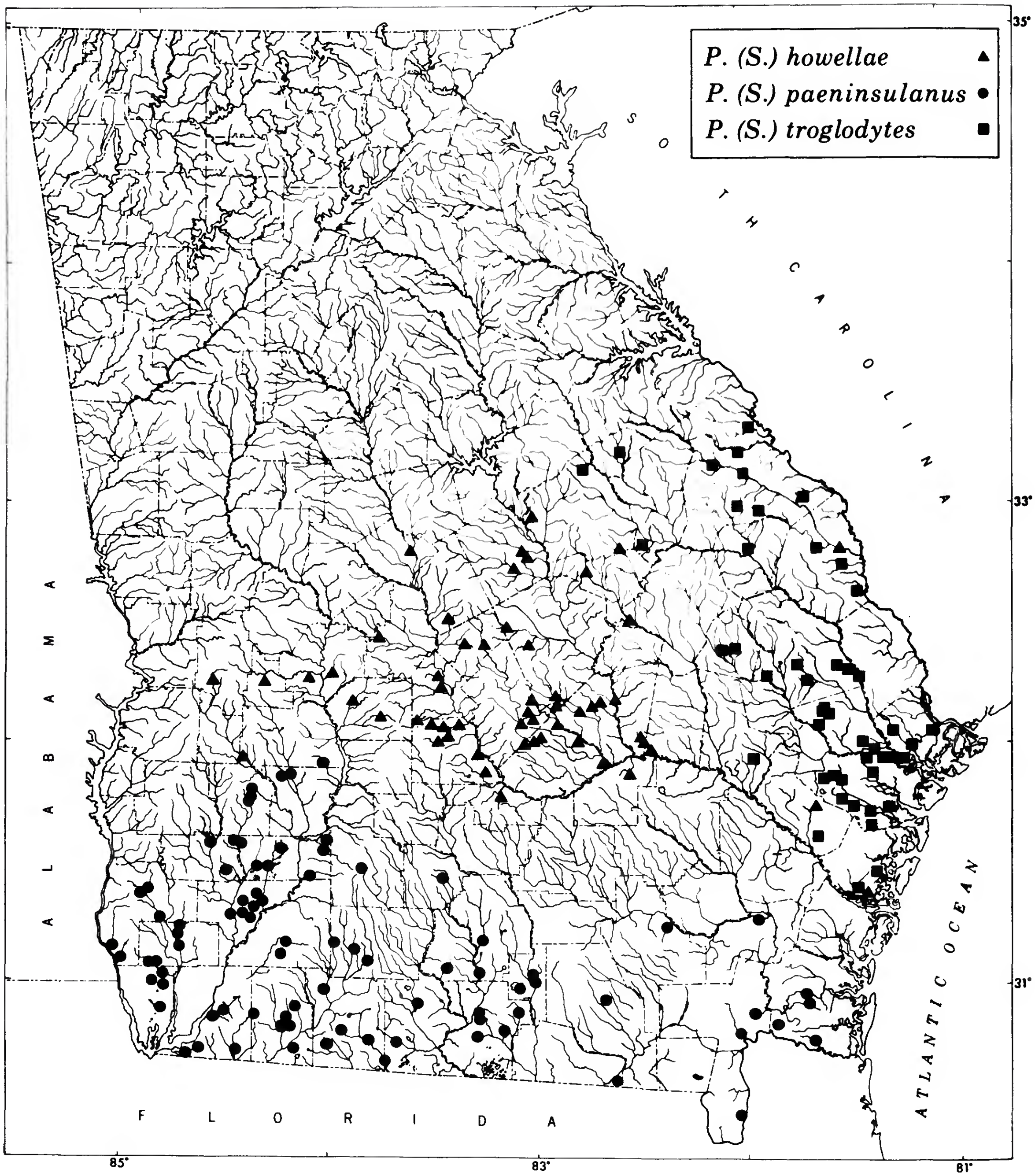


FIGURE 185.—Distribution of *Procambarus (S.) howellae, P. (S.) paeninsulanus*, and *P. (S.) troglodytes* in Georgia.

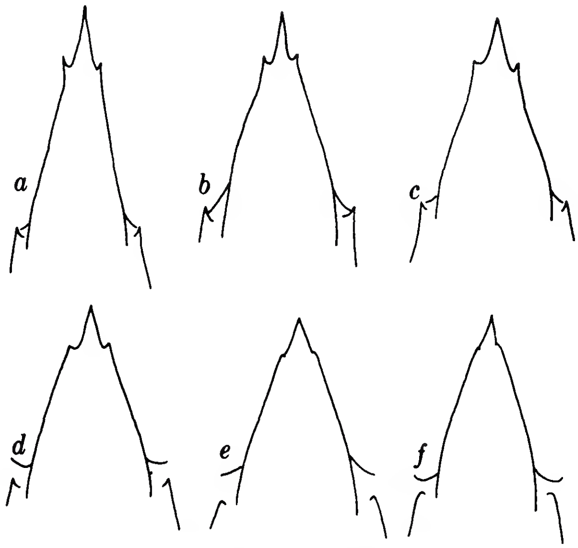


FIGURE 186.—*Procambarus (S.) howellae*, variations in rostrum: *a, c*, Dodge Co; *b*, Montgomery Co; *d, e*, Bleckley Co; *f*, Dooly Co.

to be no correlation between the width of the areola and the size of the adult animal, but there is some evidence that the young have a proportionately broader and shorter areola than do the adults and that it becomes narrower and longer with increase in carapace length up to about 30 mm. At greater carapace lengths the wide range of variation pointed out in the "Diagnosis" exists. Of the specimens measured, only two have areolae that are as much as 20 times as long as wide. The mesial margin of the palm bears a row of six to nine tubercles (seven occur most frequently). The presence of a tubercle on the basis of the fourth pereiopod of the male that opposes the hook on the ischium (Figure 184*l*) is erratic; it may be present or absent in males from the same locality. Variations in the first pleopod of the male, form I, are illustrated in Figure 187. A rather striking variation occurs in the sternum immediately anterior to the annulus ventralis in the female (Figure 188); it may bear several small, rounded tubercles, or there may be two that are much larger than the others that project caudally some distance over the anteroventral face of the annulus. In juvenile and most second form males, the shoulder on the right first pleopod is a virtual mirror image of that on the left, but in the first form male it is always bent caudomesially.

SIZE.—The largest specimen available is a first form male, having a carapace length of 45.2 (postorbital carapace length 34.1) mm. Corresponding lengths of the smallest first form male and of the only known ovigerous female are 28.3 (20.6) mm and 29.3 (22.9) mm, respectively.

LIFE HISTORY NOTES.—First form males have been collected in February, March, April, May, June, and November, and a single ovigerous female was obtained from a burrow on 21 June 1975. The latter (see measurements under "Size") carried 134 eggs (diameter ranging from 1.8 to 1.9 mm) and newly hatched young.

Seasonal Data

Sex/stage	*J*	*F*	*M*	*A*	*M*	*J*	*J*	*A*	*S*	*O*	*N*	*D*	*?*
♂I		1	5	12	1	11					4		
♂II	5	1	9	21	10	8			1		1		
♀			2	41	9	25			1		2		1
♂j			11	73	9	5			1		3		
♀j			5	82	9	7	2						
♀ ovig						1							

ECOLOGICAL NOTES.—*Procambarus (S.) howellae*, while frequenting a wide range of habitats, seems to be most common in sluggish to moderately flowing streams, where it occurs in dense growths of submergent (*Juncus repens*, *Ceratophyllum* sp., *Ludwigia* sp., *Utricularia* sp., and *Vallisneria* sp.) and emergent (*Orontium aquaticum*, *Sagittaria* sp., *Typha* sp., and sedges) plants or among debris of various kinds, ranging from leaf drifts to rock litter. It does not shun segments of streams having a clay or sandy bottom devoid of macrophytes, and whether or not the water is clear, coffee colored, or silt laden seems to have little influence on the size of the population. It also occurs in temporary roadside pools and constructs simple burrows that extend vertically, or almost so, to depths of 0.5 to more than a meter.

GEORGIA CRAYFISH ASSOCIATES.—Collected with this crayfish are the following species (the number of shared localities is noted in parenthe-

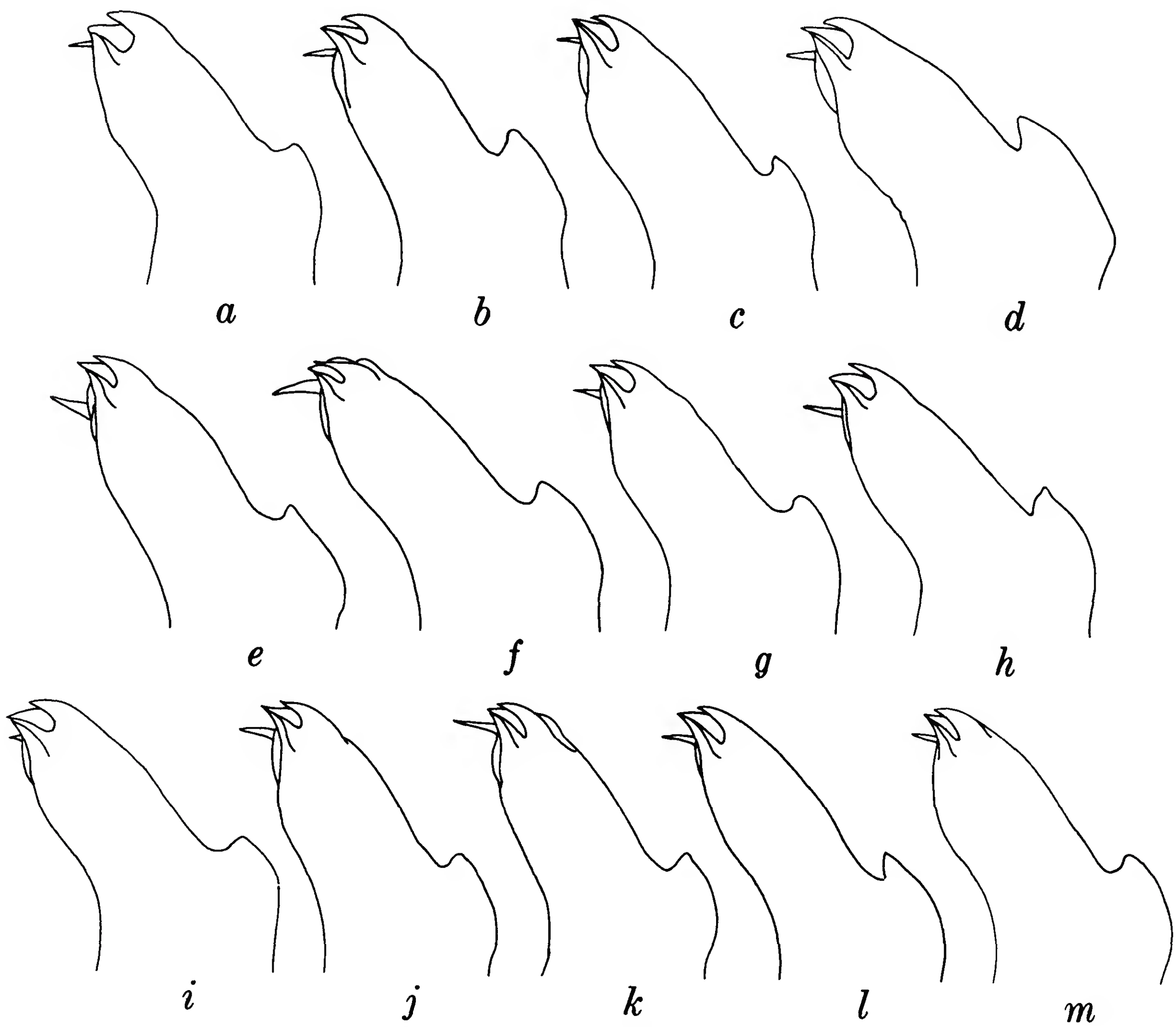


FIGURE 187.—*Procambarus (S.) howellae*, variations in left first pleopod of first form male. Flint Basin: *a*, Marion Co; *b*, Dooly Co. Ocmulgee-Altamaha Basin: *c*, Bleckley Co; *d*, Pulaski Co; *e*, Dodge Co; *f*, Wheeler Co; *g*, Telfair Co; *h*, Wilcox Co. Oconee-Altamaha Basin: *i*, Wilkinson Co; *j*, Laurens Co. Altamaha Basin: *k*, Montgomery Co; *l*, Jeff Davis Co. Ohoopee-Altamaha Basin: *m*, Washington Co.

ses): *Cambarus (D.) latimanus* (1), *C. (D.) striatus* (5), *C. (L.) diogenes diogenes* (2), *Faxonella clypeata* (16), *Procambarus (H.) caritus* (3), *P. (H.) pygmaeus* (1), *P. (O.) acutus acutus* (3), *P. (O.) pubescens* (1), *P. (O.) seminolae* (3), and *P. (Pe.) spiculifer* (10).

REMARKS.—The locality, Thompson's Fishing Lodge, 10 miles northeast of Sylvania, Screven County, should be confirmed, for it is situated in the midst of the range of *P. (S.) troglodytes*, one of its close relatives. Certainly if this is a reliable record, this crayfish must have been introduced, perhaps by fishermen.

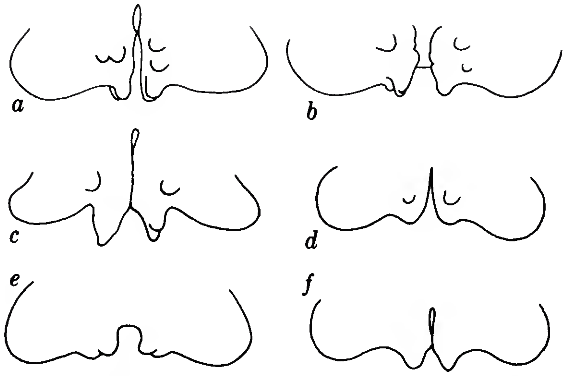


FIGURE 188.—*Procambarus (S.) howellae*, variations in sternum immediately cephalic to annulus ventralis: *a*, Jeff Davis Co; *b*, Telfair Co; *c*, Dodge Co; *d*, Dooly Co; *e*, Wilkinson Co; *f*, Wilcox Co.

Procambarus (Scapulicambarus) paeninsulanus (Faxon)

FIGURES 16*c*, 182*c*, 183*g*, 185, 189-191, 261

Cambarus Clarkii.—Faxon, 1884:136(?) [in part]; 1885a:26, 157, 167, 173 [in part].

Cambarus clarkii.—Harris, 1903a:58, 82, 137, 143 [in part].

Cambarus (Cambarus) clarki.—Ortmann, 1905a:105 (?) [in part].

Cambarus clarkii paeninsulanus Faxon, 1914:369, 414.—Hobbs, 1942b:9; 1942c:57, figs. 13, 14; 1974a:15.

Cambarus clarkipaenensulanus.—Hobbs, 1937:154 [erroneous spelling].

Cambarus clarki paeninsulanus.—Goodnight, 1941:72, 73.

Procambarus clarkii paeninsulanus.—Hobbs, 1942a:342 [by implication]; 1942b:104.

Procambarus paeninsulanus.—Hobbs, 1942b:14, 15, 20, 21, 25, 31, 45, 66, 68, 71, 72, 87, 99, 100, 103, 104, 105* [in part], 106*, 107, 109, 112, 113, 116, 118, 123, 128, 145, 155, 166, 170-172, figs. 106-110; 1952b:165, 173*, fig. 3*; 1959:885*; 1962:290*, 291, fig. 62; 1966b:70; 1968b:K-10*, fig. 22d; 1969b:343*.—Hobbs and Marchand, 1943: 22.—Hoff, 1944:337*, 340, 349, 356.—Dickinson, 1949: 23.—Hobbs and Hart, 1959:148, 154, 158-162, 164, 166, 168, 170-171, 174-176, 178, 184, 185, 188, fig. 18.—Hart, 1959:195, 198, 201, 203, 204*.—Hoffman, 1963:330*.—Anonymous, 1967h, tab. 3*; 1972f:194*; 1973a:50*, 52*; 1973c:60*, 68*.—Hobbs III, 1969:41, 45, 62.—Caine, 1974b:3, 5, 7-9, 14-16, 19, 20, 22, 25, 26, 30, 33, 34, 36-38, 42, 45, 47-49, 51-54, 56, 59, 60, 62, 69, figs. 1b, 4b, 5a.—Hobbs and Hall, 1974:202, 204*.—Hart and Hart, 1974:27, 28*, 32, 87, 88*, 90, 96, 128, 129*, 131*.—Franz, 1977a:93.—Wharton, 1978:220*.

Procambarus troglodytes.—Kilby, 1945:84.—Penn, 1950b:647, 650.

Procambarus paeninsulanis.—Anonymous, 1967b, tab. 3* [erroneous spelling].

Cambarus paeninsulanus.—Hobbs, 1972a:12.

Procambarus (Scapulicambarus) paeninsulanus.—Hobbs, 1972a: 12, figs. 1*e*,*f*, 2*n*, 3*b*, 17*a*-*g*; 1972b:71*, 151*, 154*, figs. 5e, 6b, 56b; 1974b:65-66*, fig. 280; 1977a:419.—Bouchard, 1976c:14.—Hobbs, Hobbs, and Daniel, 1977:148.

Procambarus paeninsulans.—Hart and Hart, 1974:128* [erroneous spelling].

Procambaris paeninsulanus.—Wharton, 1978:46* [erroneous spelling].

The above citations are believed to constitute a complete bibliography of the species. References to its occurrence in Georgia are marked by asterisks.

SUMMARY OF LITERATURE.—Faxon (1884) cited Florida as one of the states in which Girard's (1852) *Cambarus Clarkii* had been found and in 1885 (a) recorded it from two localities in Florida—"Pensacola" and "three miles below Horse Landing, St. John's River." On the basis of these, both Harris (1903a) and Ortmann (1905a) recorded the occurrence of the species in Florida. Faxon (1914) presented a brief diagnosis of *Cambarus clarkii paeninsulanus*, employing the specimens from the second locality listed above as types. No further references to the species appeared in the literature until Hobbs (1937:154), in summarizing notes on the crayfishes in the northern peninsular region of Florida, stated that this crayfish "inhabits the small springs and sandy bottom creeks where it often burrows into the clay or mud banks." In 1942 (a), Hobbs (by implication) referred this crayfish to the genus *Procambarus*, and later in the same year (b), he presented an account of its occurrence in Florida and Georgia and also described the Pensacola population, previously referred to by Faxon (1884, 1885a, 1885b: 357), as *Procambarus okaloosae*. The summary treatment of this crayfish by Hobbs (1942b), except for subsequent locality records, includes most of what is known about the species at the present time. In it, he presented a diagnosis, discussed its affinities, commented on variations, and reviewed in some detail the geographic and ecological distribution in Florida and Georgia, recording it from the following counties in the latter: Baker, Camden, Colquitt, Dougherty, Grady, Liberty, Thomas, and Lowndes. (The Liberty County record was based on a misidentified specimen of *Procambarus (S.) troglodytes.)* These county records include parts of all of the drainage basins in Georgia, except the Aucilla, in which *P. (S.) paeninsulanus* is now known to occur. Additional Georgia records have been reported subsequently from several counties as follows: Berrien (Anonymous, 1967b, 1973c), Calhoun (Hobbs and Hart, 1959), Camden, Colquitt, and Thomas (Hart and Hart, 1974), Cook (Anonymous, 1973c), Decatur and Early (Hobbs and Hart, 1959; Hart and Hart, 1974), Grady (Hobbs and Hart, 1959; Anonymous, 1973a), Miller (Hobbs and Hart, 1959; Anonymous, 1972f), Mitchell (Hobbs and Hart, 1959), Seminole (Hobbs and Hart, 1959; Hoffman, 1963), and Ware (Anonymous, 1967h). The occurrence of the species in Alabama has been reported by Hobbs and Hart (1959) and Bouchard (1976c). In an effort to express his views on the interrelationships of the members of the genus *Procambarus*, the largest of the crayfish genera, Hobbs (1972a) recognized several subgenera and assigned this crayfish to the subgenus *Scapulicambarus*. Hobbs and Hall (1974) stated that in preliminary experiments to determine the lower limits of oxygen concentrations tolerated by members of this species, individuals died at 1.7 to 2.3 mg/l, but in Okapilco Creek, a tributary of the Suwannee River, it occurred abundantly in an area in which the oxygen concentration was 1.5 mg/l. In the same locality a measure of 2.5 mg/l had been obtained a few days before, thus the depletion indicated by 1.5 mg/l could have been of short duration. Caine (1974b), comparing adaptations of *P. (S.) paeninsulanus* with other epigean and troglobitic crayfishes in northern Florida, presented valuable data on factors involved in its exploitation of environments there. Hobbs, Hobbs, and Daniel (1977) noted its occurrence in a cave in the Florida panhandle. A summary of the branchiobdellid worms and entocytherid ostracods harbored by this crayfish is presented in Appendix 2.

Diagnosis.—Rostrum usually with marginal spines, tubercles, or angles at base of acumen and lacking median carina. Carapace with 1 pair of cervical spines or tubercles. Areola 6.5 to 19.0 (average 13.2) times as long as broad and constituting 29.1 to 35.6 (average 32.8) percent of entire length of carapace (40.1 to 45.5, average 43.2, percent of postorbital carapace length). Antennal peduncle with spine (rarely reduced to tubercle) on ischium. Ventral surface of basis and ischium of third maxilliped lacking dense plumose setae. Basis of cheliped without mesial spine. Mesial surface of palm of chela bearing row of 6 to 9 (usually 7) prominent tubercles. Male with simple hooks on ischia of third and fourth pereiopods, that on fourth opposed by tubercle on corresponding basis, and conspicuous caudomesial bosses on coxae of fourth and fifth pereiopods. First pleopods asymmetrical and reaching coxae of third pereiopods; cephalic surface of left member of pair with highly variable shoulder (that on right member folded caudomesially in first form male) at base of distal third of shaft, latter with convex caudal margin distal to level of shoulder; subapical setae few in number and situated laterally; mesial process rather slender, acute, and directed caudally to caudodistally; cephalic process acute to rounded distally, its apex directed caudodistally, and base cephalolateral to, and partly hooding, central projection; central projection dentiform and strongly sclerotized, with apex directed caudodistally to caudally; caudal element consisting of (1) small caudal knob (often absent) situated on distal caudolateral surface of appendage at base of (2) corneous caudal process; latter somewhat lamellate and closely applied to caudolateral surface of central projection; and (3) corneous adventitious process forming ridge extending along caudal and mesial base of central projection. Female usually with annulus ventralis completely exposed, rarely minute parts hidden in ventral aspect by pair of small symmetrically arranged tubercles projecting from sternum immediately cephalic to annulus; first pleopod present.

Male, Form I (from 2.0 miles south of Folkston on State Route 121, Charlton County, Georgia).—Body (Figure 189*a,i*) subovate, compressed laterally. Abdomen narrower than thorax (14.2 and 15.3 mm). Width and height of carapace subequal at caudodorsal margin of cervical groove (15.3 and 15.6 mm). Areola 9.9 times as long as broad, with 2 punctations in narrowest part. Cephalic section of carapace 2.2 times as long as areola, length of latter 33.1 percent of total length of carapace (43.8 percent of postorbital carapace length). Rostrum subplane dorsally, with slender convergent margins bearing small spines at base of acumen; upper surface with scattered punctations between submarginal rows; acumen clearly defined basally and reaching anteriorly beyond midlength of ultimate podomere of antennular peduncle; subrostral ridges weak and evident in dorsal view along no more than basal fifth of rostrum. Postorbital ridge well defined, grooved dorsolaterally, and ending cephalically in small spine. Suborbital angle rudimentary. Branchiostegal spine clearly defined. Carapace punctate dorsally and granulotuberculate laterally, tubercles flanking cervical groove in anteroventral branchiostegal area slightly larger than most others; cervical spine comparatively small. Abdomen slightly longer than carapace (37.0 and 35.6 mm). Cephalic section of telson with 3 spines in each caudolateral corner, mesial and lateral ones fixed. Uropods with both lobes of basal podomere bearing corneous spine; mesial ramus with distinct spine on lateral margin and distomedian one far removed from margin; lateral ramus with usual row of small spines immediately proximal to transverse suture and larger ones at lateral extremity of suture. Cephalic lobe of epistome (Figure 189*g*) broadly rounded with anterolateral margins slightly undulating, ventral surface plane with few punctations; main body with median furrow extending posteriorly from fovea; epistomal zygoma arched. Antennule of usual form, with prominent spine at midlength of ventral surface. Antennal peduncle with acute lateral spine on basis and strong ventral one on ischium, flagellum extending caudally short distance beyond posterior margin of telson; antennal scale (Figure 189*h*) almost 2.6 times as long as wide, broadest at about midlength where lamellate section distinctly broader than thickened lateral part, latter terminating in moderately strong corneous-tipped spine. Third maxilliped with ventral surface of ischium not studded with conspicuous mat of long plumose setae, only those on mesial half of podomere long, most plumose setae very short, few long ones situated proximomesially.

Right chela (Figure 189*k*) about 3.5 times as long as broad, subovate in cross section, depressed. Mesial surface of palm with row of 6 tubercles subtended dorsally by another row of 6 and ventrally by row of 3; entire palm studded with tubercles. Fixed finger with rounded median longitudinal elevation dorsally and ventrally, flanked by tubercles in proximal fifth and setiferous punctations along remainder of length; lateral margin of finger with similar row of punctations; opposable margin with row of 13 tubercles along proximal two-thirds of finger, all very small except third from base, additional large tubercle present on lower level at base of distal third, and broad band of minute denticles, interrupted by third tubercle from base, extending from base of finger to corneous tip. Dactyl with dorsal and ventral surfaces similar to those of fixed finger, mesial surface with row of tubercles, decreasing in size distally, along basal third; opposable margin with dorsal row of 6 very small tubercles along basal two-fifths and ventral row of 4 larger tubercles in second fifth from base, first in latter row largest, minute denticles along distal three-fourths of fingers arranged in broad band, single row to narrow band in proximal fourth, band interrupted by ventral row of tubercles.

Carpus of right cheliped longer than broad (9.7 and 5.7 mm), tuberculate mesially and dorsomesially; subspiniform tubercle situated on distal dorsomesial margin, another near midlength of mesial surface, 1 on ventromesial angle and another on distal ventrolateral articular condyle.

