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Two New Species of Crayfishes of
the Genus *Cambarus*
(Decapoda: Cambaridae) from the
Southeastern United States

RAYMOND W. BOUCHARD
and
HORTON H. HOBBS, JR.

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SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY • NUMBER 224

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SMITHSONIAN INSTITUTION PRESS

City of Washington

1976

ABSTRACT

Bouchard, Raymond W., and Horton H. Hobbs, Jr. A New Subgenus and Two New Species of Crayfishes of the Genus *Cambarus* (Decapoda: Cambaridae) from the Southeastern United States. *Smithsonian Contributions to Zoology*, number 224, 15 pages, 3 figures, 1976.—A new subgenus *Exilicambarus* is proposed to receive a single species, *Cambarus (Exilicambarus) cracens*, described from southeastern tributaries of Guntersville Lake (impounded Tennessee River) in DeKalb and Marshall counties, Alabama. A second previously undescribed species, *Cambarus (Jugicambarus) nodosus*, is a burrowing crayfish closely allied to *Cambarus (J.) carolinus* (Erichson), and is reported from the Hiwassee, Savannah, and Chattahoochee drainage systems in Tennessee, North Carolina, and Georgia.

OFFICIAL PUBLICATION DATE is handstamped in a limited number of initial copies and is recorded in the Institution's annual report, *Smithsonian Year*. SI PRESS NUMBER 6163. SERIES COVER DESIGN: The coral *Montastrea cavernosa* (Linnaeus).

Library of Congress Cataloging in Publication Data

Bouchard, Raymond W.

A new subgenus and two new species of crayfishes of the genus *Cambarus* (Decapoda, Cambaridae) from the southeastern United States.

(Smithsonian contributions to zoology ; no. 224)

Bibliography: p.

Supt. of Docs. no.: SI 1.27:224

1. *Cambarus cracens*. 2. *Cambarus nodosus*. 3. *Cambarus*. 4. Crustacea—Southern States. I. Hobbs, Horton Holcombe, 1914– II. Title: A new subgenus and two new species of crayfishes of the genus *Cambarus* . . . III. Series: Smithsonian Institution. Smithsonian contributions to zoology ; no. 224.

QL1.S54 no. 224 [QL444.M33] 591'.08s [595'.3841] 75-619424

A New Subgenus and Two New Species of Crayfishes of the Genus *Cambarus* (Decapoda: Cambaridae) from the Southeastern United States

Raymond W. Bouchard
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Introduction

The recognition of 10 subgenera within the genus *Cambarus* (Hobbs, 1969) has received general acceptance among crayfish systematists. Only the monotypic subgenus *Barbicambarus* has been elevated to generic rank (Bouchard, 1972), suggesting a greater divergence from a common ancestry in it than in any other member or assemblage within the genus. *Cambarus (Exilicambarus) craccens*, described herein, provides evidence of a previously unknown evolutionary line within the genus; nevertheless, it bears morphological resemblances to members of three of the currently recognized subgenera. Certain characteristics of the areola, rostrum, cervical spines, and chela are similar to those in members of the subgenus *Puncticambarus*. Other characters of the chela and of the first form male gonopod are suggestive of crayfishes assigned to the subgenus *Jugicambarus*, while in some respects the chela and areola exhibit features reminiscent of those occurring in the monotypic subgenus *Veticambarus*. Details of

these characters are more completely discussed in the section on "Relationships." The array of unique and shared characters of this new species provides the rationale prompting the proposal of the recognition of the new subgenus *Exilicambarus*.

The second species described herein represents one of a growing number of burrowing crayfishes to be reported. The difficulty in obtaining specimens and the variation exhibited by numerous populations of burrowers compound the problem of their recognition as distinct taxa. Specimens of this species have been available since 1958, but its close kinship to another poorly known species, *C. carolinus* (Erichson, 1846), suggested that it was prudent not to describe it until additional specimens from other localities became available. A previous study by us (Hobbs and Bouchard, 1973) presented a better understanding of *C. carolinus* and *C. dubius*, which was previously synonymized with the former. Improved concepts of the latter two species and the accumulation of additional data on the range and variations of the undescribed species encourage a description of the latter.