Merus of right cheliped tuberculate dorsally, ventrally, and distomesially, otherwise punctate;

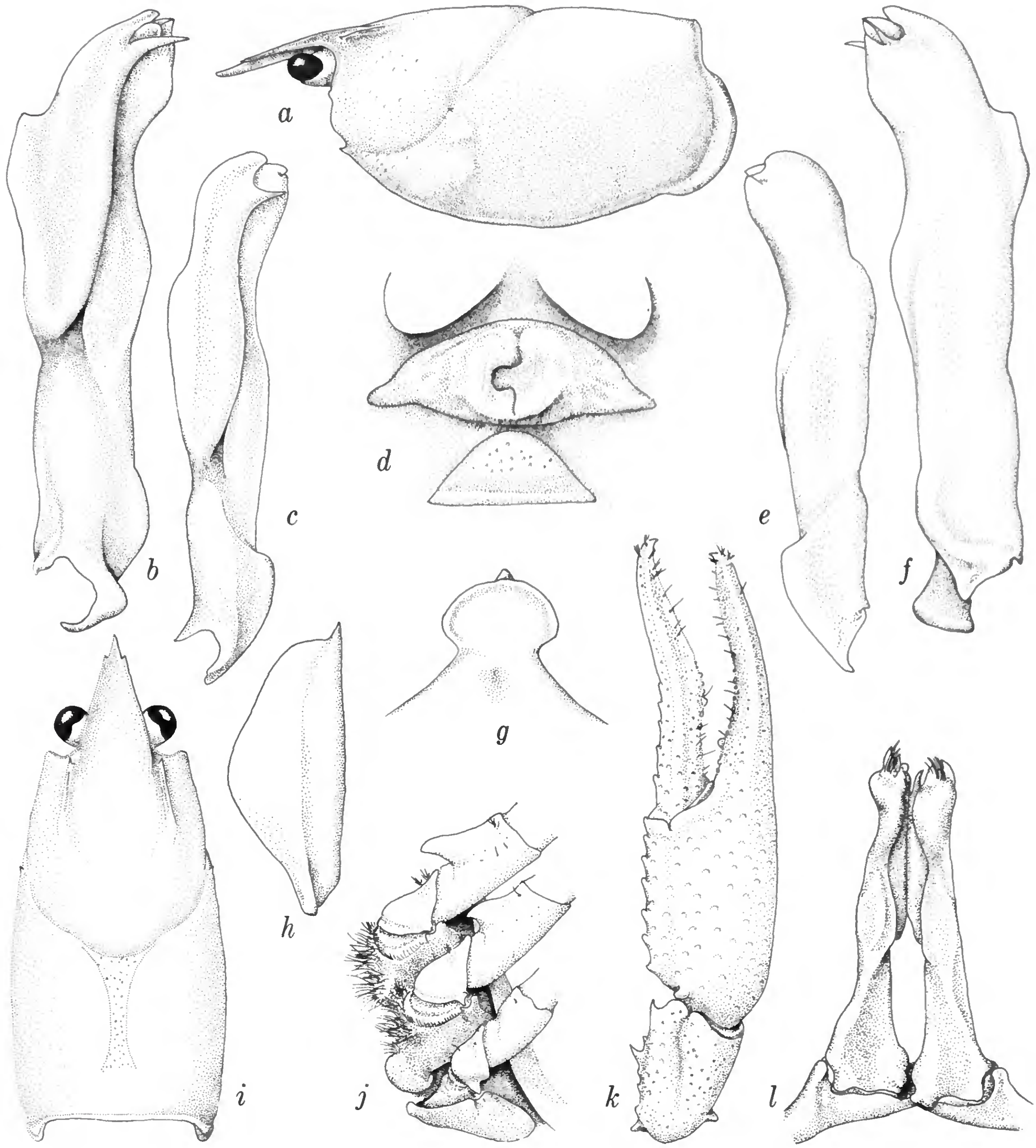


FIGURE 189.—*Procambarus (Scapulicambarus) paeninsulanus* from 2 mi S of Folkston on St Rte 121, Charlton Co (all from first form male except *c*, *e*, from second form male, and *d*, from female): *a*, lateral view of carapace; *b*, *c*, mesial view of first pleopod; *d*, annulus ventralis; *e*, *f*, lateral view of first pleopod; *g*, epistome; *h*, antennal scale; *i*, dorsal view of carapace; *j*, proximal podomeres of third, fourth, and fifth pereiopods; *k*, dorsal view of distal podomeres of cheliped; *l*, caudal view of first pleopods.

dorsal surface with 2 spiniform tubercles situated short distance proximal to distal extremity; ventral surface with irregular (in size and position) lateral row of 14 tubercles, more regular mesial row of 15 increasing in size distally, and oblique distal row of 4 joining mesial and lateral rows; distal members of latter 2 rows strong and spiniform. Ischium with row of 4 small tubercles mesially.

Hooks on ischia of third and fourth pereiopods (Figure 189*j*), both simple, and that on third overreaching basioischial articulation, neither opposed by tubercle on basis. Coxa of fourth pereiopod with prominent vertically disposed caudomesial boss; that on coxa of fifth much smaller and compressed.

Sternum between third, fourth, and fifth pereiopods moderately deep and bearing fringe of plumose setae on ventrolateral margins.

First pleopod (Figure 189*b,f,l*) as described in "Diagnosis."

Female.—Differing from first form male, other than in secondary sexual characters, as follows: cephalic section of telson with 4 spines (lateral and 2 more mesial ones fixed) in dextral corner; epistome more nearly cordiform with ventral surface convex; chela (Figure 183*g*) about 2.7 times as long as broad, mesial margin of palm with row of 7 tubercles; opposable margin of fixed finger with row of 11 tubercles, second from base largest and width of band of minute denticles much reduced (proximally to single staggered row); opposable margin of dactyl with 1 row of 10 tubercles, fourth from base largest and distal 6 diminishing in size distally (finger conspicuously broader at level of fourth tubercle than more proximally), and minute denticles arranged in single row along almost entire length of finger; most tubercles on carpus more nearly acute; 3 prominent spiniform tubercles on dorsodistal surface of merus, and ventrolateral and ventromesial rows of 13 and 15 tubercles, respectively; mesial surface of ischium with 5 tubercles. (See "Measurements.")

Annulus ventralis (Figure 189*d*) subspindle shaped, approximately 2.7 times as wide as long; weakly sculptured ventral surface with submedian depression; sinus originating near cephalomedian margin, extending caudally and slightly dextrally before making almost right-angle turn, crossing median line before making 180-degree arc and returning to median line before curving caudally to end short distance anterior to caudal margin of annulus. Postannular sclerite subtriangular, about 2.3 times as long as wide, and two-thirds as long and almost 0.6 times as wide as annulus; ventral surface punctate and caudal band less sclerotized than remainder of sclerite. First pleopod reaching level of coxa of fourth pereiopod when abdomen flexed.

Male, Form II.—Differing from first form male in following respects: cephalic section of telson with only 2 spines in caudosinistral corner, mesial one movable; cephalolateral borders of epistome with 2 pairs of subacute tubercles; mesial surface of palm of chela with row of 7 tubercles and lateral half of palm punctate dorsally and ventrally (some punctations with withdrawn tubercles); opposable margin of fixed finger with row of 5 tubercles, basal one largest, and minute denticles forming single row; opposable margin of dactyl with tubercles in dorsal row exceedingly small, and minute denticles forming single row; ventral surface of merus with lateral row of 8 tubercles and mesial one of 13, only 1 tubercle representing oblique row. Hooks on ischia of third and fourth pereiopods and bosses on coxae of fourth and fifth pereiopods much reduced. (See "Measurements.") First pleopod (Figure 189*c,e*) with shoulder on cephalic surface broadly rounded; all terminal elements represented, but cephalic process not clearly differentiated distally, and caudal knob and caudal process fused in 1 tuberculiform prominence; juvenile oblique suture present.

Color Notes (Figure 182*c*).—Carapace dark brown dorsally, with pinkish suffusion and very small black spots; rostral margins, postorbital ridges, and 2 pairs of small spots in posterior gastric region black. Narrow pinkish band extending obliquely caudoventrally from antennal region across mandibular area, and irregular pink splotches in hepatic region. Branchiostegite with black longitudinal stripe laterally, extending from level opposite base of abdominal pleura to cervical groove; posteriorly stripe continuous with black area covering caudal flange and extending along ventral margin of branchiostegite; area between black stripe and ventral margin pink, with small black and cream spots. First abdominal tergum with paired black bars in cephalic half and in posterior half, area between bars dark pinkish brown; second through sixth terga with broad median pinkish brown stripe, narrowing posteriorly and ending on cephalic fourth of sixth; lateral part of second through fifth terga and remainder of sixth pink, with irregular cream splotch abutting median stripe and with tiny cream and brown flecks. Pink pleura delimited basally from corresponding terga by pinkish brown, ventrally undulating line, and anterior 3 pleura with oblique pinkish cream splotch. Telson and uropod also pinkish brown; former with lateral parts darker than median area and lateral articular areas and spines black; rami of uropod with black lateral margins and distal margin of proximal section of lateral ramus also black. Antennular and antennal peduncles pinkish, mottled with black; flagella olive brown, with pale articular rings; antennal scale pinkish cream, with dark brown lateral margin and slightly paler stripe flanking thickened area mesially. Chelipeds dark brown and with black and orange-tipped tubercles from midlength of merus to bases of fingers; tubercles on dorsal surface of palm mostly orange; fingers of chela very dark olive brown, with orange-tipped tubercles basally, distal parts of fingers cream; ventral surface of chelipeds except for brownish fingers mostly orange. Remaining pereiopods pale olive from ischium distally, merus and carpus slightly darker than other podomeres. Ventral region of body pinkish cream.

In specimens from Early County, carapace olive, marked with red spots in gastric region; areola red, and red granules on branchiostegites, latter lacking longitudinal dorsolateral strip; abdomen greenish tan, with paired, transverse, small reddish black markings on first and second terga and small somewhat oblique red ones dorsolaterally on third through sixth; second through fifth pleura with red anteroventral markings; telson and uropods greenish tan, flecked with red; distal podomeres of cheliped bright olive, with orange tubercles.

Measurements (mm)

	Male, form I	*Female*	*Male, form II*
Carapace			
Height	15.6	19.4	12.1
Width	15.3	19.8	11.9
Entire length	35.6	43.1	27.0
Postorbital length	26.9	33.0	20.1
Areola			
Width	1.2	1.3	0.6
Length	11.8	14.7	9.0
Rostrum			
Width	5.5	6.6	4.4
Length	10.1	11.9	7.9
Chela			
Length of mesial margin of palm	10.2	9.3	4.7
Width of palm	8.6	10.6	4.2
Length of lateral margin	30.6	28.9	13.5
Length of dactyl	17.9	18.1	8.0
Abdomen			
Width	14.2	17.1	9.5
Length	37.0	46.8	29.4

TYPES.—Holotype, MCZ 3530 (♂II); paratypes, MCZ, USNM.

TYPE-LOCALITY.—Three miles below Horse Landing, Saint Johns River, Putnam County, Florida.

RANGE.—Southern Georgia, and Florida from the Choctawhatchee Basin east and south to Flagler, Marion, and Hillsboro counties. In Georgia (Figure 185), it occurs in the Coastal Plain Province in all of the river basins from the Chattahoochee southeastward to the Satilla and Saint Marys rivers. It is very common in the Flint, Ochlockonee, and western tributaries of the Suwannee River system, and is the only crayfish that has been found in the Aucilla Basin in Georgia. Although common in the Saint Marys, it does not appear to be abundant in the Satilla watershed. It occurs in part of all of the districts of the Coastal Plain Province except the Fort Valley Plateau and the Vidalia Upland. Only in the Flint Basin does it reach the Fall Line Hills.

GEORGIA SPECIMENS EXAMINED.—I have examined a total of 473 specimens from 83 localities in the following counties: Baker (7), Berrien (2), Brantley (1), Brooks (2), Calhoun (3), Camden (4), Charlton (3), Clinch (1), Colquitt (3), Cook (1), Decatur (5), Dougherty (7), Early (5), Echols (1), Grady (6), Lanier (3), Lee (2), Lowndes (5), Miller (5), Mitchell (2), Seminole (4), Sumter (1), Terrell (3), Thomas (4), Tift (1), Ware (1), and Worth (1).

VARIATIONS.—Variations in this crayfish are abundant; the rare occurrence of some of them make preparing diagnoses of the species of the subgenus *Scapulicambarus* difficult and the preparation of a key to aid in the recognition of all members of the three species occurring in Georgia virtually impossible. As pointed out in the "Diagnosis," most individuals exhibit rostra (Figure 190*a*-f) with at least angular margins at the base of the acumen, but in a few that have been found in Georgia and Florida there is hardly any interruption of the margin. The branchiostegal, cervical, and postorbital spines range from being rather well developed to very inconspicuous tubercles, and occasionally the postorbital spine is obsolete. The limits of the ratios involving the length and width of the areola are rather broad as noted in "Diagnosis," and, on the basis of the limited number of specimens available from some of the watersheds, the areolae of individuals in the Saint Marys and Satilla river basins appear, in general, to be proportionately both longer and narrower than in specimens from elsewhere in Georgia, averaging 34 percent of the total length of the carapace and 16.1 times as long as broad. Samples of populations from the Suwannee Basin appear to have the shortest areolae, constituting an average of only 31.7 percent of the entire length of the carapace, and those from the Ochlockonee and Aucilla seem to have the broadest, averaging 9.0 and 10.1 times as long as broad, respectively. To be sure, these ratios calculated on specimens from the several watersheds overlap (Table 3) so that the river basin from which a

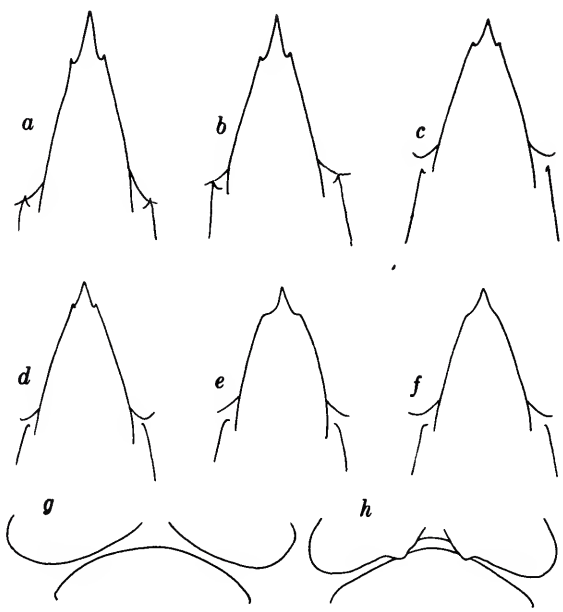


FIGURE 190.—*Procambarus (S.) paeninsulanus*, variations (*a-f*, rostrum in males; *g*, *h*, sternum and anterior margin of annulus ventralis of female): *a*, Cook Co; *b*, Charlton Co; *c*, *d*, *f*, Camden Co; *e*, Decatur Co; *g*, Bacon Co; *h*, Dougherty Co.

specimen has been taken cannot be determined by them. For example, while in no specimen from outside of the Satilla Basin does the areola constitute as much as 35.6 percent (the maximum among Georgia specimens) of the total length of the carapace, one specimen from the Suwannee Basin (in which the shortest areola occurs) exhibits a corresponding ratio of 28.8 percent.

Variations in the first pleopod of the first form male are also somewhat more extensive than in most of the Georgia crayfishes. The shoulder on the cephalic surface ranges from a broadly rounded hump (Figure 191*e*) to one in which the angle is produced distally in a subacute prominence (Figure 191*i*). The free end of the cephalic process may be acute (Figure 191*i*) or rounded (Figure 191*m*). The caudal element may include a well-developed caudal knob (Figure 191*a*) or it may be lacking (Figure 191*i*); the caudal process, although always leaflike, may be flattened or loosely folded obliquely or longitudinally (Figure

TABLE 3.—Variation in ratios involving areola length in *Procambarus (Scapulicambarus) paeninsulanus* (ratios for carapace length and postorbital carapace length × 100; averages in parentheses)

River Basins	Number of Specimens	Ratios		
		Areola length / Carapace length	Areola length / Postorbital carapace length	Areola length / Areola width
Chattahoochee-Flint	43	29.1-35.3 (32.8)	39.7-45.3 (43.2)	7.1-19.0 (13.2)
Ochlockonee	6	31.0-33.8 (32.2)	40.1-45.5 (41.8)	6.5-14.1 (9.0)
Aucilla	7	33.0-34.0 (33.2)	42.9-44.1 (43.5)	7.8-14.4 (10.1)
Suwannee	14	28.8-35.3 (31.7)	40.1-44.9 (42.7)	5.8-17.2 (13.1)
Saint Marys-Satilla	14	32.4-35.6 (34.0)	42.9-45.9 (44.3)	10.2-22.4 (16.1)

191*c*). Throughout most of the range of the species in Georgia the sternal plate immediately cephalic to the annulus ventralis in the female is usually unadorned (Figure 190*g*), but in two localities in the Flint River basin in Dougherty and Lee counties, there are small paired prominences that project caudally over the cephaloventral surface of the annulus (Figure 190*h*) as they do in certain members of the species in Florida. Such prominences, although much better developed (Figure 188), are typical of the females of *P. (S.) howellae*, and the fact that this variation occurs in a part of the Flint Basin where the ranges of the two species are not delimited by a discernible barrier suggests that a gene exchange between the two may well occur. The likelihood that such an exchange is taking place seems probable if one compares the distal part of the first pleopod of the only available specimen (first form male) from Marion County (Figure 187*a*), tentatively identified as *P. (S.) howellae*, with those of the same species and *P. (S.) paeninsulanus* (Figure 191). The identifications of juvenile specimens of the latter from Lee and Sumpter counties most assuredly are tentative, and adults of both sexes are needed from these and other localities in the Fall Line Hills and upper Dougherty Plain segments of the Flint Basin to determine whether or not a gene flow between the two assumed species is occurring where the ranges are approximate.

SIZE.—The largest specimen available from Georgia is a female from the Flint Basin in Dougherty County that has a carapace length of 49.5 (postorbital carapace length 39.2) mm. Corresponding lengths of the smallest and largest first form males are 23.9 (18.2) mm and 41.2 (30.4) mm, respectively, and those of the smallest ovigerous female, 28.3 (20.8) mm.

LIFE HISTORY NOTES.—First form males have been collected in Georgia during every month of the year except February, July, August, and December, and in Florida they were obtained during February and July (Hobbs, 1942b:105) as well; thus it is highly probable that first form males occur throughout the year. Ovigerous females have been found in August, September, and October in Georgia and Florida, and also in March, April, and November (Hobbs, 1942b:105) in Florida. Females carrying young were found in August and December in Georgia, and from August to November in Florida (Hobbs, 1942b:105). It seems likely that the life history of this species parallels that of its close relative *P. (S.) clarkii* as recounted by Penn (1943).

The following data were obtained from six females, collected in Georgia, that were carrying eggs or young:

Carapace and postorbital carapace lengths (mm)	*Number of eggs, young*	*Diameter of eggs (mm)*
23.5 (17.3)	81e	1.6–1.8
28.3 (20.8)	1e, 64y	1.8
28.6 (22.5)	211e	1.6–1.8
29.0 (22.4)	1e, 75y	1.8
32.5 (31.2)	98e	1.8–1.9
36.4 (28.0)	363e	1.8

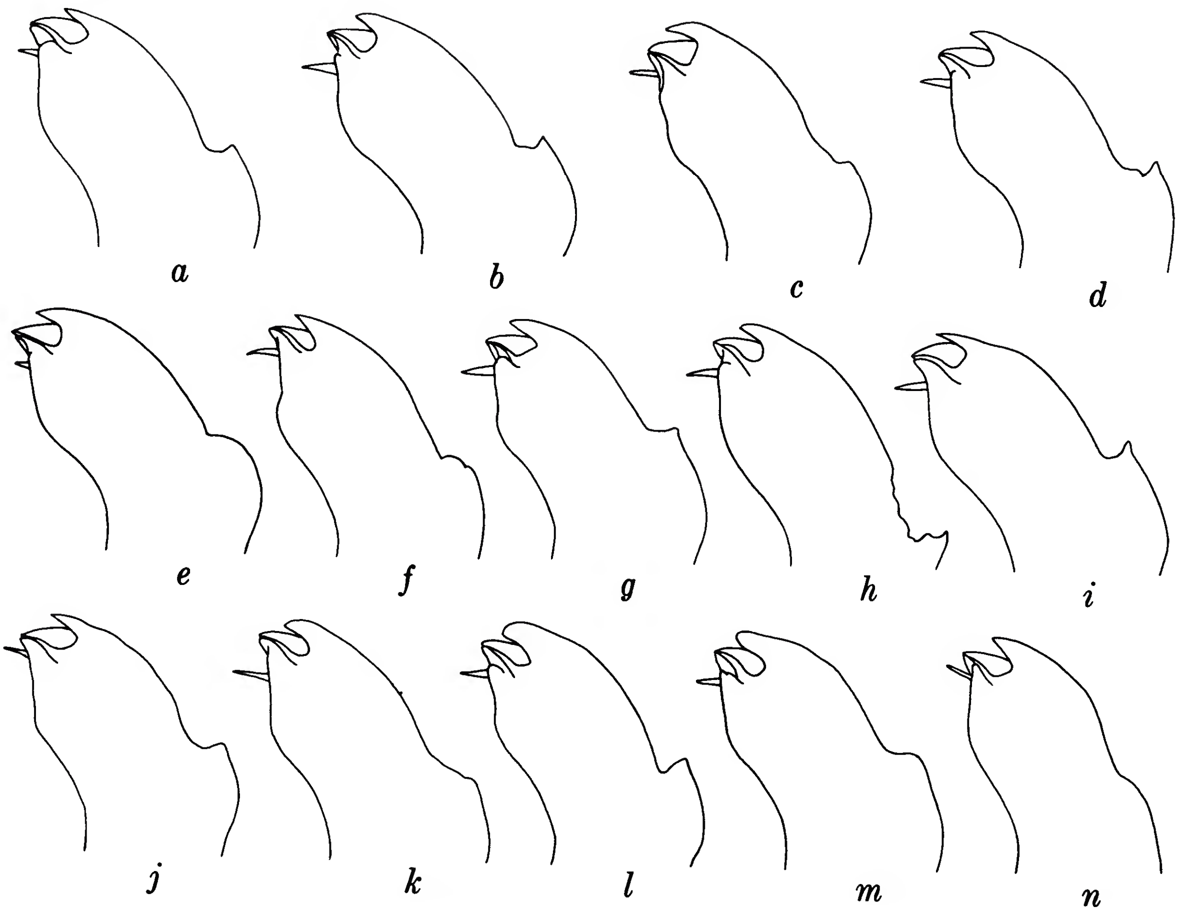


FIGURE 191.—*Procambarus (S.) paeninsulanus*, variations in left first pleopod of first form male (lateral view). Flint Basin: *a*, Seminole Co; *b*, Early Co; *c*, Dougherty Co; *d*, Mitchell Co; *e*, Decatur Co; *f*, Miller Co; *g*, Calhoun Co; *h*, Baker Co. Ochlockonee Basin: *i*, Grady Co; *j*, Colquitt Co. Aucilla Basin: *k*, Thomas Co. Suwannee Basin: *l*, Cook Co. Saint Marys Basin: *m*, Charlton Co. Satilla Basin: *n*, Camden Co.

The remarks of Hobbs (1942b:107) relative to certain reproductive habits of the species in Florida are in agreement with observations made in Georgia.

It seems probable that in many instances copulation occurs in the burrows, that the pair separates (there is evidence that it is the male which leaves the burrow) and that the female lays her eggs and remains in the burrow for a considerable period after they have hatched. First form males and females have been found together in burrows all over the range, and practically all of the females carrying eggs or young were found in burrows.

Although I have excavated literally hundreds of crayfish burrows and have found pairs of crayfishes in many of them, seldom have I found ovigerous females sharing a tunnel system with an adult member of either sex. In excavating a burrow located in a roadside ditch 6.5 miles north of Valdosta, Lowndes County, I found that it was forked instead of consisting of a single vertical passage. An ovigerous female was found at the end of one of the tunnels and a first form male in the other. This joint occupancy of a burrow suggested to me that the two had entered a simple unbranched burrow prior to a dry season, and following amplexus, when I presume the male usually departs or is driven out, the water in the ditch had receded, leaving no convenient escape.

As an alternative to moving overland in search of an unoccupied burrow or some other water source, the male constructed a secondary downward sloping gallery in which it remained, awaiting the flooding of the entrance to the original burrow, permitting its departure.

Seasonal Data

Sex/stage	*J*	*F*	*M*	*A*	*M*	*J*	*J*	*A*	*S*	*O*	*N*	*D*	*?*
♂I	3		7	6	2	8			11	3	1		
♂II	8		6	6	2	36			18	5	1	1	
♀	6		21	6	8	41	1	2	13	6	1		1
♂j	11	3	13	45	1	6			20	12	3	4	5
♀j	14	1	5	37		11		4	25	11	1	2	2
♀ ovig								1	1	3			
♀ with young										2		1	

Ecological Notes.—In commenting on the habitats occupied by this crayfish in Florida, Hobbs (1942b:106) stated that "it has been collected in ponds of all types, lakes, roadside ditches and excavations, sand bottomed and flatwoods streams, rivers, small springs, and burrows." As pointed out by him, in waters supporting vegetation, this crayfish occurs among the lower parts of the mats or in debris during the daylight hours; if macrophytes are lacking, the crayfish seeks cover during the day in debris or shallow burrows in the stream bank, abandoning their hiding places at night to wander about the stream bed. In roadside ditches and temporary ponds, the young occur in open water, ambling here and there throughout the daylight hours, and at least a limited number of adults do likewise, but when disturbed most of the latter take cover in burrows that litter the bottom of the pools. A few of the adults and most of the young scurry away from the source of a disturbance, often swimming so rapidly they find themselves propelled onto the banks. When the water recedes or prior to mating and egg laying, the crayfish, either singly or in pairs, retreat to burrows that usually consist of a single subvertical passageway that reaches depths as great as 1.5 meters and almost always extends below the water table. I have found individuals in tunnels that, while moist, contained no standing water.

Whereas there are numerous records of mass migrations of *P. (S.) clarkii* (see Penn, 1943:15), such have not been reported to occur in *P. (S.) paeninsulanus*. That members of the species do at least occasionally abandon burrows and open water was attested to by Hobbs (1942b:107): "On a cloudy day in February a specimen was taken from the middle of a road several hundred yards from the nearest body of water. At another time one was collected on high, well drained land about a quarter of a mile from the nearest body of water."

A rather unique colony of this crayfish in Alachua County, Florida, was described by Hobbs (1942b:107) as follows:

> ... in a seepage area along the edge of a small fluctuating pond... numerous burrows of *paeninsulanus* are crowded together in an acre plot. The pond is shallow and rises and falls considerably with the season. In wet weather it often covers the entire area, flooding the burrows of the crayfish, but most of the year it is not so extensive. Time and again I have endeavored to catch specimens with a dip net from the vegetation in the pond proper but have always failed. In the wide exposed margin, however, one may dig a hundred specimens in an hour. The simply constructed burrows are in water-soaked muck which is overgrown with grass and hydrophytic plants, and the digging for crayfish is not at all difficult. The burrows are seldom more than two feet deep and usually consist of a vertical shaft with one or two side passages. During the dry seasons the water table in this area is from four to twelve inches below the surface. The chimneys usually consist of a mount of the discarded muck and have no particular shape.

Georgia Crayfish Associates.—Collected with *Procambarus (S.) paeninsulanus* are the following species (the number of shared localities is noted in parentheses): *Cambarus (D.) latimanus* (1), *C. (D.) striatus* (1), *C. (L.) diogenes diogenes* (8), *Fallicambarus (C.) hedgpethi* (2), *Faxonella clypeata* (17), *Procambarus (H.) pygmaeus* (3), *P. (H.) talpoides* (3), *P. (L.) pubischelae pubischelae* (3), *P. (O.) fallax* (3), *P. (O.) seminolae* (4), *P. (Pe.) gibbus* (2), and *P. (Pe.) spiculifer* (21).

Procambarus (Scapulicambarus) troglodytes (LeConte)

Figures 16*d*, 182*a*, 183*h*, 185, 192–194, 262

Astacus troglodytes LeConte, 1856:400*.—Hagen, 1870:9*, 42*, 43.

Astacus fossarum LeConte, 1856:401* [syntypes, MCZ 3377 (♂I dry), ANSP 314 (♀); type-locality, ditches, lower Georgia].—Hagen, 1870:9*, 10, 43.—Faxon, 1884:136; 1885a: 28*.—Underwood, 1886:373*.—Harris, 1903a:107*, 130*.—Hobbs, 1972a:2*.

Astacus maniculatus LeConte, 1856:401*[types not extant; type-locality, ditches, lower Georgia].—Hagen, 1870:10.—Hobbs, 1972a:2*; 1974b:66*.

Cambarus troglodytes.—Hagen, 1870:20, 37, 38, 41-43* [in part], 44, 45, 48, 97*, 100*, 106, pl. I: figs. 11-14, pl. III: fig. 141.—Forbes, 1876:18.—Faxon, 1884:136-137*, 138; 1885a:8, 10, 21, 22, 26-28*, 29, 37, 157*, 167*, 169, 173*, 179; 1885b:358; 1914:414*.—Underwood, 1886:373*.—Hay, 1899b:959*.—Ortmann, 1902:277.—Harris, 1903a: 58*, 107, 130*, 138*, 142, 143, 151, 152*, 154, 156.—Newcombe, 1929:279.—Crocker, 1957:30.—Hobbs, 1972a:2.

Cambarus troglodytus.—Hagen, 1870:33 [erroneous spelling].

Cambarus maniculatus.—Hagen, 1870:34, 52-53*, 83, 97*, 100*, 107.—Faxon, 1884:137*; 1885a:8, 19, 29, 158*, 167*, 173*; 1914:427*.—Underwood, 1886:370*.—Harris, 1903a:107*, 151, 152*.—Hobbs, 1972a:2.

Cambarus fossarum.—Hagen, 1870:53, 100*.—Faxon, 1885a: 27.

Cambarus troglodyles.—Herrick, 1882:254 [erroneous spelling].

Cambarus (Cambarus) troglodytes.—Ortmann, 1905a:102, 105*, 128*, 129; 1905d:437.

Cambarus (Ortmannicus) troglodytes.—Fowler, 1912:341 [by implication].—Creaser, 1934:4 [by implication].

Procambarus troglodytes.—Hobbs, 1942a:342 [by implication]; 1942b:99, 100, 105; 1952b:165, 173*, fig. 2; 1958a:88; 1958b:163; 1959:885*; 1962:273, 290*, 291, fig. 61; 1966b: 68, 70, 71; 1968b:K-11*, fig. 22c.—Hobbs and Freeman, 1956:10.—Crocker, 1957:30.—Crawford, 1959:150, 151, 156, 162, 171, 172, 177, 180, 181.—Hobbs III, 1969:42.—Hart and Hart, 1974:21*, 22, 28, 32*, 33, 71, 88*, 91, 131*.—Page, 1974:97*.—Peters, 1975:20, 22.—Wharton, 1978:46*.

Procambarus paeninsulanus.—Hobbs, 1942b:105* [in part].

Procambarus (Scapulicambarus) troglodytes.—Hobbs, 1972a:12; 1972b:72*, 152*, 154*, 155, fig. 56e; 1974b:66*, fig. 284; 1977a:419.—Hobbs III, Thorp, and Anderson, 1976:3, 10, 43*-44, figs. 19, 24.

These citations are believed to constitute a complete bibliography for the species; those followed by an asterisk contain references to Georgia.

SUMMARY OF LITERATURE.—Following the description of this crayfish by LeConte (1856), apparently there was some confusion on the parts of several of the earlier workers as to the identity of the species (Faxon, 1884:137-138), but with the appearance of Hagen's (1870) monograph, except for erroneous localities (all of those outside of Georgia and South Carolina), the identity of LeConte's species became clear, and both Hagen and Faxon (1885a) agreed that LeConte's *Astacus fossarum* was a synonym of the species they called *Cambarus troglodytes.* There is no evidence that any subsequent student of crayfishes saw one of LeConte's specimens of his *Astacus maniculatus*, and his description of it does not permit its separation from subsequently obtained specimens of his *A. troglodytes*, in which the areola suture is very slender, virtually reduced to a line, apparently the only character prompting Hagen (1870:53) to recognize *Cambarus maniculatus.* Faxon (1884:137) listed *Cambarus maniculatus* as occurring in "Lower Georgia," but noted that it was "known only through LeConte's description, which perhaps was drawn up from an immature specimen of *C. troglodytes.*" Faxon (1885a:29) also listed it in his revision of the Astacidae but reiterated the above statement, and, in 1914 (p. 427), listed it as a "doubtful species." No further disposition of, or comments on, LeConte's *A. maniculatus* appeared until Hobbs (1974b:66) included it along with *Astacus fossarum* under the synonomy of *Procambarus (Scapulicambarus) troglodytes.*

Faxon (1885a:27-28) summarized the known locality records including three in South Carolina (Charleston, Oakley, and Columbia), two in Georgia (neighborhood of Augusta, Richmond County, and "Lower Georgia"), and one in Illinois, the latter based on a specimen for which he questioned the accuracy of the locality label. Certainly this species does not occur in Illinois. Although several subsequent new records of the occurrence of this crayfish in South Carolina have appeared (Hobbs and Freeman, 1956; Crawford, 1959; Hart and Hart, 1974; and Hobbs III, Thorp, and Anderson, 1976), only four additional records have been cited for Georgia (Hart and Hart, 1974): in Burke, Chatham, Liberty, and McIntosh counties. The studies of Crawford and of Hart and Hart are directed toward a knowledge of the ostracod symbionts of crayfishes, and the ostracods reported by the latter in Georgia were obtained from crayfishes used in the present study. The best existing account of what little is known of the species is that of Hobbs III, Thorp, and Anderson (1976). All other references prior to 1972 that are cited in the synonomy consist of keys, repeat information presented by Hagen or Faxon, are concerned with statements of affinities of this crayfish with other, for the most part, new species, or involve nomenclatural changes. Those appearing subsequent to 1972 add little to our knowledge of the species.

Diagnosis.—Rostrum usually with marginal spines, tubercles, or angles at base of acumen, and rarely with low median carina. Carapace with 1 pair of cervical spines or tubercles. Areola 13.9 (rarely less than 18) to more than 50 (average 29.1) times as long as wide and constituting 31.9 to 37.6 (average 35.0) percent of entire length of carapace (41.5 to 47.7, average 44.9, percent of postorbital carapace length). Antennal peduncle with or without tubercle (adults rarely with strong spine) on ischium. Ventral surface of basis and usually proximal half of ischium of third maxilliped with variable quantity of long plumose setae among simple stiff ones. Basis of cheliped without mesial spine. Mesial surface of palm of chela of male with row of 5 to 8 (usually 6) prominent tubercles. Male with simple hook on ischia of third and fourth pereiopods, neither opposed by tubercle on corresponding basis, and conspicuous caudomesial boss on coxae of fourth and fifth pereiopods. First pleopods asymmetrical and reaching coxae of third pereiopods; cephalic surface of left member of pair with prominent shoulder (that of right member folded caudomesially in first form male) at base of distal third of shaft; latter with convex caudal margin distal to level of shoulder; subapical setae moderately abundant and situated laterally; mesial process acute, rather short, directed caudodistally, its tip often bent mesially; cephalic process, most conspicuous of terminal elements, forming large, laterally compressed, distally rounded lobe borne on cephalodistal half of shaft; central projection corneous, acute, and usually largely obscured, particularly in lateral aspect, by caudal element; latter highly variable with caudal knob and corneous process usually not clearly delimited, latter either forming prominent caudodistal ridge or scooplike prominence on caudodistal extremity of shaft; adventitious process consisting of corneous ridge mesially. Female with sternum anterior to annulus ventralis usually unadorned, very rarely bearing single pair of low, symmetrically arranged prominences; cephalomedian part of annulus with paired, rounded elevations, together forming oval to rounded eminence almost bisected by cephalic part of sinus; first pleopod present.

Male, Form I (from 7.6 miles west of Midway on State Route 38, Liberty County, Georgia).—Body (Figure 192*a,h*) subovate, compressed laterally. Abdomen narrower than thorax (16.3 and 19.5 mm). Width of carapace slightly greater than depth at caudodorsal margin of cervical groove (19.5 and 18.7 mm). Areola 38.3 times as long as broad, with 1 punctation in narrowest part. Cephalic section of carapace 1.7 times as long as areola, length of latter 37.4 percent of total length of carapace (46.2 percent of postorbital carapace length). Rostrum subplane dorsally with slender convergent margins weakly angulate at base of acumen, lacking marginal spines or tubercles; upper surface with scattered punctations between submarginal rows; acumen clearly defined basally and reaching anteriorly to base of ultimate podomere of antennular peduncle; subrostral ridges weak and evident in dorsal view along no more than basal fifth of rostrum. Postorbital ridges well developed, grooved dorsolaterally, and ending cephalically in very small tubercles. Suborbital angle rounded and almost obsolete. Branchiostegal spine moderately strong. Carapace punctate dorsally and tuberculate laterally, thickly so in anteroventral branchiostegal area, tubercles rather sparse cephalolaterally except in mandibular adductor region and along cervical groove in mandibular region; cervical spine acute, rather small, and flanked dorsally by tubercle slightly larger than others nearby. Abdomen subequal in length to carapace (39.2 and 40.9 mm). Cephalic section of telson with 4 spines in right and 3 in left caudal corners, all fixed except that immediately lateral to mesialmost on

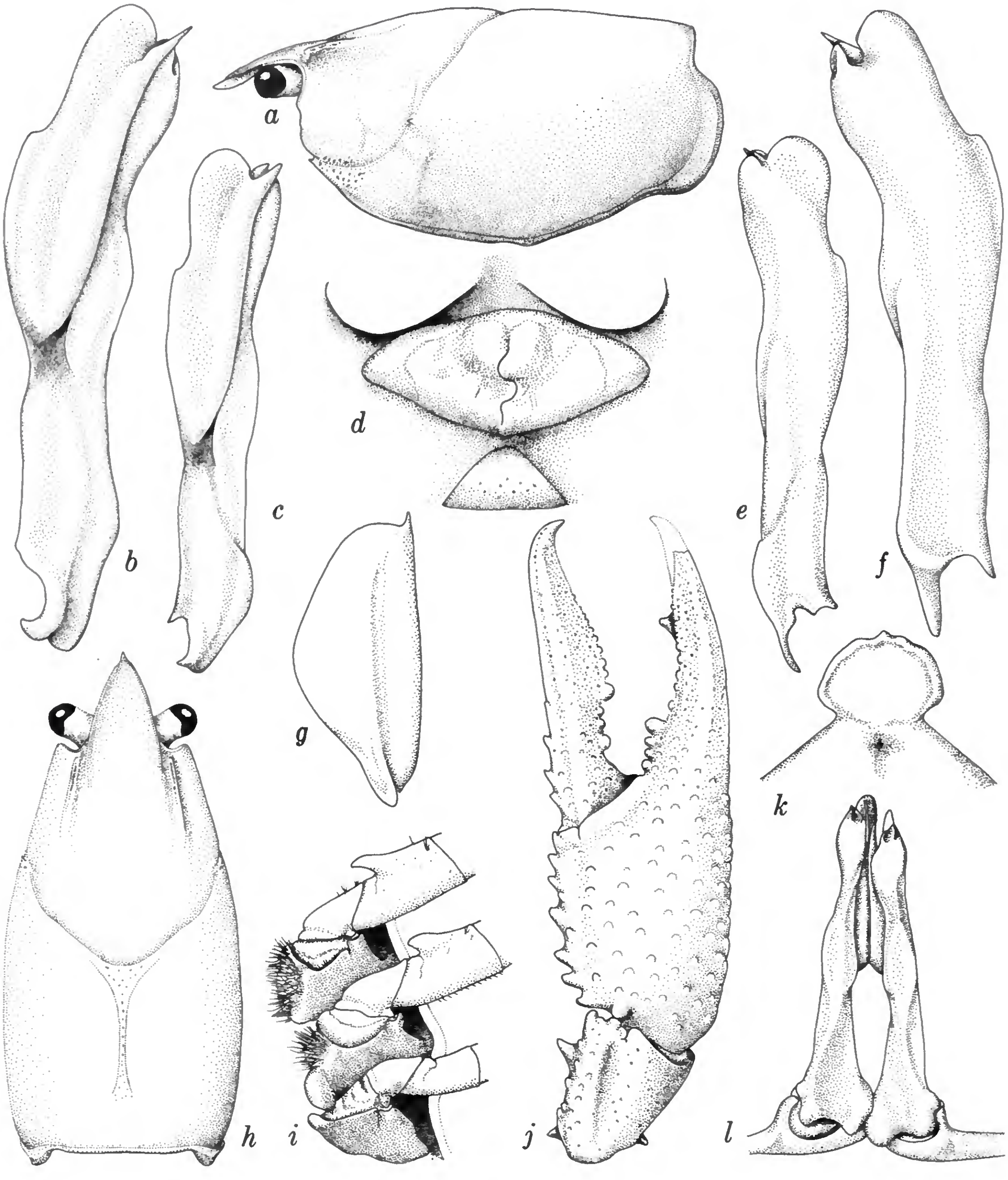


FIGURE 192.—*Procambarus (Scapulicambarus) troglodytes* from Liberty Co, Georgia (*c, e,* second form male from Gouldins Creek about 5 mi SW of Wilderness Church off US Hwy 82; *d,* from female; all others from first form male from 7.6 mi W of Midway on St Rte 38): *a,* lateral view of carapace; *b, c,* mesial view of first pleopod; *d,* annulus ventralis; *e, f,* lateral view of first pleopod; *g,* antennal scale; *h,* dorsal view of carapace; *i,* proximal podomeres of third, fourth, and fifth pereiopods; *j,* dorsal view of distal podomeres of cheliped; *k,* epistome; *l,* caudal view of first pleopods.

both sides. Uropods with both lobes of basal podomere bearing corneous spine; mesial ramus with distinct spine on lateral margin and distomedian one far removed from margin; lateral ramus with usual row of small spines immediately proximal to transverse suture and larger ones at lateral extremity of suture. Cephalic lobe of epistome (Figure 192*k*) broadly rounded, with short, subangular anteromedian prominence, flanked laterally by weak marginal undulations; main body with conspicuous fovea in suboval depression; epistomal zygoma arched. Antennule of usual form, with rather prominent spine near midlength of ventral surface. Antenna extending caudally slightly beyond base of telson; peduncle with acute lateral spine on basis and rather small acute tubercle on ventral surface of ischium; antennal scale (Figure 192*g*) about 2.3 times as long as wide, broadest at about midlength, where lamellate section about 2.4 times as broad as thickened lateral part, latter terminating in moderately strong corneous-tipped spine. Ventral surface of ischium of third maxilliped studded with conspicuous mat of long and short plumose setae (becoming somewhat shorter in distal third) among and outnumbering stiff simple ones.

Right chela (Figure 192*j*) about 3.0 times as long as broad, subovate in cross section and somewhat depressed. Mesial surface of palm with row of 7 tubercles subtended dorsally and ventrally by irregular rows of 3 to 5; entire palm tuberculate. Fixed finger with low, rounded median longitudinal elevation dorsally and ventrally, flanked by tubercles proximally and setiferous punctations along at least distal four-fifths; lateral margin of finger with row of similar punctations; opposable margin with row of 13 tubercles along proximal two-thirds, proximal 4 increasing in size distally, fifth much smaller than fourth, and more distal ones decreasing in size distally; additional row of 7 (6 on left chela) tubercles present on lower level, penultimate member, situated near base of distal third, largest; minute denticles forming single row along middle third of finger and arranged in band along distal third. Dactyl with dorsal and ventral surfaces similar to those of fixed finger, mesial surface with row of 4 tubercles, decreasing in size distally, along basal third of finger; opposable margin with row of 14 tubercles extending along proximal two-thirds, fourth from base largest, first next, otherwise decreasing in size distally; width of dactyl narrower proximal to level of fourth tubercle than in middle third; minute denticles occurring between all tubercles distal to fourth from base and forming band between distalmost tubercle and corneous tip of finger.

Carpus of right cheliped longer than broad (12.2 and 8.3 mm), mesial and dorso- and ventromesial surfaces tuberculate, otherwise punctate; larger tubercles as follows: 1 on mesial surface, 1 at dorsomesial distal angle, 1 on ventrolateral condyle, and another on ventral distomesial margin.

Merus of right cheliped tuberculate dorsally, ventrally, and distomesially, punctate elsewhere; dorsal surface with 2 subspiniform tubercles near distal margin and smaller one distomesially on margin; ventral surface with irregular lateral row of 14 (left with 12) tubercles, more regular mesial row of 16 (left with 18) and oblique distal row of 5 joining mesial and lateral rows; tubercles of mesial and lateral rows not graduated in size, but in general more distal ones larger. Ischium with row of 5 small tubercles.

Hooks on ischia of third and fourth pereiopods (Figure 192*i*), both simple and that on third overreaching basioischial articulation, neither opposed by tubercle on basis. Coxa of fourth pereiopod with conspicuous, vertically oriented caudomesial boss; that on coxa of fifth less prominent and compressed in longitudinal plane of body.

Sternum between third, fourth and fifth pereiopods moderately deep and bearing fringe of plumose setae on ventrolateral margins.

First pleopod (Figure 192*b,f,l*) as described in "Diagnosis."

FEMALE (also from 7.6 miles west of Midway, Liberty County, Georgia).—Differing from first form male, other than in secondary sexual characters, as follows: rostrum with minute marginal tubercles at base of acumen; suborbital angle obsolete; cervical and branchiostegal spines very small; cephalic section of telson with 3 spines in each caudolateral corner but with rudiment of fourth (mesially) in both; epistome with small spine on anterodextral border; spines on basis and ischium of antennal peduncle reduced in size, rather inconspicuous; chela (Figure 183*h*) about 2.4 times as long as broad, mesial margin of palm with row of 6 tubercles; opposable margin of fixed finger with single row of 10, third from base largest, and more ventral row represented by single large tubercle at base of distal third, minute denticles arranged in single row; opposable margin of dactyl with row of 11 tubercles; both fingers with moderately conspicuous tufts of plumose setae at ventral base; tubercle on dorsodistal margin of merus very small, mesial and lateral rows on ventral surface consisting of 13 tubercles each and 4 in oblique row; ischium with row of 4 tubercles. (See "Measurements.")

Annulus ventralis (Figure 192*d*) subspindle shaped, approximately 2.2 times as wide as long, lateral parts less strongly sclerotized than median three-fifths; weakly sculptured except in cephalomedian area, where paired elevations (together forming subcircular prominence) bisected by cephalic part of sinus, latter, following slightly tilted S-shaped course along median line, terminating short distance anterior to caudal margin of annulus. Postannular sclerite subtriangular, about 1.9 times as broad as long, and half as long and almost 0.42 as wide as annulus, and rather strongly arched transversely near midlength. Sternum immediately anterior to annulus lacking tubercles or prominences. First pleopod reaching slightly anterior to caudal margin of sternum between fourth pereiopods.

MALE, FORM II (from Gouldins Creek off State Route 82, Liberty County, Georgia).—Differing from first form male in following respects: marginal spines on rostrum well defined, acumen slightly overreaching antennular peduncle; postorbital, cervical, and branchiostegal spines well developed; cephalic section of telson with 3 spines in each caudolateral corner; epistome more truncate anteriorly, with anterolateral acute prominences; antennal peduncle with well-developed spines on basis and ischium; third maxilliped with less conspicuous plumose setae on lateral half of ventral surface of ischium; opposable surface of fixed finger of chela with 13 tubercles in dorsal row and only 2 representing ventral row, corresponding surface of dactyl with row of 12 tubercles; distal part of band of minute denticles on opposable margins of both fingers narrower than in first form male; ventral surface of merus with lateral row of 14 tubercles, mesial of 15, and oblique one represented by 2; ischium with 4; hooks on ischia of third and fourth pereiopods and bosses on coxae of fourth and fifth pereiopods greatly reduced in size. (See "Measurements.") First pleopod (Figure 192*c*,*e*) with distal part less caudally inclined, anterior-posterior plane of cephalic process longer, and caudal knob area of caudal element not so distinctly delimited from caudal process; left pleopod with cephalic shoulder not folded mesially; juvenile oblique suture clearly defined.

COLOR NOTES (Figure 182*a*).—Carapace reddish brown with brick red to black markings dorsally, fading to pinkish cream ventrally; rostrum, more red than brown dorsally, with black margins; postorbital ridges, paired spots on gastric region, and paired dorsolateral stripes on branchiostegites also black; these stripes extending from, or almost from, areola caudally to caudal flange, flange and ventral margin of carapace black; cephalic triangular part of areola brick red; anterior part of antennal, mandibular, and anteroventral branchiostegal regions pinkish cream to white. Abdomen with broad, median dorsal dark brown stripe extending from first to sixth abdominal tergum, it, in turn, flanked by narrower pinkish cream stripes flecked with red, and these stripes delimited ventrally by black, somewhat undulating (often broken) line at base of pleura; remainder of latter dark brown, flecked with red and occasionally with cream to white spot adjacent to ventral margin. Dark dorsomedian stripe on abdomen sometimes bisected by lighter median one extending from second onto sixth tergum. First through fifth terga with dark red caudal margin. Telson and uropods tan to brown, flecked with red. Antennule and antenna mostly reddish brown. Cheliped, from midlength of merus distally, dark brown with reddish orange to orange tubercles, and ventral surface orange red; remaining pereiopods orange cream proximally, becoming dark brown on distal part of merus, then progressively lighter distally; ventral surface of body orange to pinkish cream.

Measurements (mm)

	Male, form I	*Female*	*Male, form II*
Carapace			
Height	18.7	16.5	14.9
Width	19.5	16.4	15.0
Entire length	40.9	35.0	33.1
Postorbital length	33.1	27.9	25.5
Areola			
Width	0.4	0.4	0.4
Length	15.3	12.1	11.2
Rostrum			
Width	6.2	5.6	5.4
Length	8.6	8.2	8.5
Chela			
Length of mesial margin of palm	13.5	7.3	6.1
Width of palm	14.0	8.6	6.2
Length of lateral margin	39.5	22.2	19.2
Length of dactyl	23.6	13.6	11.7
Abdomen			
Width	16.3	15.1	12.8
Length	39.2	35.9	32.4

TYPES.—Syntypes, MCZ 3375 (♂I dry), ANSP 4175 (fragments).

TYPE-LOCALITY.—Rice fields in Georgia. Inasmuch as LeConte owned a plantation in the vicinity of Riceboro, in Liberty County, it seems reasonable to assume that his specimens came from somewhere in the vicinity of his home.

RANGE.—Between the Altamaha and Pee Dee rivers in Georgia and South Carolina. In Georgia it is largely confined to the Canoochee, Newport, Ogeechee, and Savannah basins, although it has been found in other short tributaries of the lower Altamaha River. Within the Savannah Basin it ranges from the Fall Line Hills through the Vidalia Upland to the Barrier Island Sequence districts, and in the other watersheds it appears to be confined to the latter two physiographic areas.

GEORGIA SPECIMENS EXAMINED.—I have examined a total of 420 specimens from 47 localities (Figure 185) in the following counties in Georgia: Bryan (10), Bulloch (4), Burke (6), Candler (2), Chatham (4), Effingham (1), Glascock (1), Jefferson (1), Jenkins (1), Liberty (8), Long (1), McIntosh (2), Richmond (1), Screven (3), Tattnall (1), and Washington (1).

VARIATIONS.—The most conspicuous variations appear to be those associated with age and stage in the molting cycle. In general, the young have longer rostra with better developed marginal spines than do most adults, and in many of the older specimens, especially those in late intermolt stages (with heavily encrusted exoskeletons), the marginal spines are frequently obsolete, leaving little if any evidence of their position (Figure 193 *a–d*) when the animal was smaller. The size of the cervical and postorbital spines seems to follow a similar pattern, both occasionally being reduced to tubercles. At least in some localities, the areola is proportionately broader in juveniles than in adults, and a tendency (although far from absolute among adults) is suggested that with increase in size of the individual the areola becomes narrower, in some reduced almost to a line.

Among the conspicuous variations are those in the first pleopod of the first form male. Although larger series must become available to determine whether or not any of those pointed out are restricted to a part of the range, the major differences are as follows: (1) the mesial process may be almost straight, directed caudodistally, or its distal part may be weakly or strongly bent mesially; (2) the cephalic process, although always occurring in the form of a somewhat compressed rounded lobe, has a caudodistal margin that may be evenly convex (Figure 194*j*) or strongly concave (Figure 194*l*); the gap left between it and the caudal process may be broad or very narrow (Figure 194*i,j*); and (3) the caudal process may extend caudally in the form of a submedian ridge (Figure 194*h*) or it may be

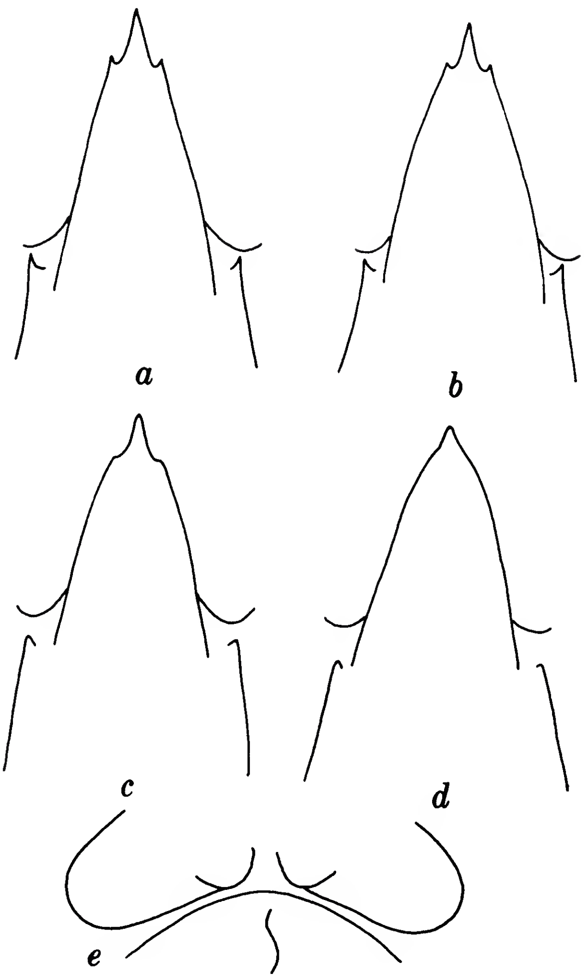


FIGURE 193.—*Procambarus (S.) troglodytes*, variations (*a-d*, rostrum; *e*, sternum and anterior part of annulus ventralis): *a*, *b*, Russell Swamp Creek, North Newport Basin, Liberty Co; *c–e*, Brier Creek, Savannah Basin, Burke Co.

broadly concave (Figure 194*o*). There is perhaps less variation in the annulus ventralis than in that of many species, and the comparatively flattened surface interrupted by a suboval or subcircular elevation bisected by the sinus and anteromedian furrow are unique among the Georgia crayfishes. The sternum immediately anterior to the annulus is unadorned except in a few specimens from Burke County, in which rather low, paired lobes flank the median trough (Figure 193*e*). The usual variations occur in the disposition of spines and tubercles on the chelipeds and telson.

SIZE.—The largest specimen available is a first form male from Chatham County, having carapace length of 44.7 (postorbital carapace length 35.9) mm. Corresponding lengths of the smallest first form male are 30.9 (24.0) mm. Females with eggs or young are unknown.

LIFE HISTORY NOTES.—First form males have been collected from February to June and in December. Few specimens were collected from July to November, when it is probable that ovigerous females are likely to be present in the population. Even among the several hundred specimens of the species available from South Carolina, obtained throughout most of the year, neither females carrying eggs nor ones with young are represented. Thus, as pointed out by Hobbs III, Thorp, and Anderson (1976:44), females "...probably burrow prior to ovulation." Such seems to be characteristic in the life cycle of *P. (S.) clarkii*, *P. (S.) howellae*, and *P. (S.) paeninsulanus* and might well be anticipated in this related species. The few ovigerous females available, of the latter two species from Georgia, would lead one to suspect that in all the members of the subgenus occurring in the state, ovulation takes place in the summer or early fall, and, if the life cycle is similar to that of *P. (S.) clarkii* (see Penn, 1943), they reach adulthood by late spring or early summer of the following year. Most individuals probably do not survive more than two and a half to three years.

Seasonal Data

Sex/stage	*J*	*F*	*M*	*A*	*M*	*J*	*J*	*A*	*S*	*O*	*N*	*D*	*?*
♂I		1	1	6	2	1						4	7
♂II	4		3	14	25	8	1		2		1	12	5
♀	6	2	6	21	28	11	1	1	1			17	16
♂j	11		7	46	16			3	1			18	3
♀j	17		6	38	20	4		5	5	1		9	3

ECOLOGICAL NOTES.—Judging by its crayfish associates alone, one might correctly conclude that *P. (S.) troglodytes* has a broad ecological tolerance, occurring in such diverse habitats as

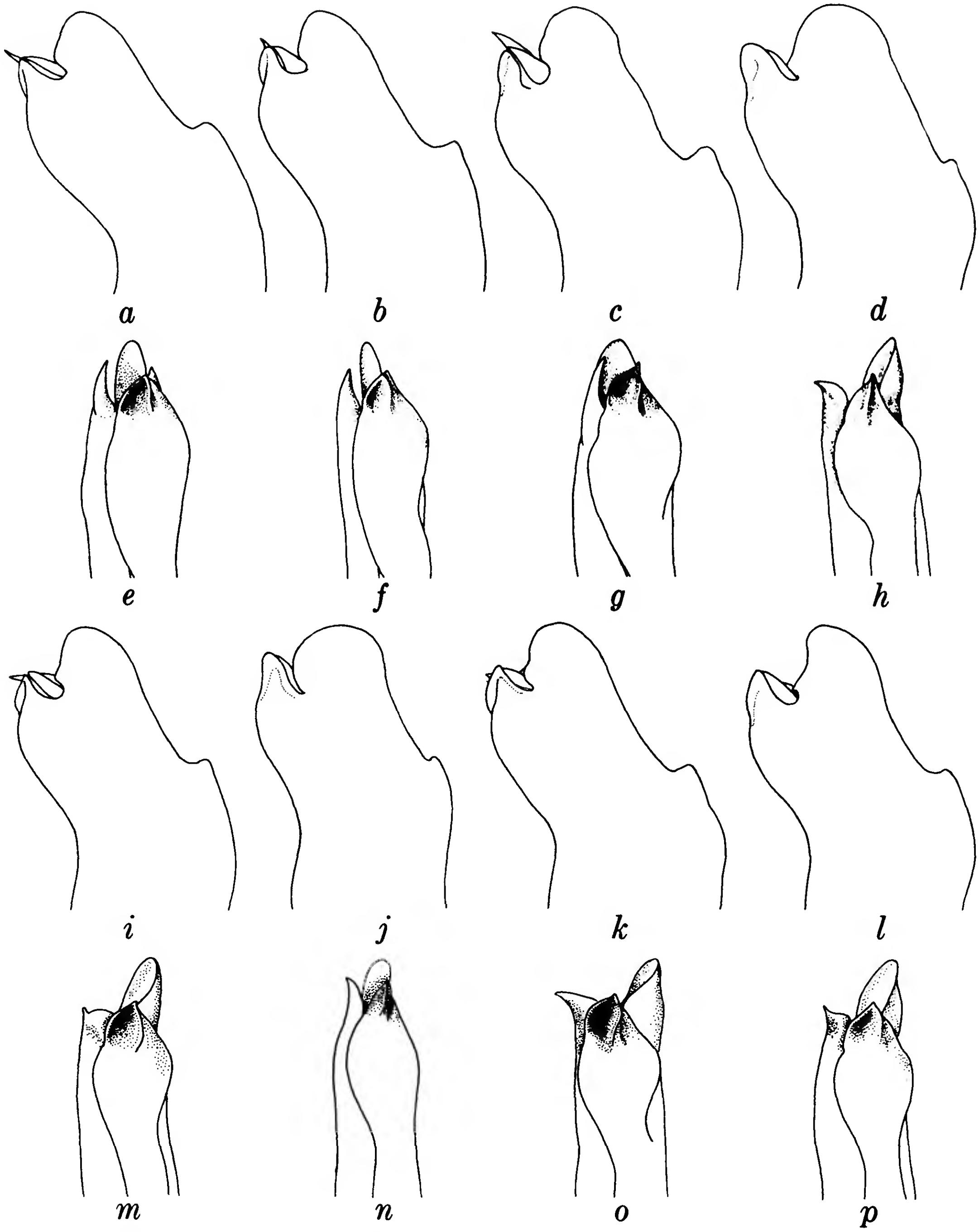


FIGURE 194.—*Procambarus (S.) troglodytes*, variations in left first pleopod of first form male (*a–d*, *i–l*, lateral view; *e–h*, *m–p*, caudal view). Midway Basin: *a*, *e*, Bryan Co. Savannah Basin: *b*, *f*, Chatham Co; *d*, *h*, Screven Co; *i*, *j*, *m*, *n*, Burke Co. Altamaha Basin: *c*, *g*, Tattnall Co. Ogeechee Basin: *k*, *o*, Burke Co; *l*, *p*, Glascock Co.

spring-fed creeks, rivers, swamps, and in burrows. Certainly like most, if not all, members of the subgenus *Scapulicambarus,* there is evidence that it is an opportunistic species that, while dominating swamps, to some degree has taken advantage of almost every type of habitat occurring within its range. In swamp habitats, it occurs in pools that support no macroscopic plants, seeking cover in tree litter or in burrows in the bottom of pools or ponds, but it appears to occur equally abundantly in vegetation-choked pools and sluggish streams. In Brier Creek, north of Waynesboro in Burke County, I found it hiding beneath rocks, chunks of asphalt discarded from the repair of the bridge, and under submerged boards. In roadside ditches, particularly in flatwoods, specimens have been obtained with the aid of seines, dip nets, and by hand in temporary pools and burrows in similar habitats. The burrows are simple, usually unbranched, subvertical tunnels that reach the water table. Chimneys, if present, are irregular and lack any obvious symmetry. I know nothing of the burrowing habits of those individuals occurring in permanent streams. In Chatham County, one specimen was taken from a (presumably submerged) hollow log.

GEORGIA CRAYFISH ASSOCIATES.—*Procambarus (S.) troglodytes* was found with the following species (the number of localities shared is noted in parentheses): *Cambarus (D.) latimanus* (3), *C. (L.) diogenes diogenes* (1), *Faxonella clypeata* (2), *Procambarus (H.) advena* (4), *P. (H.) pygmaeus* (8), *P. (L.) barbatus* (10), *P. (O.) acutus acutus* (2), *P. (O.) enoplosternum* (3), *P. (O.) epicyrtus* (2), *P. (O.) litosternum* (6), *P. (O.) lunzi* (9), *P. (O.) pubescens* (4), *P. (Pe.) petersi* (2), and *P. (Pe.) raneyi* (1).

Appendix 1

Georgia Crayfishes and the Counties in Which They Occur

(In the "List of Crayfishes," the numbers after the taxa refer to the numbered counties in the "List of Counties" immediately following; in the "List of Counties," the numbers following the county names refer to the numbered taxa in the "List of Crayfishes.")

List of Crayfishes

1. *Cambarus (A.) hamulatus*
2. *Cambarus (C.) bartonii:* 6, 29, 41, 42, 55, 59, 61, 68, 69, 73, 93, 95, 105, 119, 127, 139, 144, 146, 154, 157
3. *Cambarus (C.) howardi:* 33, 44, 48, 58, 60, 69, 93
4. *Cambarus (D.) cymatilis:* 105
5. *Cambarus (D.) englishi:* 71
6. *Cambarus (D.) halli:* 22, 71, 110
7. *Cambarus (D.) harti:* 99
8. *Cambarus (D.) latimanus:* 5–8, 11, 16–18, 22, 26–31, 33, 36, 38, 39, 41, 42, 44, 48, 51, 52, 55–62, 64, 66–75, 78, 79, 81, 82, 84, 85, 88, 90, 93, 95, 97, 99, 102, 104–110, 112, 114–118, 120, 121, 124, 126–128, 130, 131, 135, 141, 145–147, 149, 150, 154, 155, 157, 158
9. *Cambarus (D.) reflexus:* 17, 51, 62, 149
10. *Cambarus (D.) striatus:* 8, 23, 27, 28, 31, 38, 41, 42, 46, 49, 57, 64, 67, 71, 72, 74, 84, 87, 94, 100, 102, 105, 107, 112, 114, 115, 118, 128, 131, 143, 146, 150, 155, 158
11. *Cambarus (D.) strigosus:* 52, 109, 157
12. *Cambarus (D.) truncatus:* 87, 158
13. *Cambarus (H.) coosawattae:* 61
14. *Cambarus (H.) fasciatus:* 8, 28, 42, 93, 112, 115
15. *Cambarus (H.) girardianus:* 23, 41, 146, 155
16. *Cambarus (H.) longirostris:* 41, 144, 146
17. *Cambarus (H.) manningi:* 27, 57, 105, 155
18. *Cambarus (H.) speciosus:* 61, 105, 112
19. *Cambarus (J.) asperimanus:* 119, 127
20. *Cambarus (J.) conasaugaensis:* 42, 55, 61, 93, 105, 112
21. *Cambarus (J.) cryptodytes:* 43
22. *Cambarus (J.) distans:* 41
23. *Cambarus (J.) nodosus:* 93, 119, 139, 144, 154
24. *Cambarus (J.) parvoculus:* 41
25. *Cambarus (J.) unestami:* 27, 41, 146
26. *Cambarus (L.) acanthura:* 8, 22, 23, 27, 44, 55, 57, 61, 64, 105, 115, 146, 147, 155
27. *Cambarus (L.) d. diogenes:* 12, 19, 30, 43, 49, 51, 84, 88, 100, 116, 118, 120, 121, 123, 128–130, 135, 141
28. *Cambarus (P.) chaugaensis:* 119
29. *Cambarus (P.) coosae:* 8, 27, 57, 64, 105, 110, 112, 115, 146, 155
30. *Cambarus (P.) extraneus:* 23, 146, 155
31. *Cambarus (P.) georgiae:* 119
32. *Cambarus (P.) hiwasseensis:* 139, 144
33. *Cambarus (P.) parrishi:* 139
34. *Cambarus (P.) scotti:* 27, 146
35. *Fallicambarus (C.) hedgpethi:* 49, 125
36. *Faxonella clypeata:* 4, 12, 16, 17, 19, 40, 45–47, 49, 51, 53, 72, 80, 82, 83, 87, 88, 94, 100, 103, 116, 124, 125, 129, 134, 135, 137, 142, 143, 150, 153, 158, 159
37. *Orconectes erichsonianus:* 8, 23, 27, 41, 57, 146, 155
38. *Orconectes forceps:* 23
39. *Orconectes spinosus:* 8, 57, 64, 105, 115, 144, 155
40. *Procambarus (D.) devexus:* 109, 157
41. *Procambarus (H.) advena:* 15, 25, 51, 54, 89, 91, 98, 103, 124, 132, 138
42. *Procambarus (H.) caritus:* 1, 3, 34, 45, 80, 87, 103, 134, 151, 153
43. *Procambarus (H.) pygmaeus:* 2, 10, 15, 21, 24, 25, 32, 34, 51, 80, 89, 91, 98, 134, 137, 148, 151, 159
44. *Procambarus (H.) talpoides:* 2, 3, 9, 10, 13, 14, 20, 24, 32, 34, 35, 37, 40, 46, 50, 63, 77, 86, 92, 113, 136, 137, 142, 148, 156, 159
45. *Procambarus (H.) truculentus:* 16, 21, 53, 82, (87?), 140, 150
46. *Procambarus (L.) barbatus:* 15, 16, 21, 25, 51, 53, 54, 82, 89, 91, 98, 124, 132, 138
47. *Procambarus (L.) pubischelae deficiens:* 1, 20, 34, 63, 80, 103, 151
48. *Procambarus (L.) p. pubischelae:* 2, 3, 10, 20, 24, 32, 34, 35, 37, 50, 77, 86, 92, 113, 137, 148
49. *Procambarus (O.) acutissimus:* 118
50. *Procambarus (O.) acutus acutus:* 17, 24, 45, 52, 53, 62, 81–83, 87, 99, 103, 109, 121, 124, 140, 143, 150, 157, 158
51. *Procambarus (O.) angustatus:* ?
52. *Procambarus (O.) enoplosternum:* 1, 15, 16, 21, 25, 45, 53, 54, 83, 87, 91, 98, 103, 121, 124, 132, 134, 138, 140, 150, 153, 158
53. *Procambarus (O.) epicyrtus:* 15, 16, 25, 51, 82, 124
54. *Procambarus (O.) fallax:* 2, 13, 24, 32, 34, 50, 86, 92
55. *Procambarus (O.) leonensis*
56. *Procambarus (O.) litosternum:* 15–17, 21, 53, 54, 82, 89, 124, 132

57. *Procambarus (O.) lophotus:* 23, 27, 64, 146, 155
58. *Procambarus (O.) lunzi:* 15, 25, 51, 63, 89, 91, 98, 132
59. *Procambarus (O.) pubescens:* 5, 15, 17, 53, 62, (67?), 70, 81, 82, 87, 97, 109, 121, 124, 131, 149, 150, 157, 158
60. *Procambarus (O.) seminolae:* 1-3, 9, 10, 13-15, 20, 24, 32, 34, 35, 37, 40, 46, 50, 63, 77, 80, 86, 92, 103, 113, 137, 138, 142, 148, 151, 156, 159
61. *Procambarus (Pe.) gibbus:* 4, 39, 88, 96, 123, 129
62. *Procambarus (Pe.) petersi:* 15-17, 62, 70, 81, 124, 131, 149, 150
63. *Procambarus (Pe.) raneyi:* 6, 17, 44, 52, 59, 67, 73, 95, 107, 109, 121, 124, 127, 147, 157
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67. *Procambarus (S.) paeninsulanus:* 4, 10, 13, 14, 19, 20, 24, 32, 35, 37, 43, 47, 49, 50, 65, 86, 88, 92, 100, 101, 125, 129, 135-137, 148, 159
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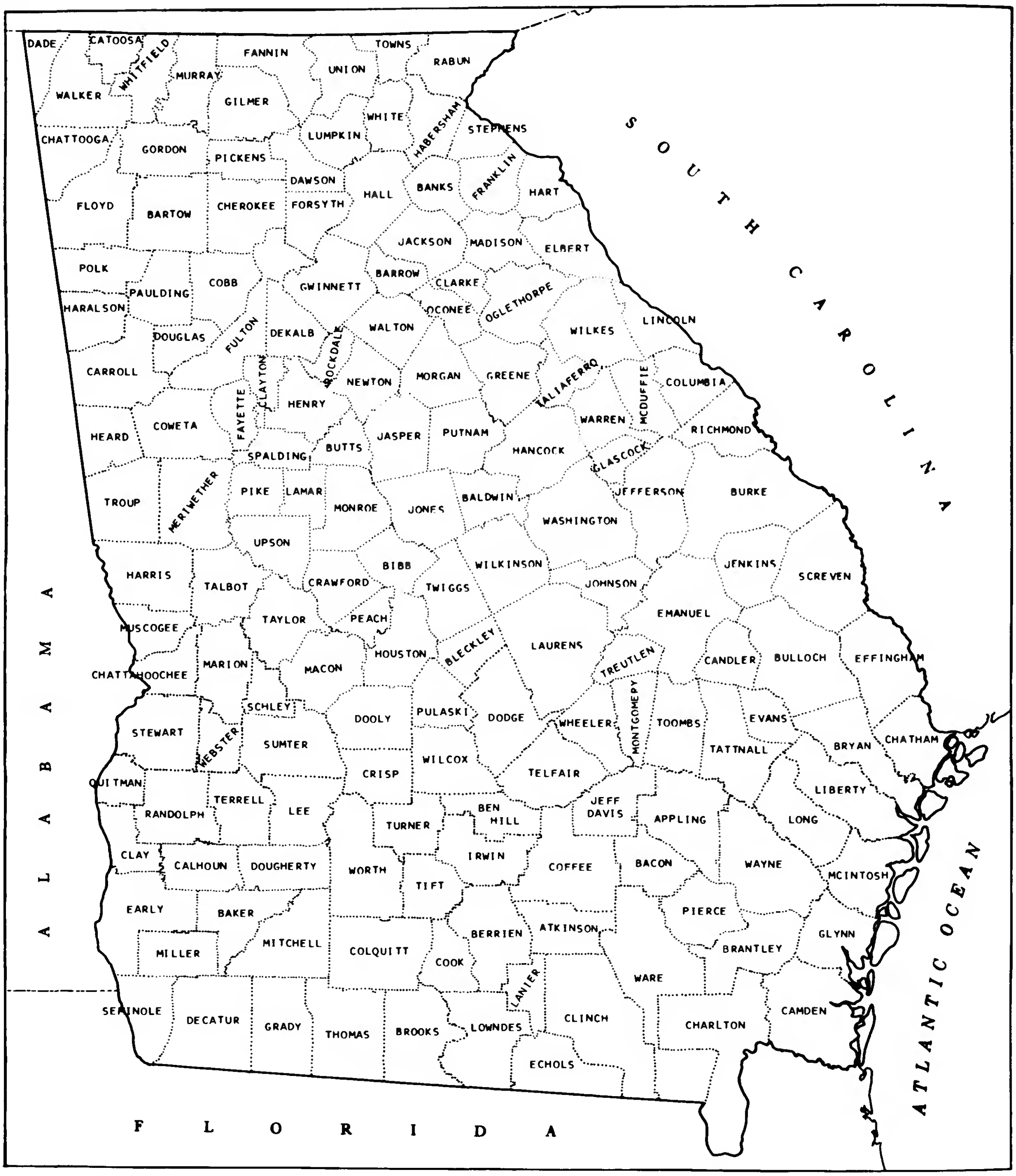

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Appendix 2

Symbionts of Georgia Crayfishes

Only nine references have been found that treat the symbionts of the crayfishes occurring in Georgia, and extracted from them is the following list, consisting of one microsporidian, one trematode, three branchiobdellid worms, and 25 entocytherid ostracods.

Hoff (1944) described four new entocytherids from the southern part of the state, and, 15 years later, Hart (1959), treating the same group in the lower Chattahoochee-Flint watershed, reported the occurrence of a fifth species and added new locality records for two of those described by Hoff. Hoffman (1963) described a new branchiobdellid worm from the southwestern part of Georgia, and Holt (1968a,b) added two additional ones from the Tallapoosa and Hiwassee watersheds. Hobbs and Walton (1968) reported the occurrence of a new entocytherid that infests the troglobitic crayfish in Climax Cave in Decatur County. The only parasites, of which I am aware, that have been reported to occur in Georgia crayfishes are those described by Sprague (1950) and Sullivan and Heard (1969). (The latter author kindly advised me of the change in the generic assignment of this fluke from *Macroderoides* to *Allogossidium*.) Hobbs III (1970) added a new entocytherid record for the Chattahoochee Basin. The remaining 18 ostracods known to occur in Georgia were reported in the studies of Hart and Hart (1971, 1974).

In the following compilation, the crayfishes are listed alphabetically, and their symbionts (currently employed combinations are used throughout) are alphabetized in each of the four groups (B = branchiobdellid worms; E = entocytherid ostracods; S = sporozoans; T = trematode worms). The author, publication date, and page reference for each symbiont follow the name the first time it appears in the list. In addition, county records are included, and the bibliographic citation to the first reported locality in the county (or counties) is given in parentheses.

Cambarus (C.) bartonii

- S *Thelohania cambari* Sprague (1950:46): Towns (Sprague, 1950:46)
- B *Pterodrilus simondsi* Holt (1968b:23): Fannin (Holt, 1968b:23)
  - *Pterodrilus* sp.: Union (Holt, 1968b:32)
- E *Dactylocythere leptophylax* (Crawford, 1961:238): Banks, Hart, Union, White (Hart and Hart, 1974:61)
  - *Donnaldsoncythere donnaldsonensis* (Klie, 1931:334): Banks, Dade, Lumpkin (Hart and Hart, 1974:79)
  - *Entocythere elliptica* Hoff (1944:328): Fannin (Hart and Hart, 1974:88)
  - *Uncinocythere simondsi* (Hobbs and Walton, 1960a:17): Fannin, Hart (Hart and Hart, 1974:134)

Cambarus (D.) halli

- E *Ankylocythere tallapoosa* Hart and Hart (1971:107): Carroll, Haralson, Paulding (Hart and Hart, 1971: 107–108)
  - *Entocythere internotalus* (Crawford, 1959:152): Paulding (Hart and Hart, 1971:107)
  - *Uncinocythere simondsi:* Haralson, Paulding (Hart and Hart, 1971:107, 108)

Cambarus (D.) harti

- E *Ankylocythere ancyla* Crawford (1965:148): Meriwether (Hart and Hart, 1974:21)

Cambarus (D.) latimanus

- B *Sathodrilus megadenus* Holt (1968a:302): Haralson (Holt, 1968a:302)
  - *Pterodrilus* sp.: Union Co. (Holt, 1968b:32)
- E *Ankylocythere ancyla:* Burke, Madison, Meriwether (Hart and Hart, 1974:21)
  - *Ankylocythere tallapoosa:* Carroll, Paulding (Hart and Hart, 1971:107, 108)
  - *Ankylocythere telmoecea* (Crawford, 1959:167): Heard, Twiggs (Hart and Hart, 1974:32)
  - *Dactylocythere leptophylax:* Banks, Hart, Jackson, Putnam (Hart and Hart, 1974:61)
  - *Dactylocythere suteri* (Crawford, 1959:150): Banks, Morgan (Hart and Hart, 1974:73)

Donnaldsoncythere donnaldsonensis: Banks (Hart and Hart, 1974:79)
Entocythere elliptica: Burke, Decatur, Gwinnett, Heard, Madison (Hart and Hart, 1974:88)
Entocythere internotalus: Paulding (Hart and Hart, 1971: 107)
Uncinocythere lucifuga (Walton and Hobbs, 1959:118): Burke, Cherokee (Hart and Hart, 1974:131)
Uncinocythere simondsi: Carroll (Hart and Hart, 1971: 108); Fannin, Hart, Heard, Madison, Monroe, Newton, Paulding, Polk, Troup (Hart and Hart, 1974:134)
Uncinocythere stubbsi Hobbs and Walton (1966:9): Troup (Hart and Hart, 1974:136)

Cambarus (D.) striatus
E *Cymocythere cyma* (Hobbs and Walton, 1960a:18): Gordon (Hart and Hart, 1974:44)
Dactylocythere falcata (Hobbs and Walton, 1961:379): Whitfield (Hart and Hart, 1974:58)
Dactylocythere mecoscapha (Hobbs and Walton, 1960a: 19): Walker (Hart and Hart, 1974:63)
Dactylocythere suteri: Murray (Hart and Hart, 1974:73)
Entocythere elliptica: Murray, Whitfield (Hart and Hart, 1974:88)
Entocythere internotalus: Dooly (Hart and Hart, 1974: 90)
Uncinocythere simondsi: Carroll, Floyd, Murray, Walker (Hart and Hart, 1974:134)

Cambarus (D.) truncatus
E *Ankylocythere tiphophila* (Crawford, 1959:173): Wilkinson (Hart and Hart, 1974:33)

Cambarus (H.) longirostris
B *Pterodrilus* sp.: Union (Holt, 1968b:32)

Cambarus (J.) cryptodytes
B unidentifiable branchiobdellid: Decatur (Holt, 1973a:248)
E *Uncinocythere warreni* Hobbs and Walton (1968:250): Decatur (Hobbs and Walton, 1968:251)

Cambarus (J.) nodosus
B *Pterodrilus* sp.: Union (Holt, 1968b:32)

Cambarus (L.) acanthura
E *Cymocythere cyma:* Gordon (Hart and Hart, 1974:44)
Uncinocythere simondsi: Floyd (Hart and Hart, 1974: 134)

Cambarus (L.) diogenes diogenes
E *Geocythere geophila* (Hart, 1959:195): Decatur (Hart, 1959:198)
Hartocythere torreya (Hart, 1959:198): Randolph (Hobbs III, 1970:182)
Uncinocythere equicurva (Hoff, 1944:332): Decatur, Early (Hart and Hart, 1974:129)

Cambarus (P.) coosae
E *Dactylocythere falcata:* Floyd, Murray, Whitfield (Hart and Hart, 1974:58)
Dactylocythere suteri: Murray (Hart and Hart, 1974:73)
Entocythere elliptica: Murray, Whitfield (Hart and Hart, 1974:88)
Entocythere internotalus: Floyd (Hart and Hart, 1974: 90)
Uncinocythere simondsi: Floyd, Murray, Polk (Hart and Hart, 1974:134)

Cambarus (P.) scotti
E *Dactylocythere falcata:* Chattooga (Hart and Hart, 1974: 58)

Fallicambarus (C.) hedgpethi
B *Cambarincola osceola* Hoffman (1963:330): Seminole (Hoffman, 1963:330)
E *Uncinocythere equicurva:* Seminole (Hart and Hart, 1974: 129)

Faxonella clypeata
E *Ankylocythere ancyla:* Wheeler (Hart and Hart, 1974:22)
Ankylocythere hobbsi (Hoff, 1944:330): Laurens (Hart and Hart, 1974:28)
Ankylocythere sinuosa (Rioja, 1942:203): Bleckley, Crisp, Twiggs (Hart and Hart, 1974:30)
Ankylocythere telmoecea: Twiggs (Hart and Hart, 1974: 129)
Ankylocythere tiphophila: Montgomery, Telfair, Wilkinson (Hart and Hart, 1974:33)
Uncinocythere equicurva: Twiggs (Hart and Hart, 1974: 129)
Uncinocythere lucifuga: Bleckley (Hart and Hart, 1974: 131)

Orconectes erichsonianus
E *Dactylocythere falcata:* Walker (Hart and Hart, 1974: 58)
Dactylocythere mecoscapha: Walker (Hart and Hart, 1974:63)
Uncinocythere simondsi: Walker (Hart and Hart, 1974: 134)

Orconectes spinosus
E *Dactylocythere falcata:* Chattooga, Whitfield (Hart and Hart, 1974:58)
Dactylocythere suteri: Murray (Hart and Hart, 1974:73)
Entocythere elliptica: Murray, Whitfield (Hart and Hart, 1974:88)
Uncinocythere simondsi: Murray, Polk (Hart and Hart, 1974:134)

Procambarus (H.) advena
E *Ankylocythere ancyla:* Liberty, Long (Hart and Hart, 1974:21)
Ankylocythere hobbsi: McIntosh (Hart and Hart, 1974: 28)
Entocythere elliptica: Liberty, McIntosh (Hart and Hart, 1974:88)

Procambarus (H.) caritus
E *Ankylocythere hobbsi:* Laurens (Hart and Hart, 1974:28)

Procambarus (H.) talpoides
E *Ankylocythere ancyla:* Atkinson, Worth (Hart and Hart, 1974:21, 22)

Ankylocythere hobbsi: Ben Hill (Hoff, 1944:356), Cook, Echols, Thomas (Hart and Hart, 1974:27, 28)
Entocythere dentata Crawford (1965:151): Cook (Hart and Hart, 1974:86)
Entocythere dorsorotunda Hoff (1944:332): Ben Hill, Clinch, Pierce (Hoff, 1944:345); Echols (Hart and Hart, 1974:87)
Entocythere internotalus: Atkinson, Echols, Glynn, Worth (Hart and Hart, 1974:90)

Procambarus (H.) truculentus
E *Ankylocythere ancyla:* Treutlen (Hart and Hart, 1974:21)
Entocythere internotalus: Treutlen (Hart and Hart, 1974:90)

Procambarus (L.) barbatus
E *Ankylocythere ancyla:* Liberty (Hart and Hart, 1974:21)
Ankylocythere hobbsi: McIntosh (Hart and Hart, 1974:28)
Entocythere elliptica: Liberty, McIntosh (Hart and Hart, 1974:88)

Procambarus (L.) pubischelae deficiens
E *Ankylocythere ancyla:* Jeff Davis (Hart and Hart, 1974:21)

Procambarus (L.) pubischelae pubischelae
E *Ankylocythere ancyla:* Coffee, Lowndes, Ware (Hart and Hart, 1974:21)
Entocythere dentata: Ware (Hart and Hart, 1974:86)
Entocythere internotalus: Atkinson, Glynn, Lowndes (Hart and Hart, 1974:90)

Procambarus (O.) acutus acutus
E *Ankylocythere ancyla:* Burke, Montgomery, Treutlen (Hart and Hart, 1974:21)
Ankylocythere sinuosa: Twiggs (Hart and Hart, 1974:30)
Entocythere internotalus: Montgomery, Treutlen (Hart and Hart, 1974:90)
Uncinocythere equicurva: Twiggs (Hart and Hart, 1974:129)
Uncinocythere lucifuga: Dodge (Hart and Hart, 1974:131)

Procambarus (O.) enoplosternum
E *Ankylocythere ancyla:* Emanuel, Montgomery, Treutlen (Hart and Hart, 1974:21)
Ankylocythere telmoecea: Twiggs (Hart and Hart, 1974:32)
Entocythere elliptica: Emanuel (Hart and Hart, 1974:88)
Entocythere internotalus: Montgomery, Treutlen (Hart and Hart, 1974:90)
Uncinocythere lucifuga: Dodge (Hart and Hart, 1974:131)

Procambarus (O.) epicyrtus
E *Ankylocythere ancyla:* Screven (Hart and Hart, 1974:21)
Entocythere elliptica: Screven (Hart and Hart, 1974:88)

Procambarus (O.) litosternum
E *Ankylocythere ancyla:* Evans (Hart and Hart, 1974:21)
Entocythere elliptica: Emanuel (Hart and Hart, 1974:88)

Procambarus (O.) lophotus
E *Dactylocythere mecoscapha:* Walker (Hart and Hart, 1974:63)
Uncinocythere simondsi: Walker (Hart and Hart, 1974:134)

Procambarus (O.) pubescens
E *Ankylocythere ancyla:* Laurens (Hart and Hart, 1974:21)
Ankylocythere telmoecea: Burke (Hart and Hart, 1974:32)
Entocythere elliptica: Burke, Screven (Hart and Hart, 1974:88)
Uncinocythere equicurva: Laurens (Hart and Hart, 1974:129)

Procambarus (O.) seminolae
E *Ankylocythere ancyla:* Atkinson, Coffee, Jeff Davis, Worth (Hart and Hart, 1974:21, 22)
Ankylocythere sinuosa: Crisp (Hart and Hart, 1974:30)
Entocythere dorsorotunda: Clinch (Hart and Hart, 1974:87)
Entocythere elliptica: Clinch (Hoff, 1944:345)
Entocythere internotalus: Atkinson, Brantley, Worth (Hart and Hart, 1974:90)

Procambarus (Pe.) petersi
E *Ankylocythere ancyla:* Burke (Hart and Hart, 1974:21)

Procambarus (Pe.) raneyi
E *Ankylocythere ancyla:* Madison (Hart and Hart, 1974:21)
Dactylocythere leptophylax: Banks (Hart and Hart, 1974:61)
Donnaldsoncythere donnaldsonensis: Banks (Hart and Hart, 1974:79)
Entocythere elliptica: Madison (Hart and Hart, 1974:88)
Uncinocythere simondsi: Madison (Hart and Hart, 1974:134)

Procambarus (Pe.) spiculifer
T *Allogossidium progeneticus* (Sullivan and Heard, 1969:305): Oconee (Sullivan and Heard, 1969:307)
E *Ankylocythere ancyla:* Laurens (Hart and Hart, 1974:21)
Ankylocythere tallapoosa: Haralson (Hart and Hart, 1971:107)
Ankylocythere telmoecea: Heard, Twiggs (Hart and Hart, 1974:32)
Ankylocythere tiphophila: Wilkinson (Hart and Hart, 1974:33)
Cymocythere cyma: Gordon (Hart and Hart, 1974:44)
Dactylocythere leptophylax: Pulaski, Putnam, White (Hart and Hart, 1974:61)
Dactylocythere suteri: Morgan (Hart and Hart, 1974:73)
Entocythere elliptica: Clark, Decatur, Gwinnett, Heard, White (Hart and Hart, 1974:88)
Entocythere internotalus: Chattahoochee, Dooly, Randolph (Hart and Hart, 1974:90)

Geocythere geophila: Decatur (Hart, 1959:198)
Uncinocythere clemsonella (Crawford, 1961:236): Putnam (Crawford, 1961:238)
Uncinocythere equicurva: Decatur, Early, Laurens (Hart and Hart, 1974:129)
Uncinocythere lucifuga: Bibb, Cherokee, Colquitt, Pike, Randolph, Stewart, Twiggs (Hart and Hart, 1974:131)
Uncinocythere simondsi: Baldwin, Carroll, Haralson, Heard, Monroe, Newton, Stewart (Hart and Hart, 1974:134)
Uncinocythere stubbsi: Troup (Hart and Hart, 1974:136)
Uncinocythere zancla Hobbs and Walton (1963:456): Fayette (Hart and Hart, 1974:141)

Procambarus (S.) howellae
E *Ankylocythere ancyla:* Wheeler (Hart and Hart, 1974:22)
Ankylocythere hobbsi: Laurens (Hart and Hart, 1974:28)
Ankylocythere sinuosa: Bleckley (Hart and Hart, 1974:30)
Ankylocythere telmoecea: Twiggs (Hart and Hart, 1974:32)
Ankylocythere tiphophila: Telfair, Wilkinson (Hart and Hart, 1974:33)
Entocythere internotalus: Dooly (Hart and Hart, 1974:90)
Uncinocythere lucifuga: Bibb, Bleckley, Dodge, Twiggs (Hart and Hart, 1974:131)

Procambarus (S.) paeninsulanus
B *Cambarincola osceola:* Seminole (Hoffman, 1963:330)
E *Ankylocythere hobbsi:* Thomas (Hart and Hart, 1974:28)
Entocythere elliptica: Decatur (Hart and Hart, 1974:88)
Uncinocythere equicurva: Camden (Hoff, 1944:337), Decatur, Early, Seminole (Hart, 1959:204)
Uncinocythere lucifuga: Colquitt (Hart and Hart, 1974:131)

Procambarus (S.) troglodytes
E *Ankylocythere ancyla:* Burke, Liberty (Hart and Hart, 1974:21)
Ankylocythere telmoecea: Chatham (Hart and Hart, 1974:32)
Entocythere elliptica: Liberty, McIntosh (Hart and Hart, 1974:88)
Uncinocythere lucifuga: Burke, McIntosh (Hart and Hart, 1974:131)

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Figures 195–262

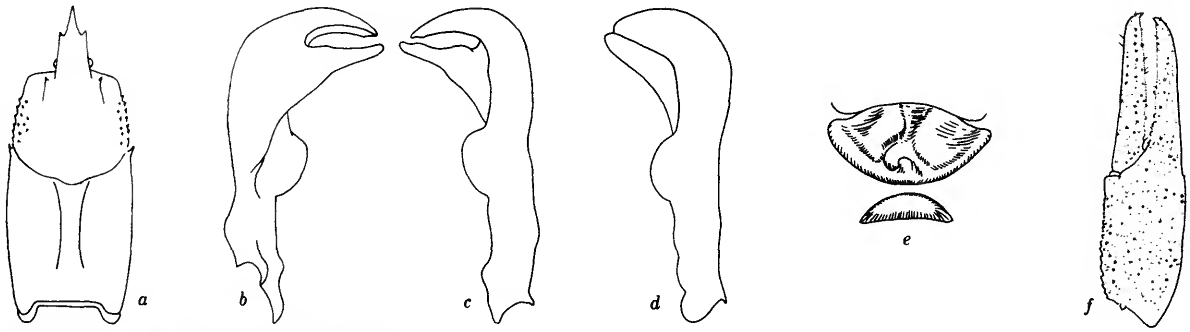
Comparative Illustrations of Georgia Crayfishes

(All scaled to same size)

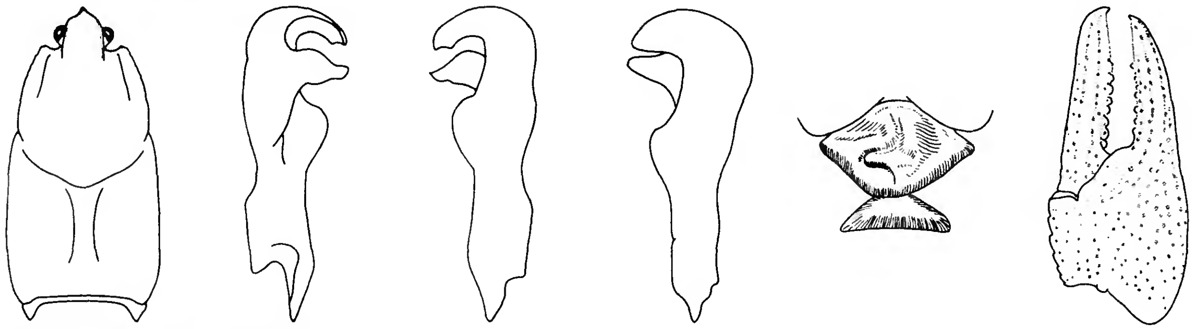
FIGURES 195–229, 231–233.—*a*, Dorsal view of carapace of male, form I; *b*, mesial view of first pleopod of male, form I; *c*, lateral view of same; *d*, lateral view of first pleopod of male, form II; *e*, annulus ventralis; *f*, dorsal view of chela of male, form I.

FIGURE 230.—*a*, Dorsal view of carapace of male, form I; *b*, mesial view of first pleopod of male, form I; *c*, caudal view of same; *d*, caudal view of first pleopod of male, form II; *e*, annulus ventralis; *f*, dorsal view of chela of male, form I.

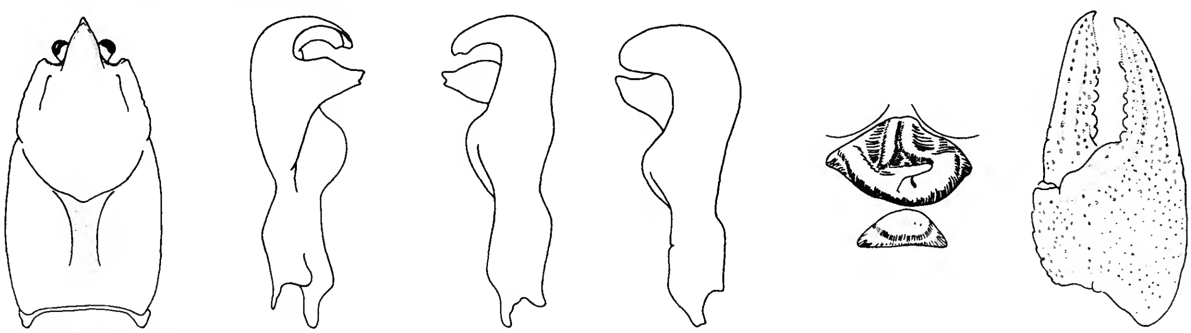
FIGURES 234–262.—*a*, Dorsal view of carapace of male, form I; *b*, lateral view of first pleopod of male, form I; *c*, lateral view of distal part of same; *d*, mesial view of distal part of same; *e*, lateral view of first pleopod of male, form II; *f*, annulus ventralis, *g*, dorsal view of chela of male, form I.



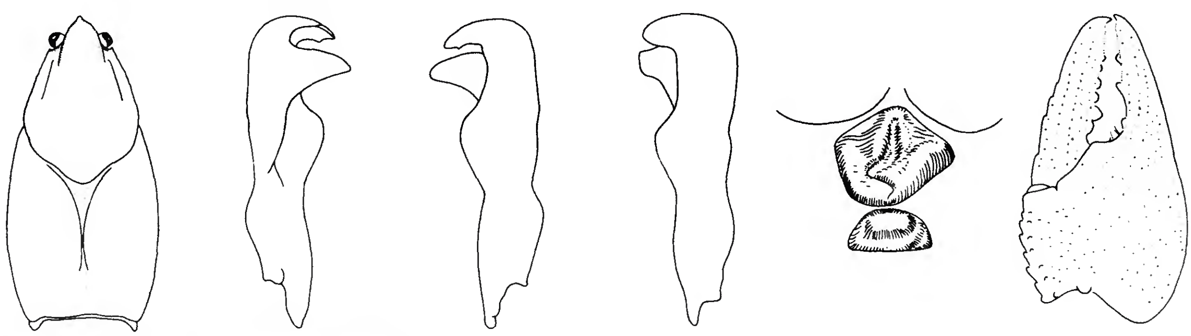
195. Cambarus (Aviticambarus) hamulatus



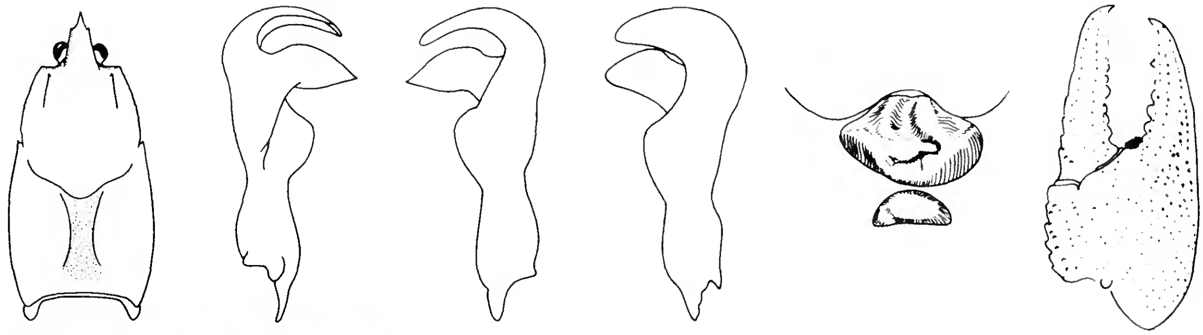
196. Cambarus (Cambarus) bartonii



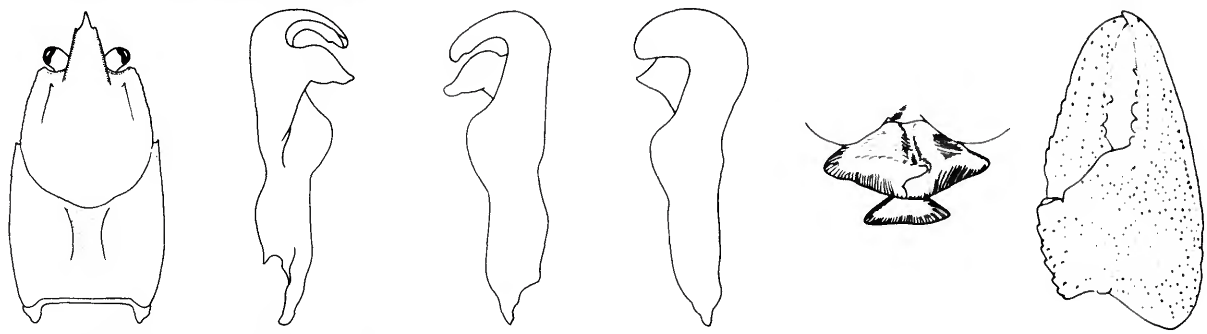
197. Cambarus (Cambarus) howardi



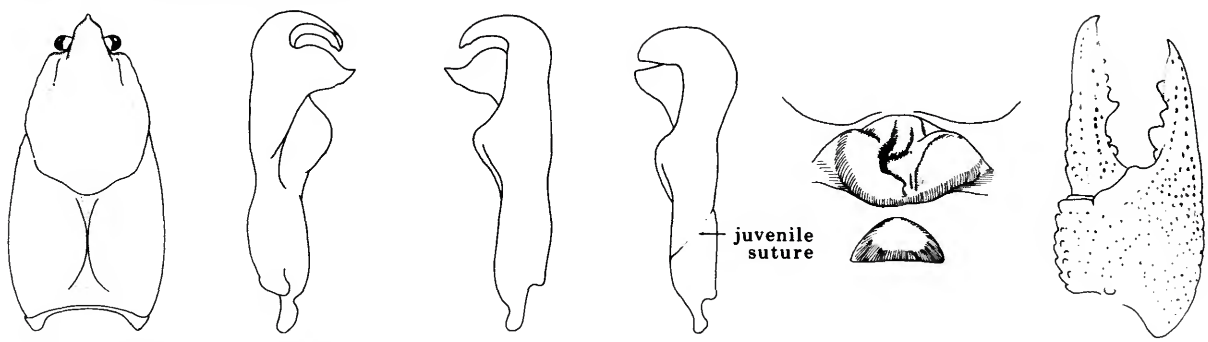
198. Cambarus (Depressicambarus) cymatilis



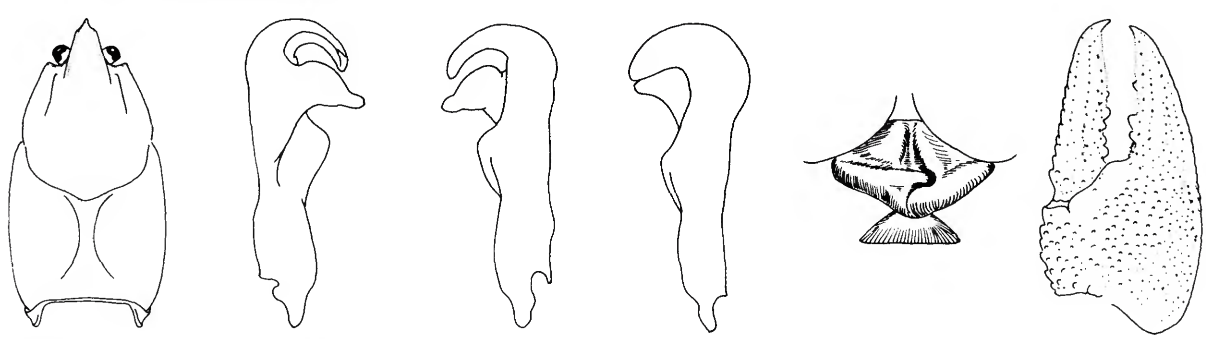
199. Cambarus (Depressicambarus) englishi



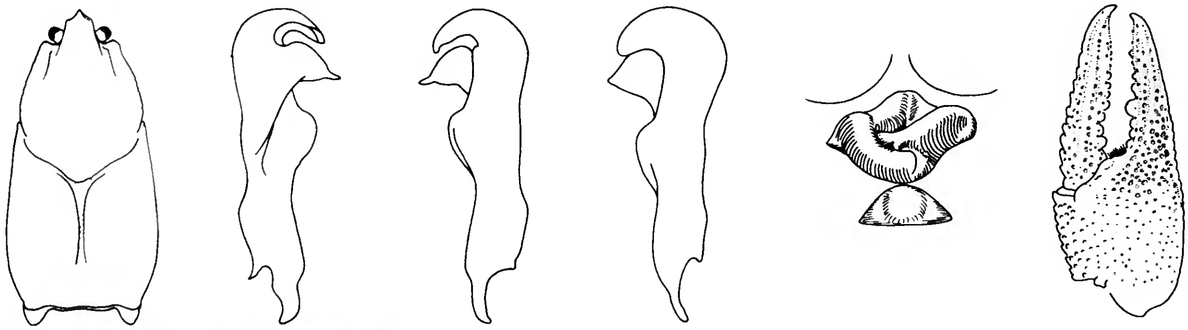
200. Cambarus (Depressicambarus) halli



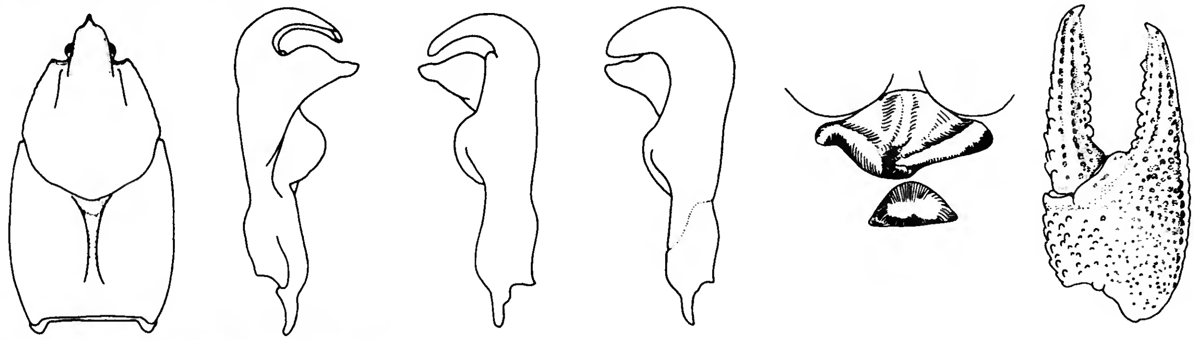
201. Cambarus (Depressicambarus) harti



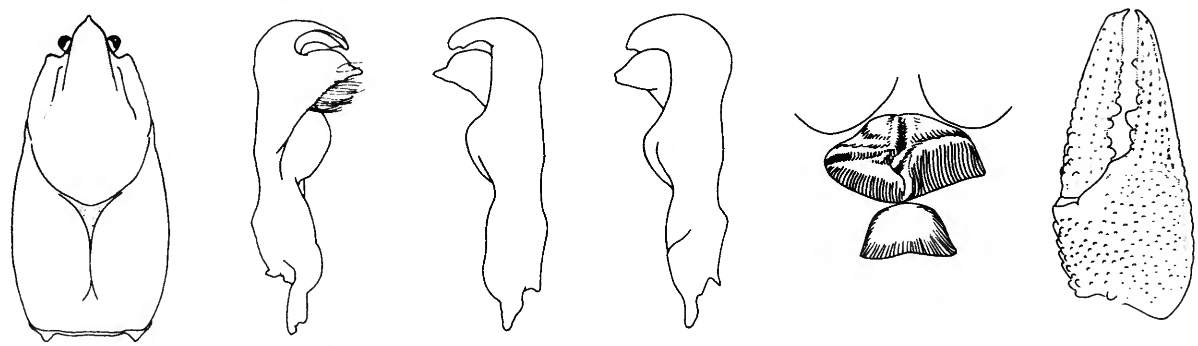
202. Cambarus (Depressicambarus) latimanus



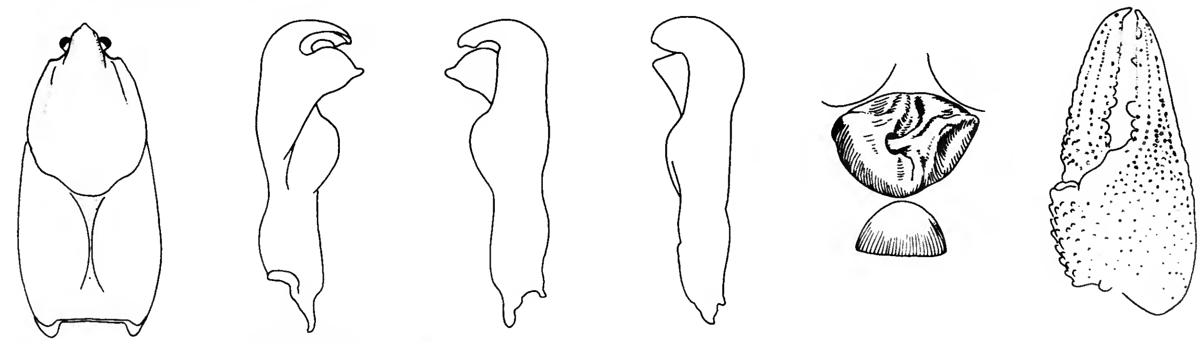
203. Cambarus (Depressicambarus) reflexus



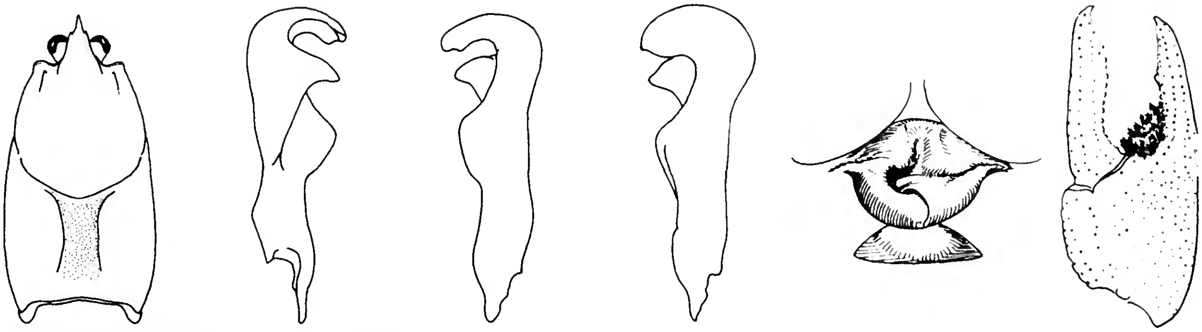
204. Cambarus (Depressicambarus) striatus



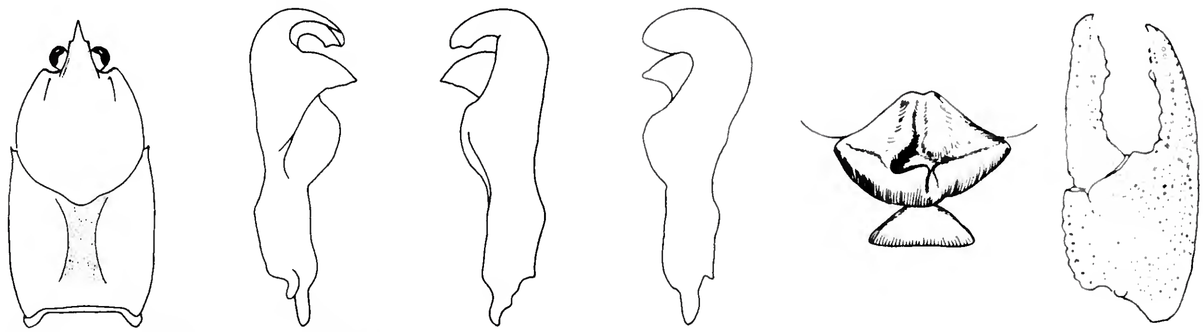
205. Cambarus (Depressicambarus) strigosus



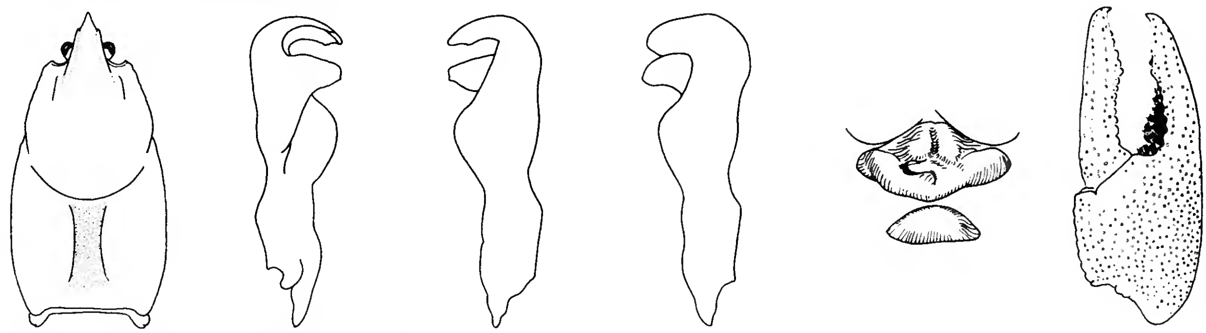
206. Cambarus (Depressicambarus) truncatus



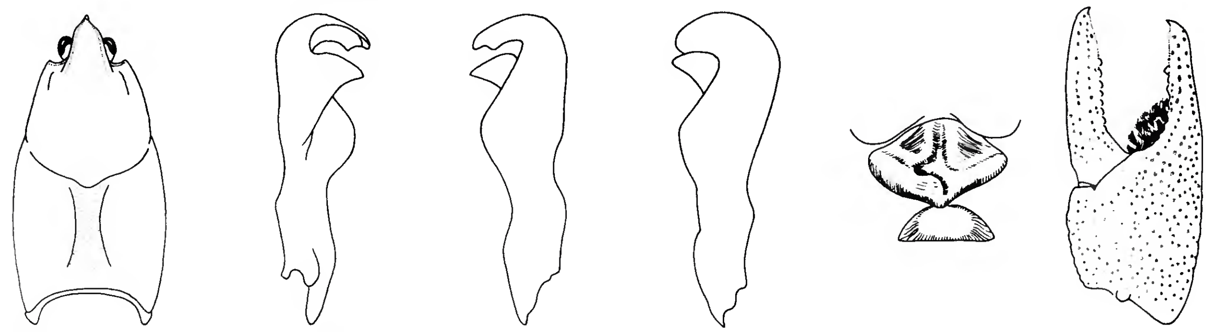
207. Cambarus (Hiaticambarus) coosawattae



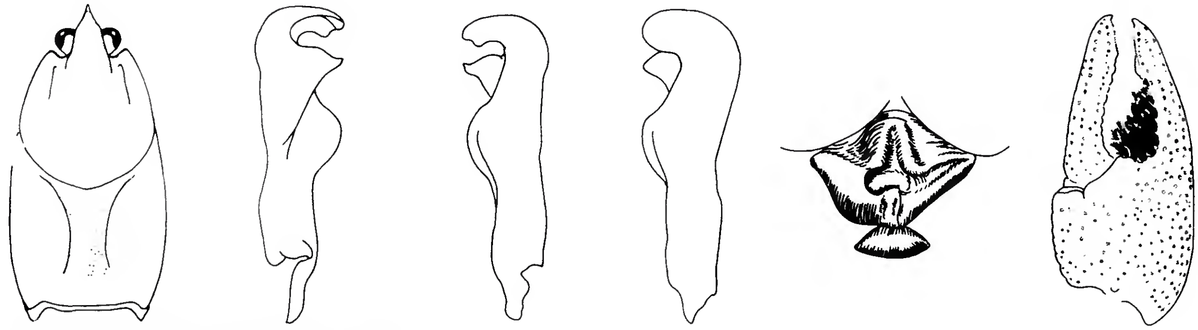
208. Cambarus (Hiaticambarus) fasciatus



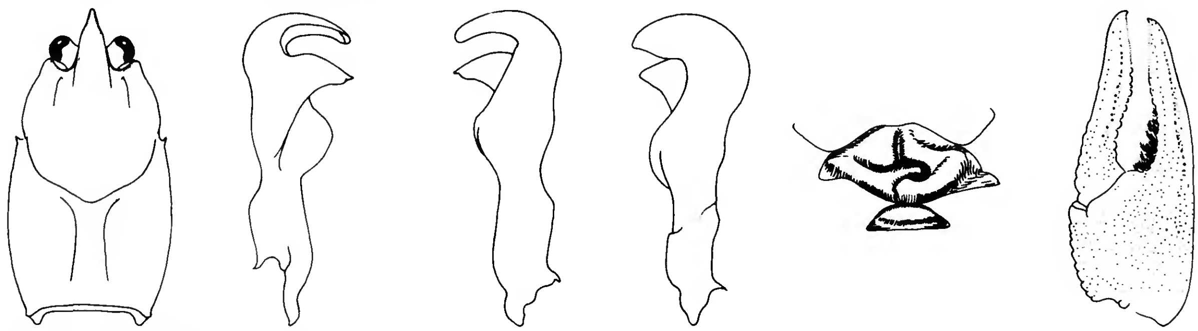
209. Cambarus (Hiaticambarus) girardianus



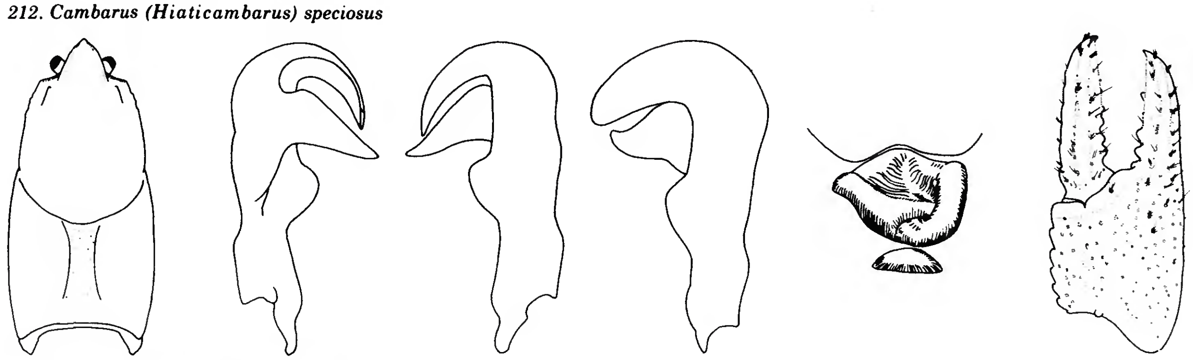
210. Cambarus (Hiaticambarus) longirostris



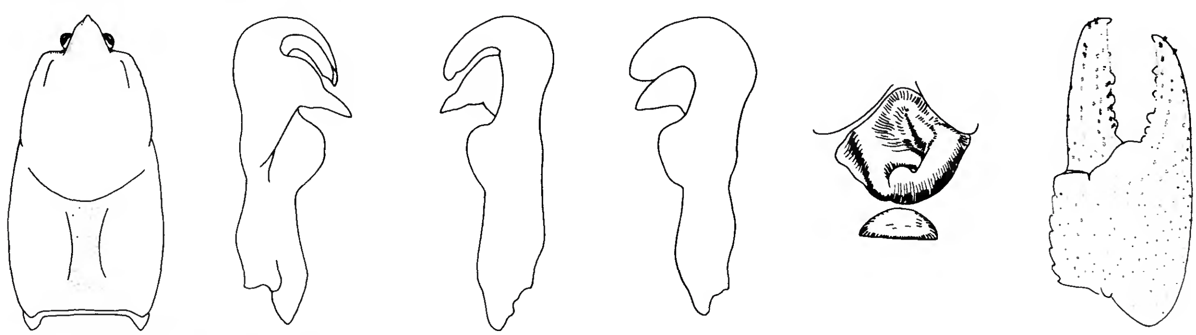
211. Cambarus (Hiaticambarus) manningi



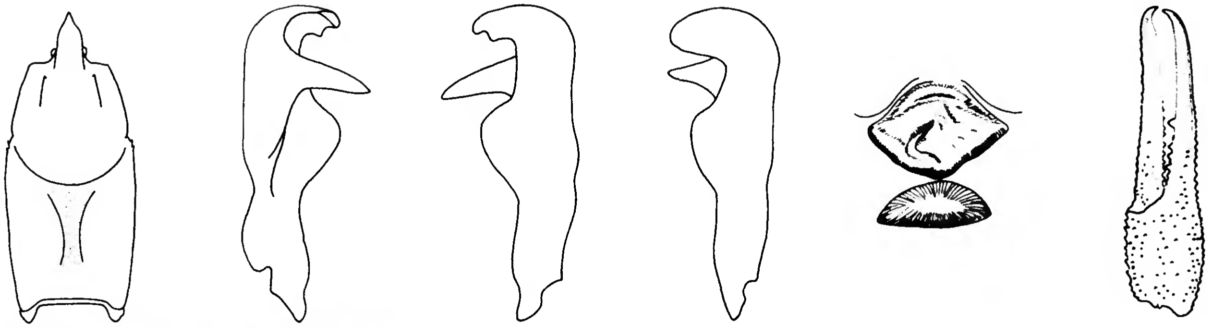
212. Cambarus (Hiaticambarus) speciosus



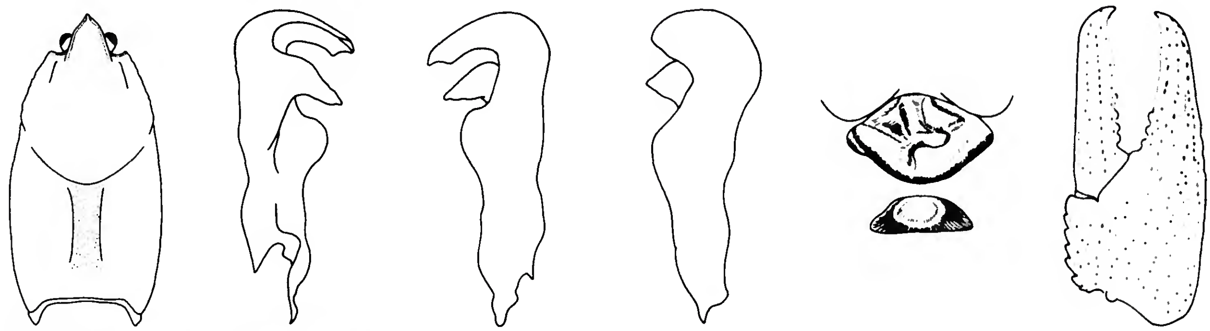
213. Cambarus (Jugicambarus) asperimanus



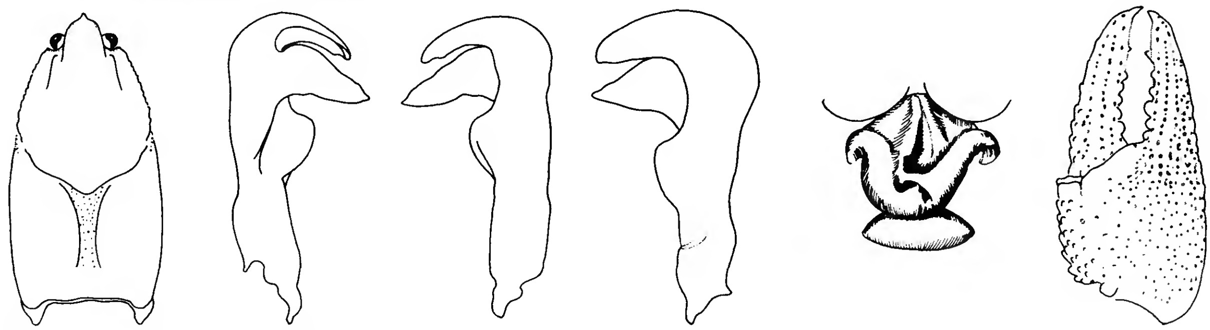
214. Cambarus (Jugicambarus) conasaugaensis



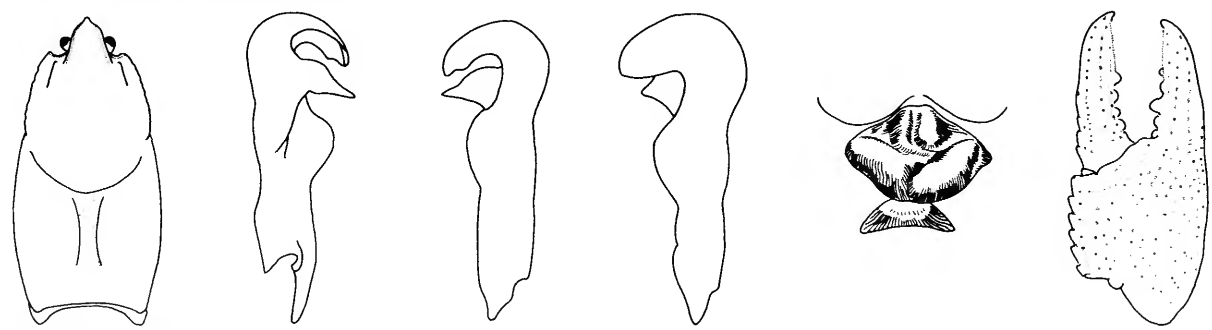
215. Cambarus (Jugicambarus) cryptodytes



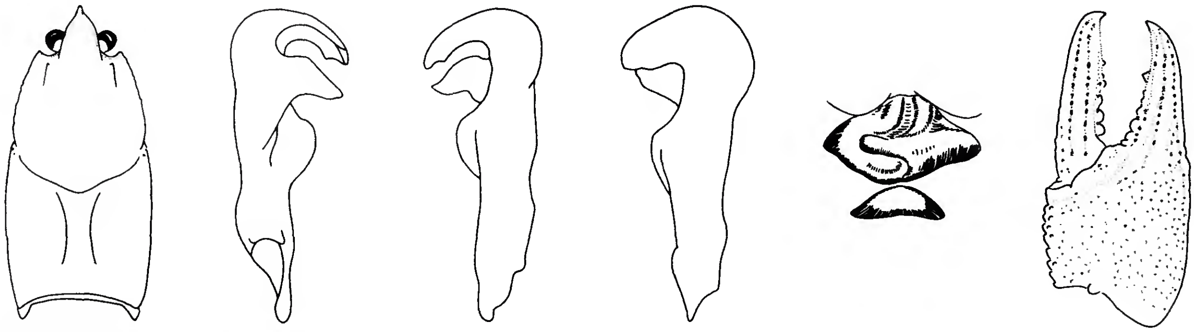
216. Cambarus (Jugicambarus) distans



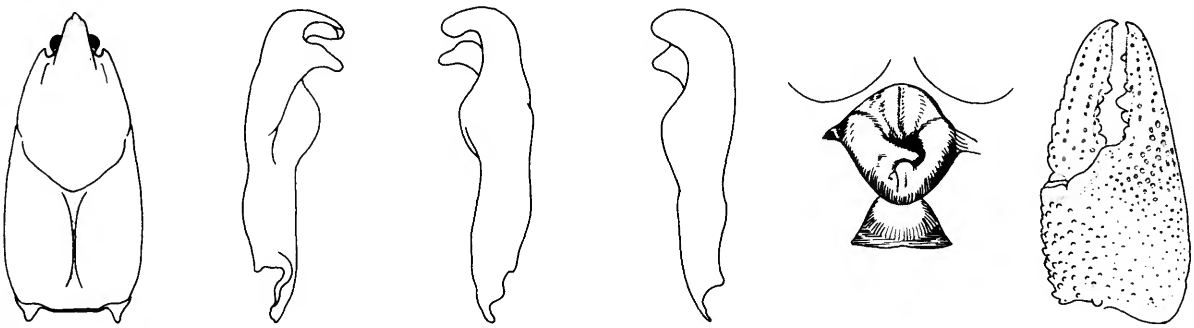
217. Cambarus (Jugicambarus) nodosus



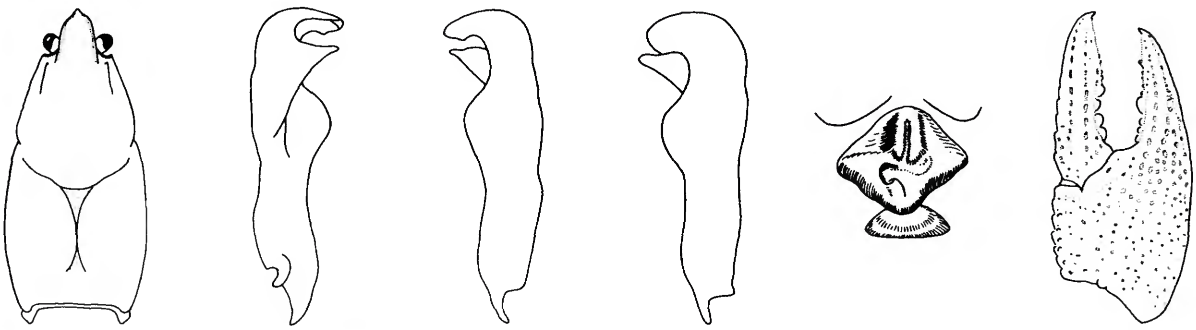
218. Cambarus (Jugicambarus) parvoculus



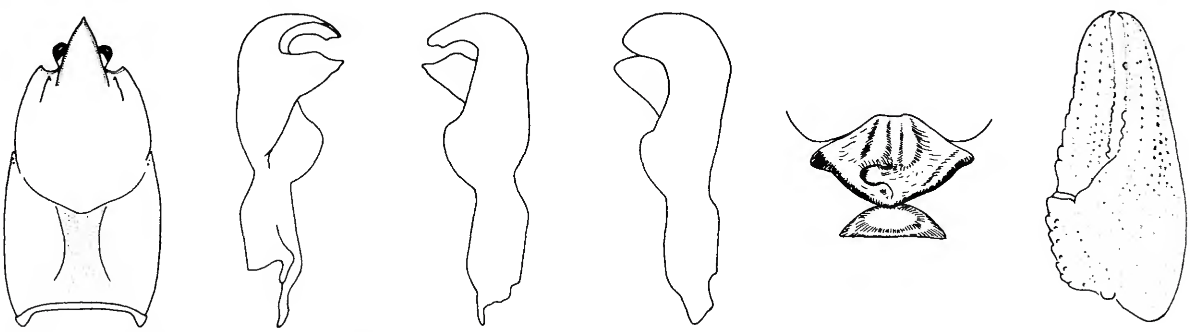
219. Cambarus (Jugicambarus) unestami



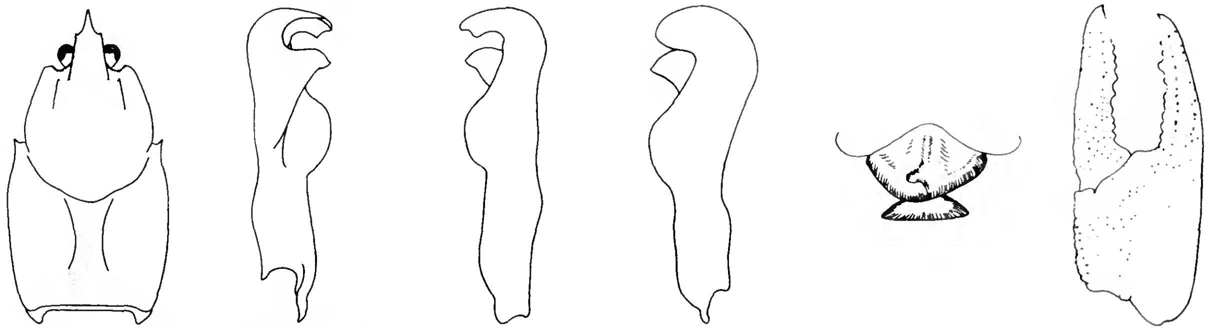
220. Cambarus (Lacunicambarus) acanthura



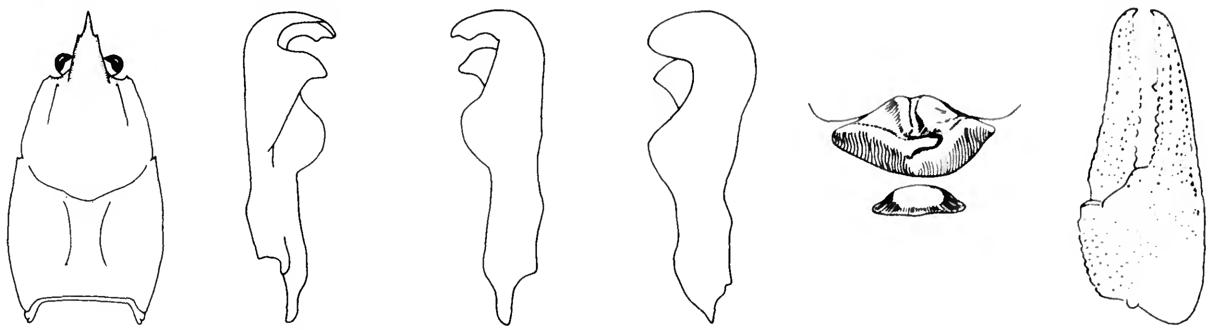
221. Cambarus (Lacunicambarus) diogenes diogenes



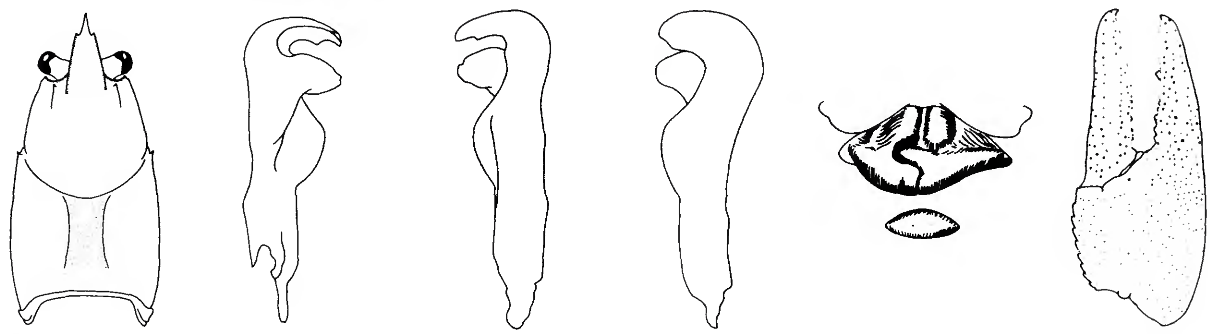
222. Cambarus (Puncticambarus) chaugaensis



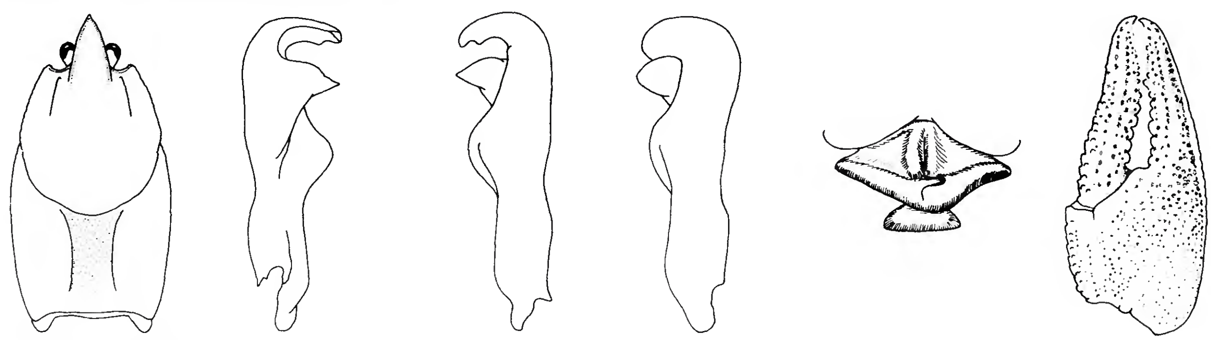
223. Cambarus (Puncticambarus) coosae



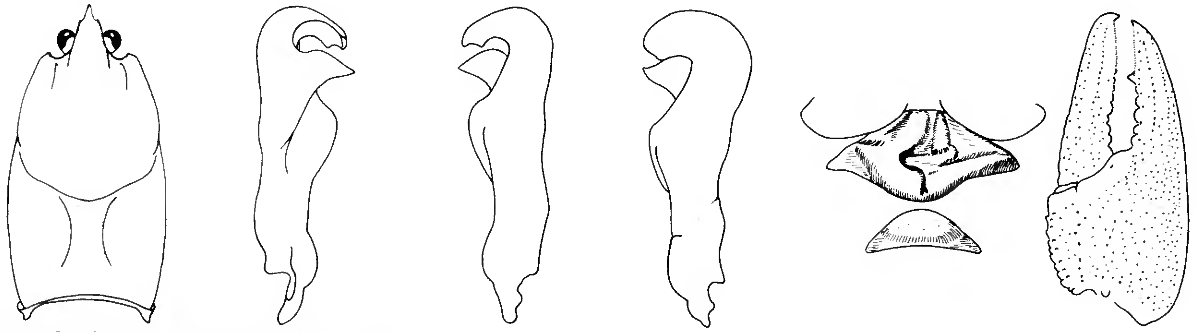
224. Cambarus (Puncticambarus) extraneus



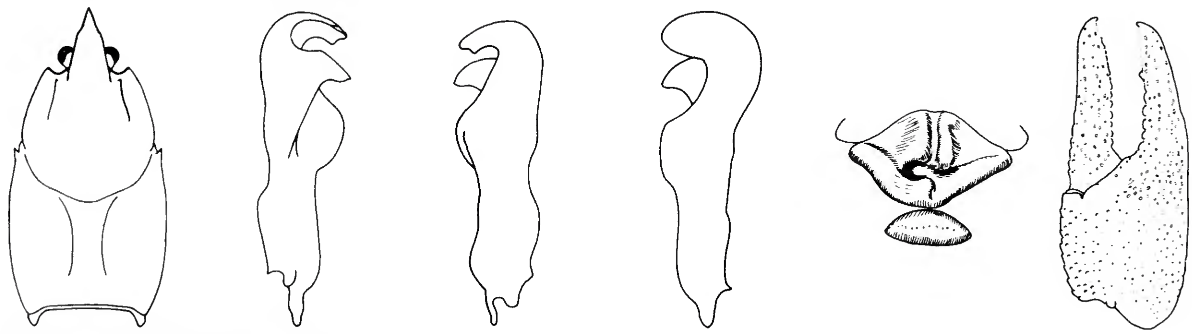
225. Cambarus (Puncticambarus) georgiae



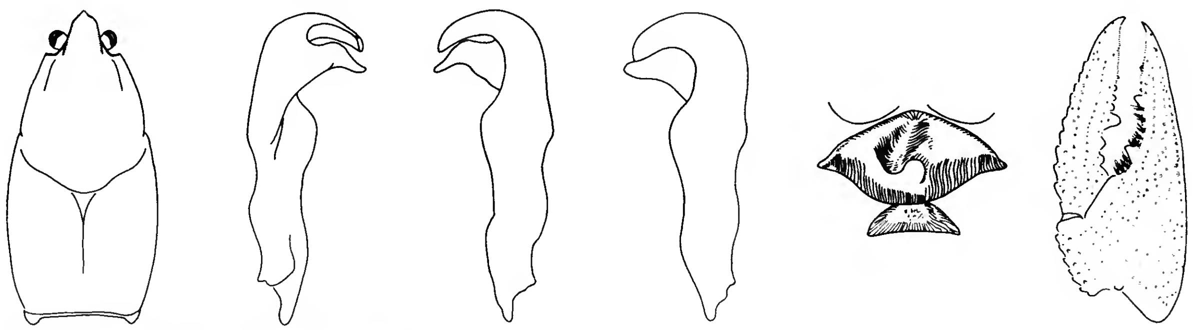
226. Cambarus (Puncticambarus) hiwasseensis



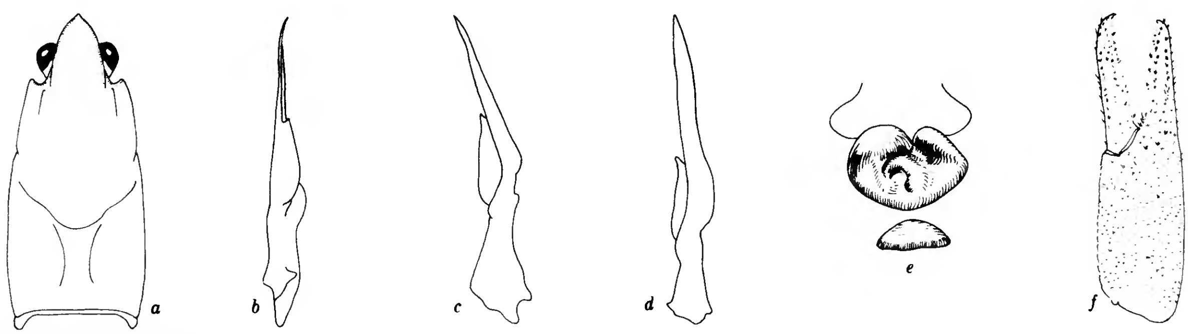
227. Cambarus (Puncticambarus) parrishi



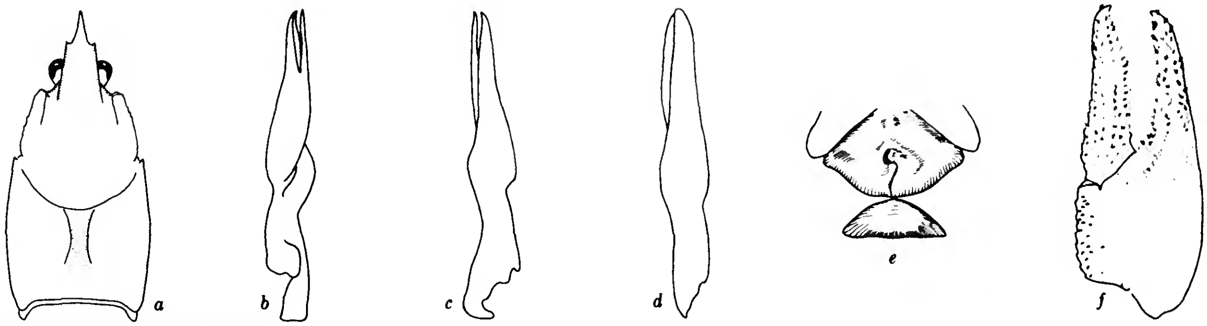
228. Cambarus (Puncticambarus) scotti



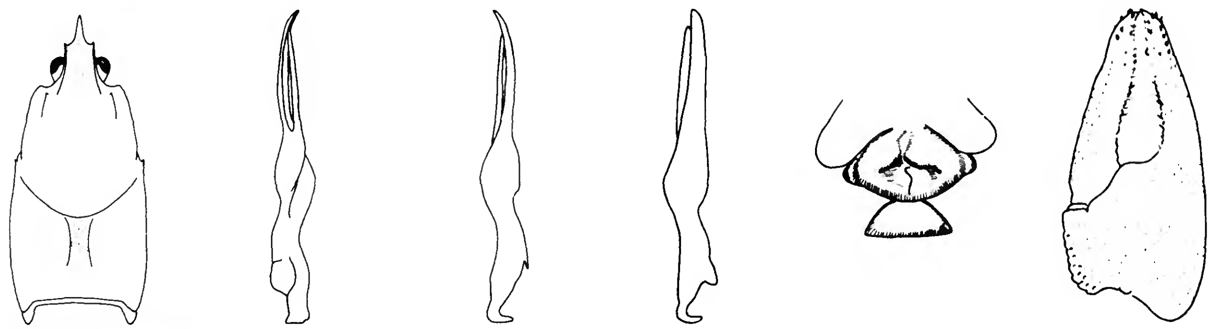
229. Fallicambarus (Creaserinus) hedgpethi



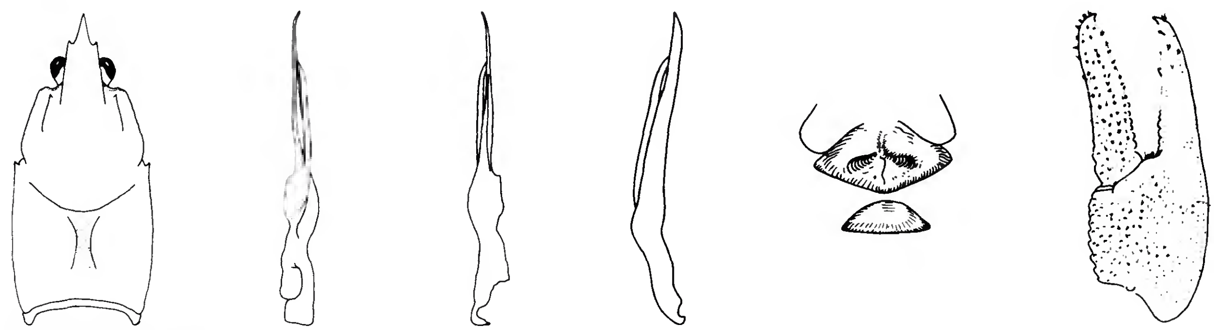
230. Faxonella clypeata



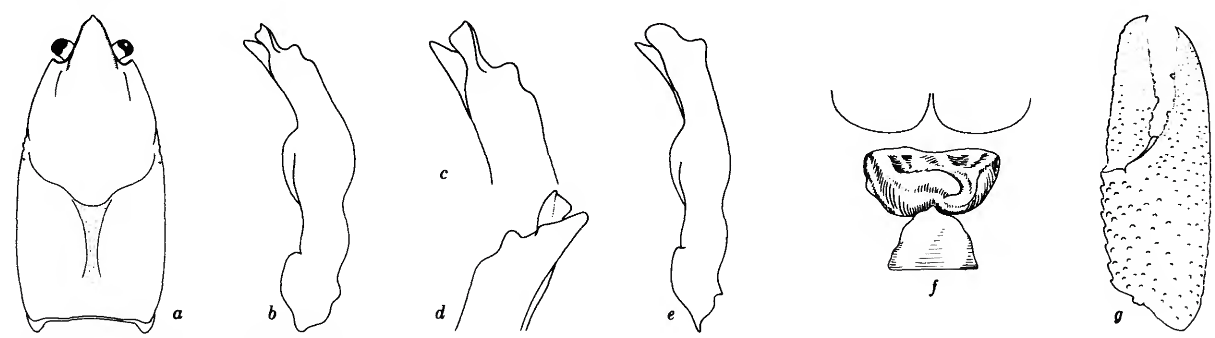
231. Orconectes erichsonianus



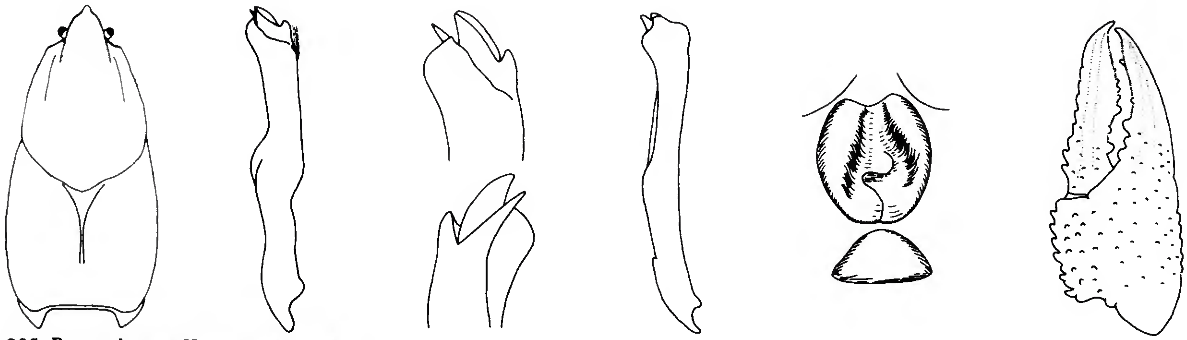
232. Orconectes forceps



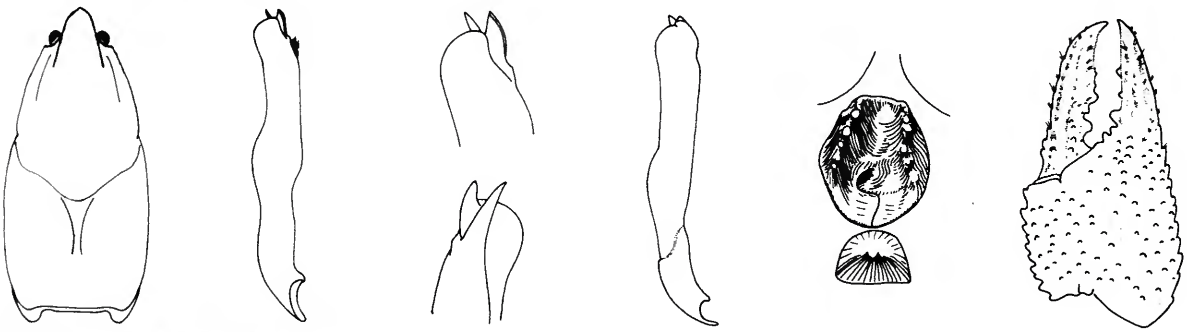
233. Orconectes spinosus



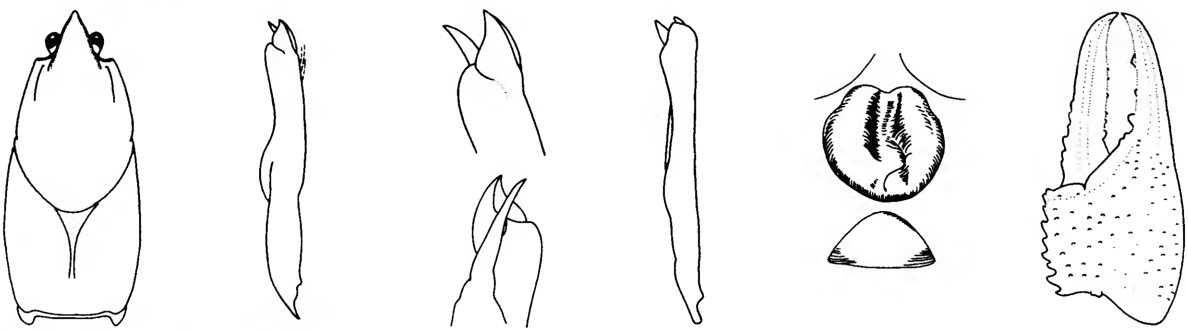
234. Procambarus (Distocambarus) devexus



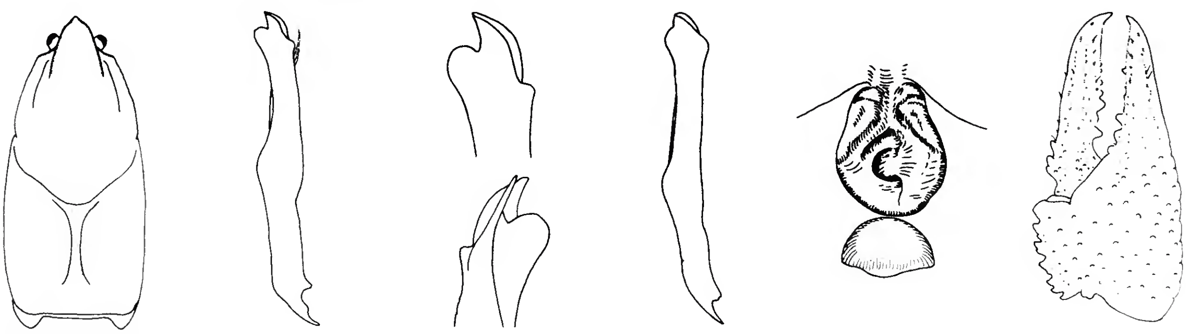
235. *Procambarus (Hagenides) advena*



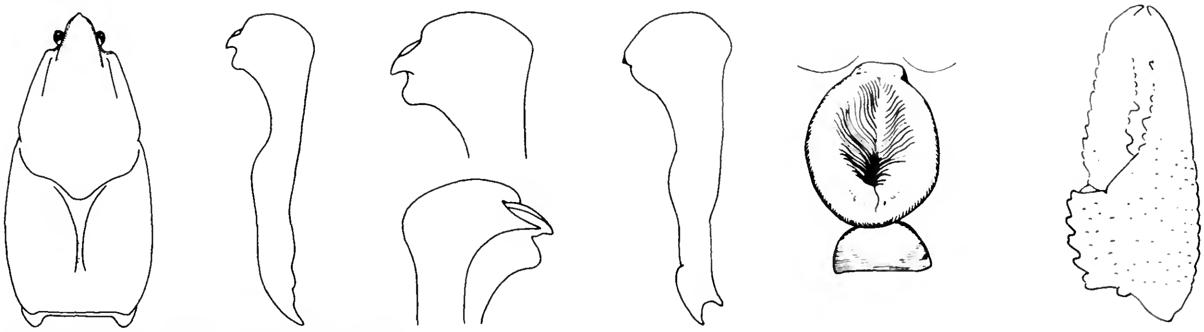
236. *Procambarus (Hagenides) caritus*



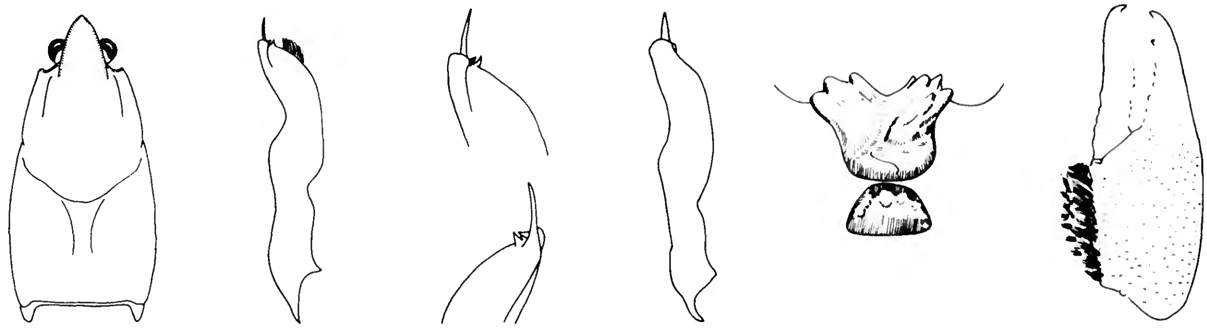
237. *Procambarus (Hagenides) pygmaeus*



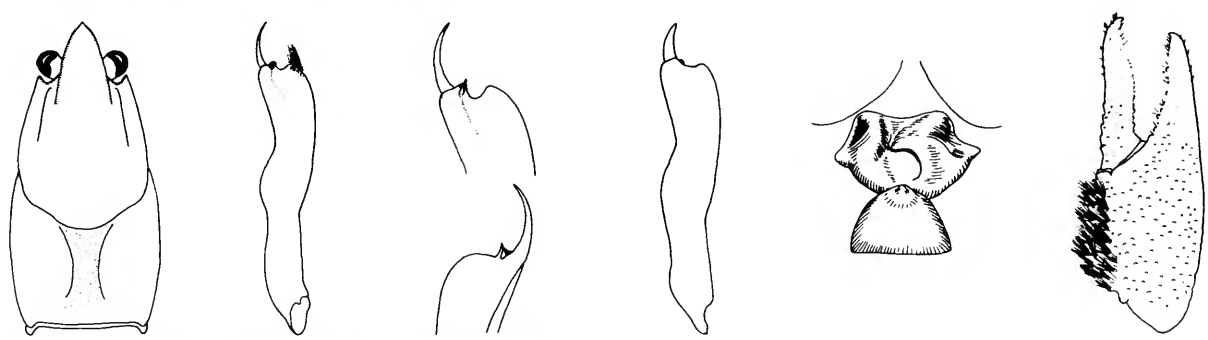
238. *Procambarus (Hagenides) talpoides*



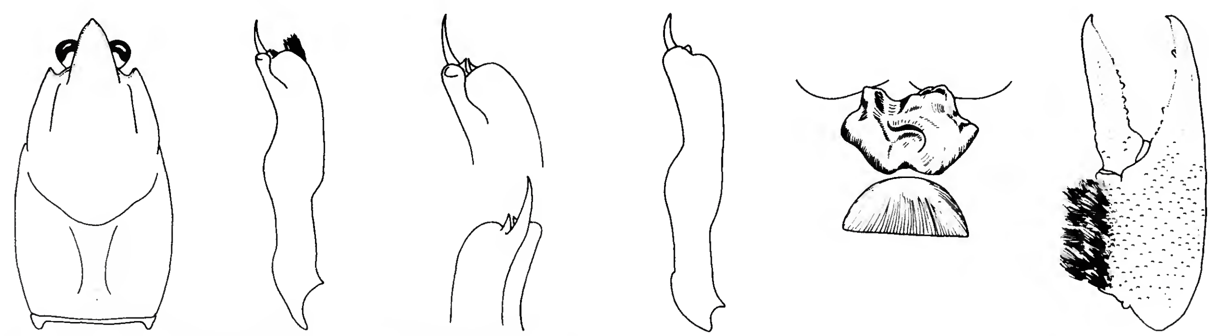
239. Procambarus (Hagenides) truculentus



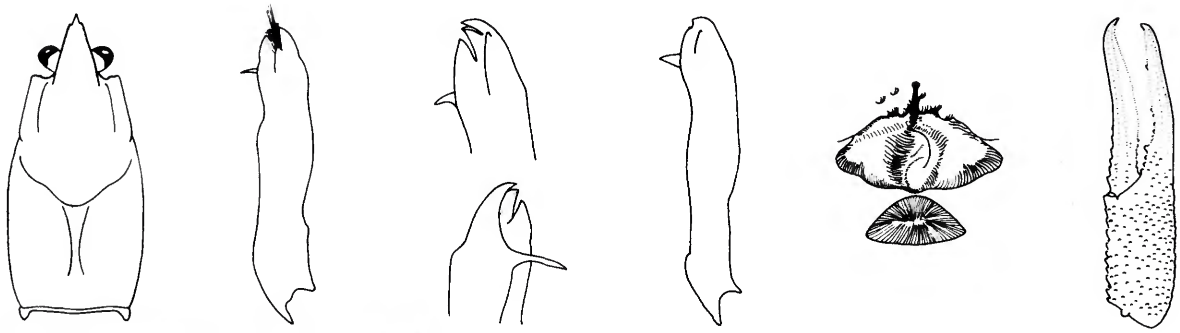
240. Procambarus (Leconticambarus) barbatus



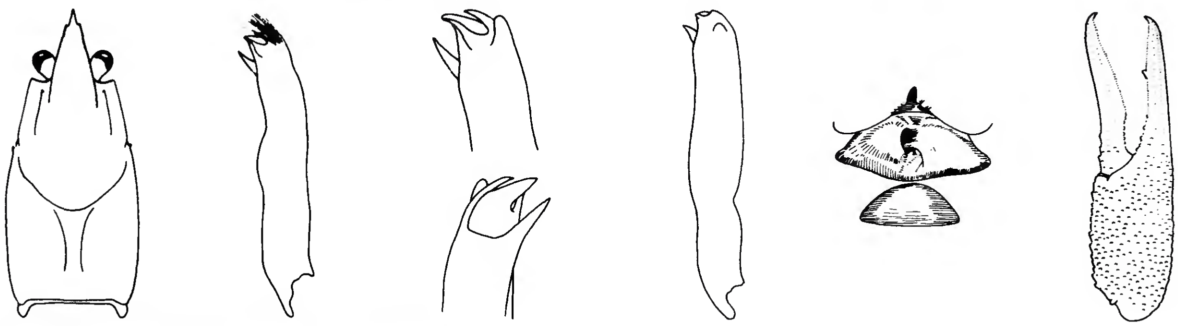
241. Procambarus (Leconticambarus) pubischelae deficiens



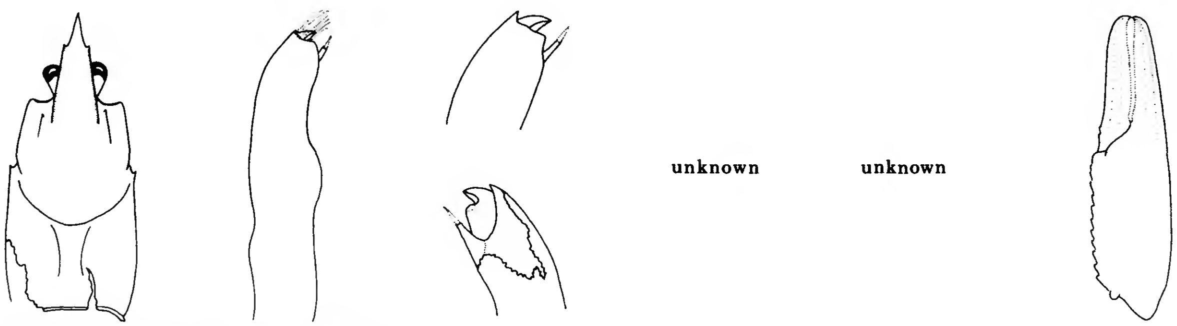
242. Procambarus (Leconticambarus) pubischelae pubischelae



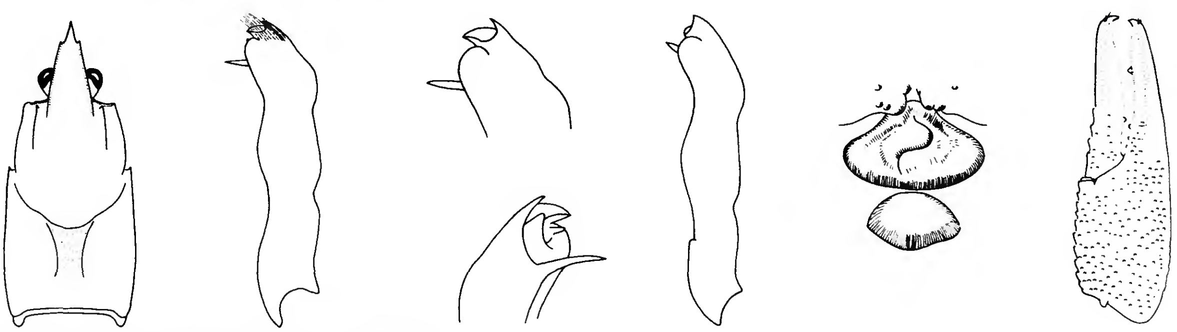
243. Procambarus (Ortmannicus) acutissimus



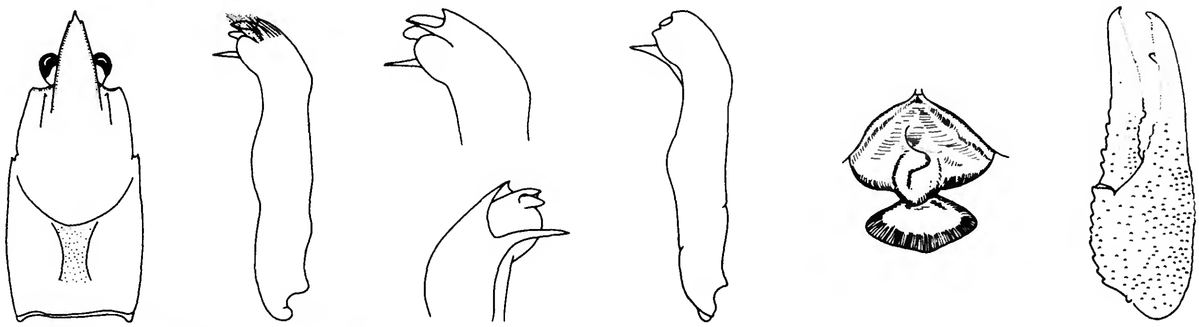
244. Procambarus (Ortmannicus) acutus acutus



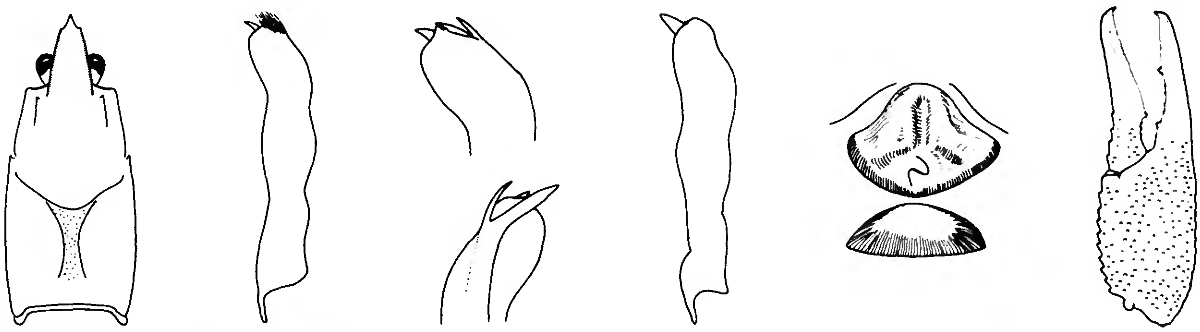
245. Procambarus (Ortmannicus) angustatus



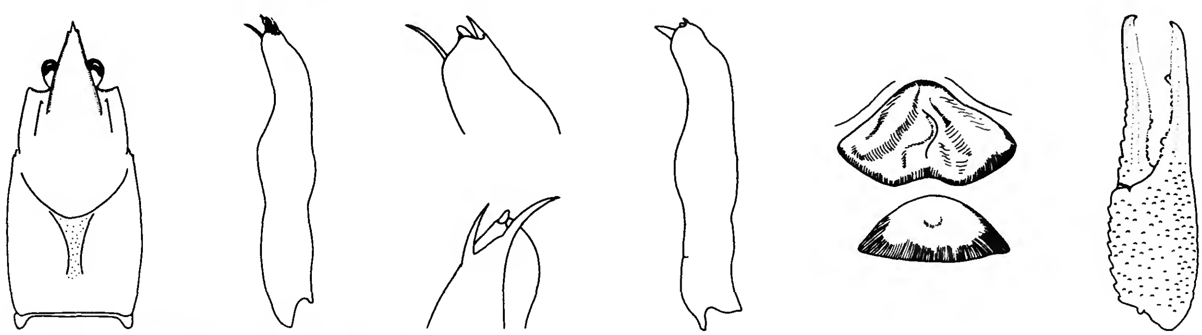
246. Procambarus (Ortmannicus) enoplosternum



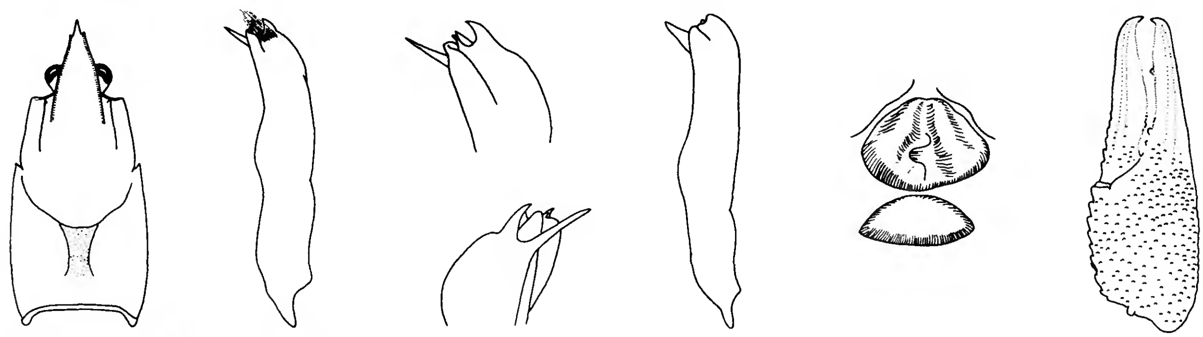
247. Procambarus (Ortmannicus) epicyrtus



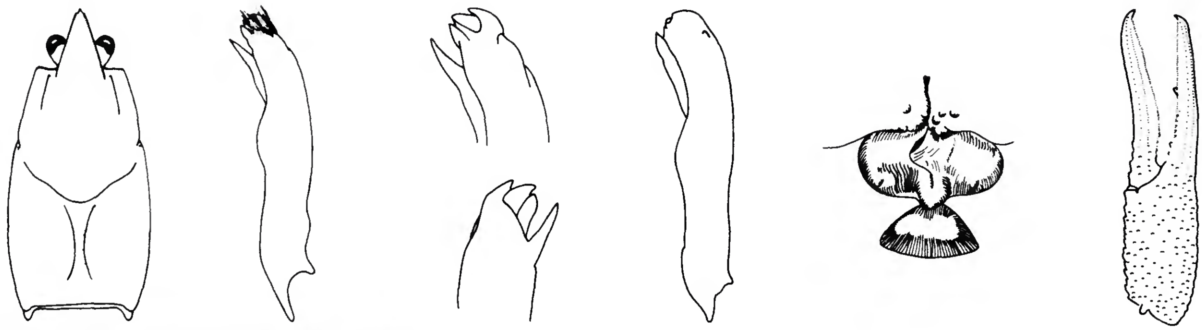
248. Procambarus (Ortmannicus) fallax



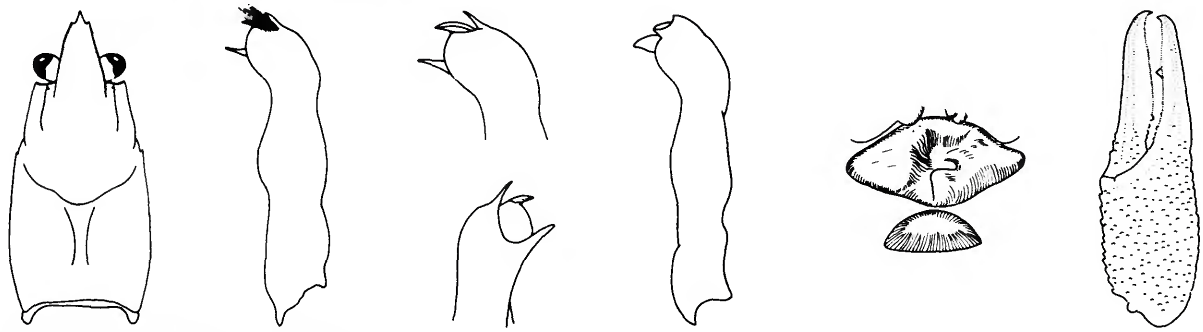
249. Procambarus (Ortmannicus) leonensis



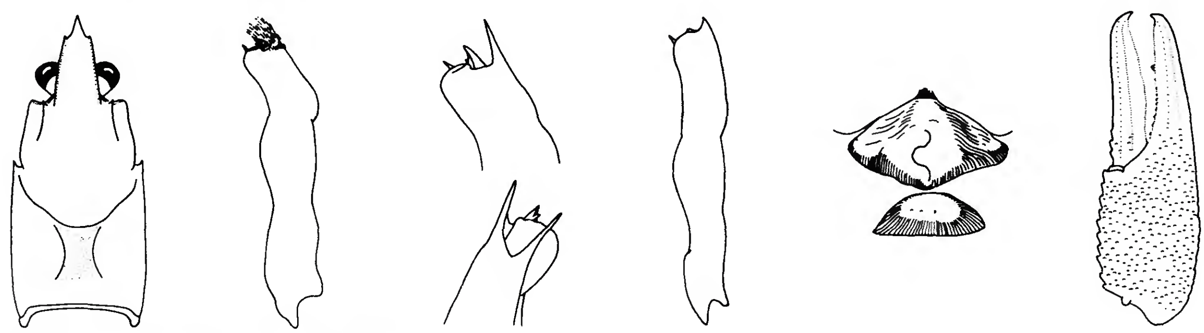
250. Procambarus (Ortmannicus) litosternum



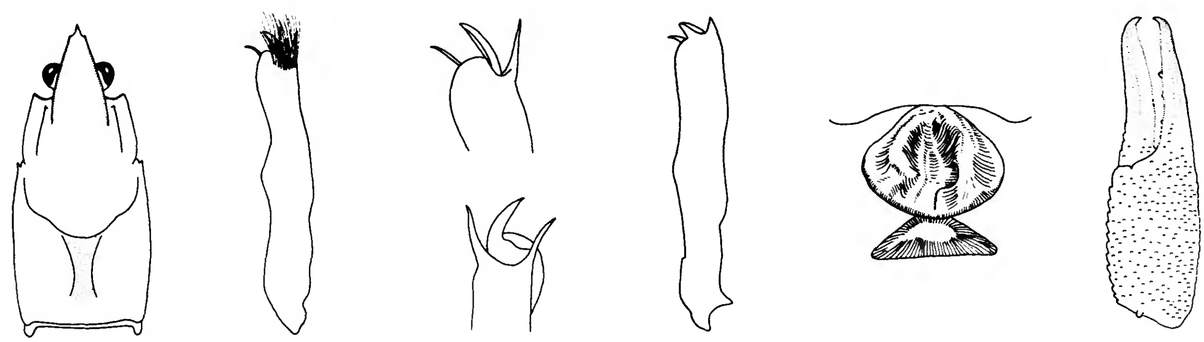
251. Procambarus (Ortmannicus) lophotus



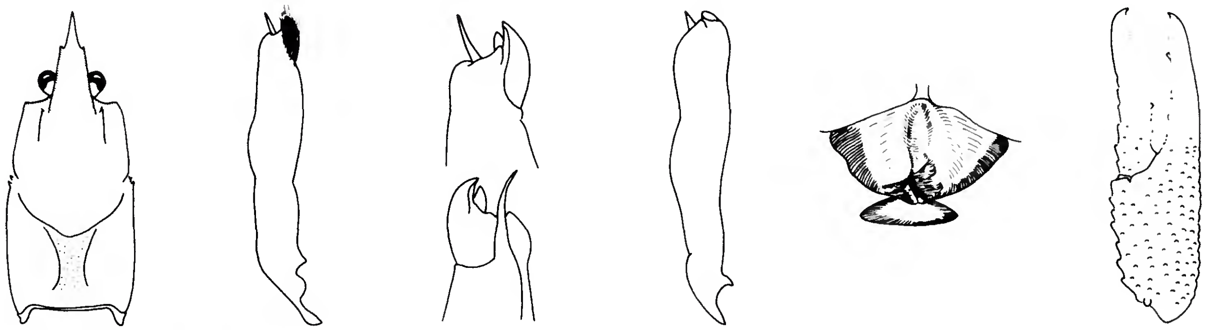
252. Procambarus (Ortmannicus) lunzi



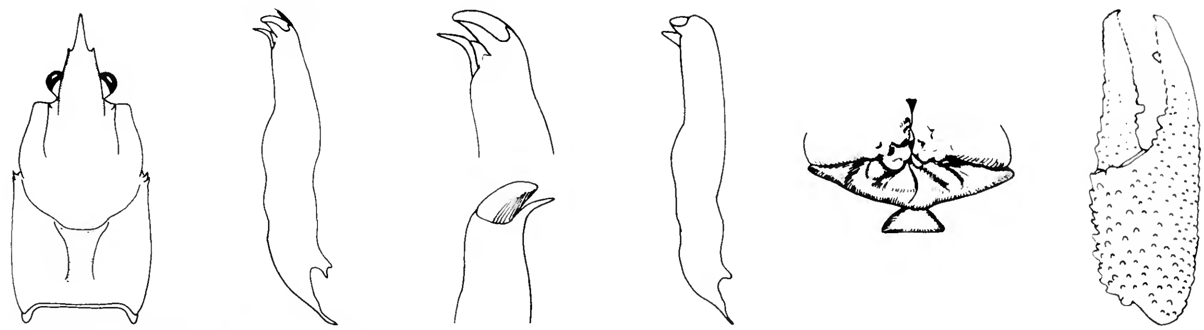
253. Procambarus (Ortmannicus) pubescens



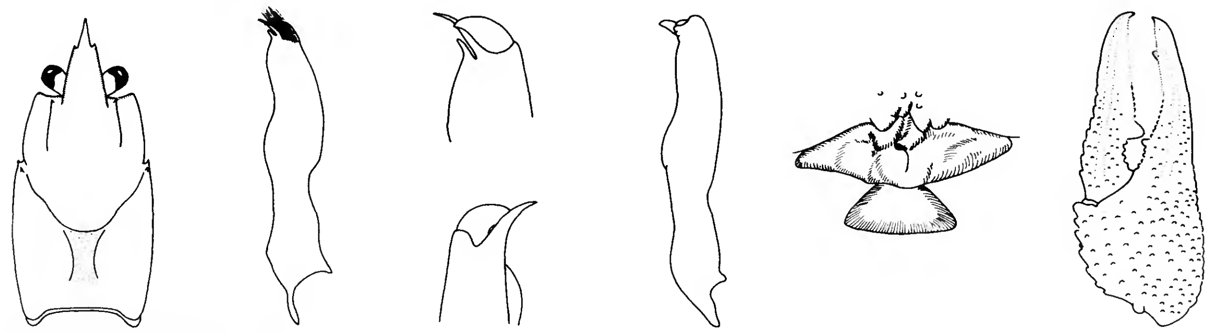
254. Procambarus (Ortmannicus) seminolae



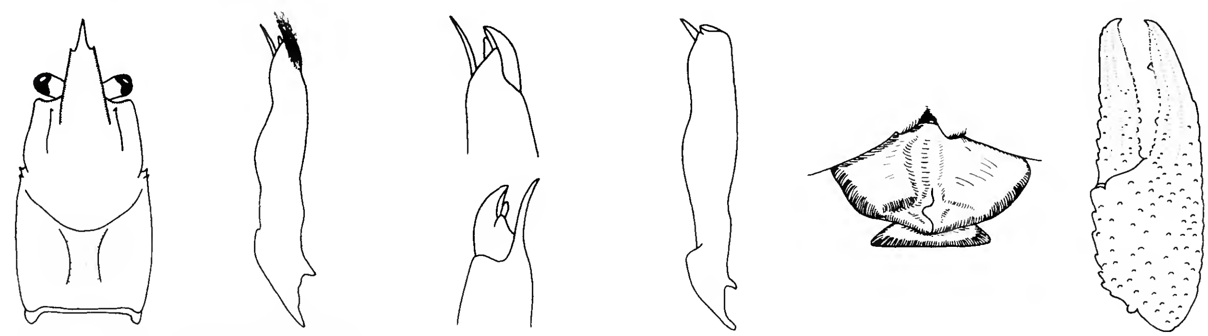
255. Procambarus (Pennides) gibbus



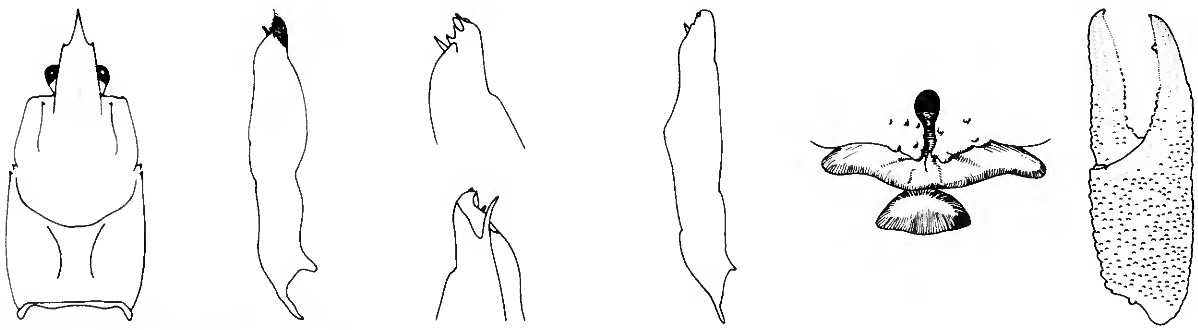
256. Procambarus (Pennides) petersi



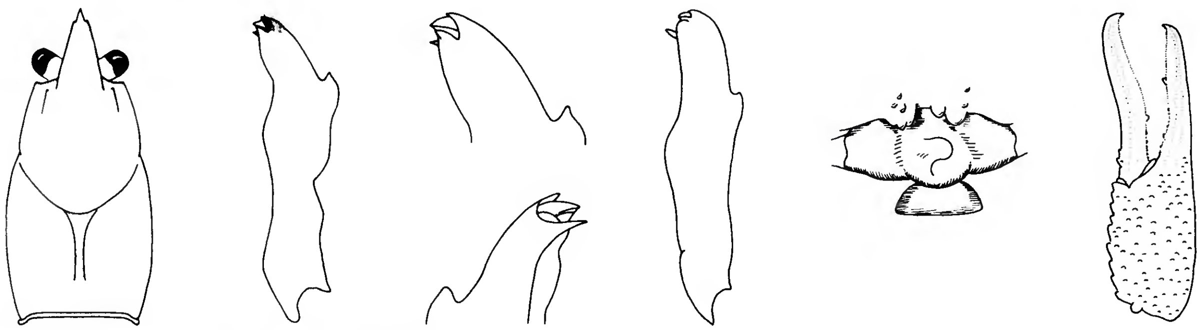
257. Procambarus (Pennides) raneyi



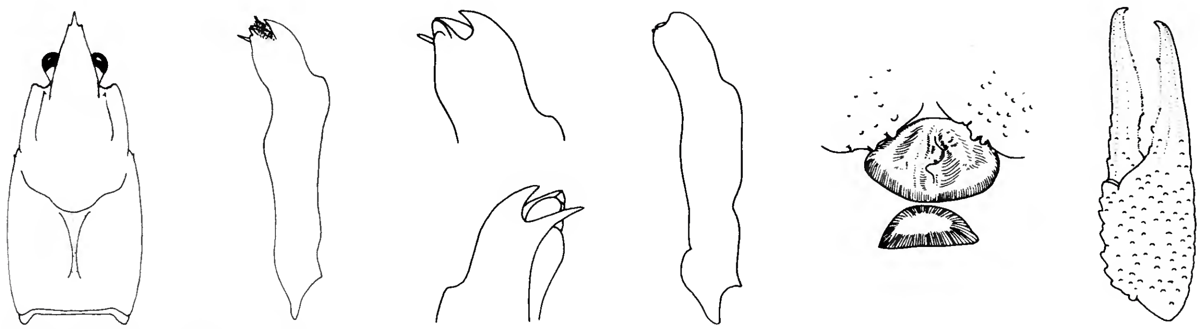
258. Procambarus (Pennides) spiculifer



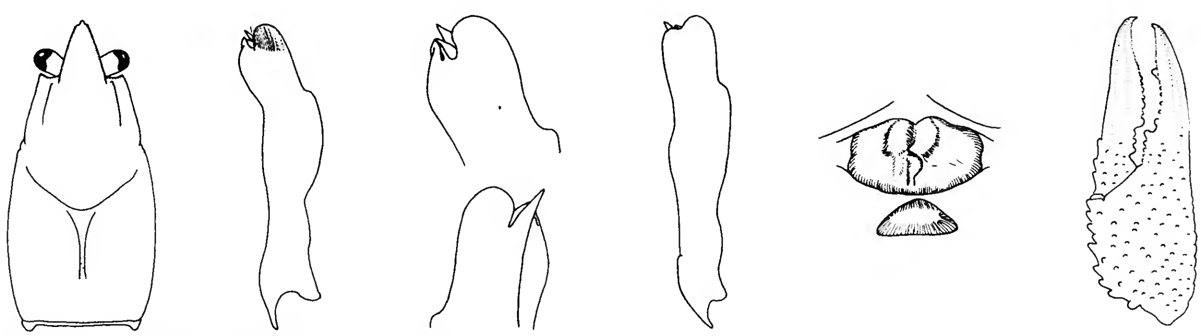
259. Procambarus (Pennides) versutus



260. Procambarus (Scapulicambarus) howellae



261. Procambarus (Scapulicambarus) paeninsulanus



262. Procambarus (Scapulicambarus) troglodytes

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Manuscripts intended for series publication receive substantive review within their originating Smithsonian museums or offices and are submitted to the Smithsonian Institution Press with approval of the appropriate museum authority on Form SI–36. Requests for special treatment—use of color, foldouts, casebound covers, etc.—require, on the same form, the added approval of designated committees or museum directors.

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Front matter (preceding the text) should include: **title page** with only title and author and no other information, **abstract page** with author/title/series/etc., following the established format, **table of contents** with indents reflecting the heads and structure of the paper.

First page of text should carry the title and author at the top of the page and an unnumbered footnote at the bottom consisting of author's name and professional mailing address.

Center heads of whatever level should be typed with initial caps of major words, with extra space above and below the head, but with no other preparation (such as all caps or underline). Run-in paragraph heads should use period/dashes or colons as necessary.

Tabulations within text (lists of data, often in parallel columns) can be typed on the text page where they occur, but they should not contain rules or formal, numbered table heads.

Formal tables (numbered, with table heads, boxheads, stubs, rules) should be submitted as camera copy, but the author must contact the series section of the Press for editorial attention and preparation assistance before final typing of this matter.

Taxonomic keys in natural history papers should use the alined-couplet form in the zoology and paleobiology series and the multi-level indent form in the botany series. If cross-referencing is required between key and text, do not include page references within the key, but number the keyed-out taxa with their corresponding heads in the text.

Synonymy in the zoology and paleobiology series must use the short form (taxon, author, year:page), with a full reference at the end of the paper under "Literature Cited." For the botany series, the long form (taxon, author, abbreviated journal or book title, volume, page, year, with no reference in the "Literature Cited") is optional.

Footnotes, when few in number, whether annotative or bibliographic, should be typed at the bottom of the text page on which the reference occurs. Extensive notes must appear at the end of the text in a notes section. If bibliographic footnotes are required, use the short form (author/brief title/page) with the full reference in the bibliography.

Text-reference system (author/year/page within the text, with the full reference in a "Literature Cited" at the end of the text) must be used in place of bibliographic footnotes in all scientific series and is strongly recommended in the history and technology series: "(Jones, 1910:122)" or ". . . Jones (1910:122)."

Bibliography, depending upon use, is termed "References," "Selected References," or "Literature Cited." Spell out book, journal, and article titles, using initial caps in all major words. For capitalization of titles in foreign languages, follow the national practice of each language. Underline (for italics) book and journal titles. Use the colon-parentheses system for volume/number/page citations: "10(2):5–9." For alinement and arrangement of elements, follow the format of the series for which the manuscript is intended.

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