ACKNOWLEDGMENTS.—We wish to express our

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gratitude to the many persons who either contributed specimens or assisted us in the field: J. W. Bouchard, T. A. English, Jr., P. L. Holcomb, B. E. Oakberg, F. L. Oakberg, F. K. Parrish, D. J. Peters, J. E. Pugh, K. W. Simonds, T. Unestam, and C. H. Wharton. Our appreciation is also extended to Judith W. Bouchard and Fenner A. Chace, Jr., for reviewing the manuscript and to Carolyn B. Gast for the rendition of Figures 2 and 3.

Exilicambarus, new subgenus

DIAGNOSIS.—Eyes pigmented and of moderate size. Rostrum with margins slightly thickened and almost always bearing marginal tubercles or spines. Postorbital ridge with spine or tubercle. Cervical spine well developed, often flanked dorsally by secondary small acute tubercle. Suborbital angle rounded or obsolete. Hepatic spines absent, branchiostegal spine well developed or vestigial. Areola broad (about 3 or 4 times as long as wide), constituting 31.1 to 34.8 percent of entire length of carapace (41.5 to 44.6 percent of postorbital carapace length) with 6 to 10 punctations across narrowest part. Antennal scale 2 to 2.5 times as long as broad, broadest at or distal to midlength. Chela comparatively slender with mesial surface of elongate palm bearing 2, usually irregular, rows of tubercles (mesialmost consisting of 7 to 9); at least mesial half of dorsal surface, as well as ventral surface of palm, studded with squamous tubercles; lateral margin of fixed finger costate. Hook on ischium of third pereopod of male overreaching basioischial articulation, not opposed by tubercle on basis. First pleopod of first form male with central projection corneous, bladelike, somewhat tapering from base, bearing distinct subapical notch, bent caudoproximally at angle of about 135 degrees (distal half almost straight), and, if straightened, constituting approximately one-fifth total length of appendage; mesial process swollen, tapering distally, directed at 90 to 110 degrees to main shaft of appendage, and usually bearing 1 or 2 acute apical prominences; caudal element represented by small rounded lobe at caudolateral base of central projection. Annulus ventralis shallowly embedded in sternum, subspindle shaped. First pleopod reaching or almost reaching midlength of annulus when abdomen flexed.

TYPE-SPECIES.—*Cambarus (Exilicambarus) cracens*, here described.

LIST OF SPECIES.—Monotypic.

ETYMOLOGY.—*Exilis* (L., = slender) in combination with *Cambarus*; in reference to the comparatively elongate, slender, chela.

Cambarus (Exilicambarus) cracens, new species

FIGURES 1, 2

DIAGNOSIS.—Identical to diagnosis of subgenus.

HOLOTYPE MALE, FORM I.—Cephalothorax (Figure 1*e*, see also Figure 2*a*, *j*) subcylindrical in cross section. Abdomen narrower than thorax (18.4 and 19.9 mm). Greatest width of carapace greater than height at caudodorsal margin of cervical groove (17.6 and 14.8 mm). Areola 3.4 times as long as broad with 6 widely spaced punctations across narrowest part; length of areola 31.9 percent of entire length of carapace (41.9 percent of postorbital carapace length). Rostrum with slightly thickened, convergent margins bearing prominent acute corneous tubercles at base of acumen; latter almost reaching distal end of ultimate podomere of antennular peduncle and terminating in corneous, subspiculiform tip, acumen slightly upturned apically; dorsal surface of rostrum concave and bearing small setiferous punctations, latter more numerous in depression at level of caudal margin of orbit. Subrostral ridge weak and evident in dorsal aspect almost to base of marginal tubercle of rostrum. Postorbital ridge moderately strong with prominent knob at caudal extremity, grooved dorsolaterally, and with spiniform corneous tubercle cephalically. Suborbital angle broadly rounded, virtually nonexistent; branchiostegal spine moderately large, acute, and curved cephalodorsally. Cervical spine well developed and flanked by several small tubercles, at least one of which acute; hepatic area with scattered tubercles; cephaloventral part of branchiostegite with crowded tubercles and few adjacent and caudoventral to cervical spine, remaining lateral portion of branchiostegite granulate and dorsolateral portion finely, but densely, punctate.

Abdomen (Figure 1*a*) shorter than carapace (35.0 and 35.4 mm); pleura of moderate length, broad with caudoventral extremity of second through fifth rounded. Cephalic section of telson

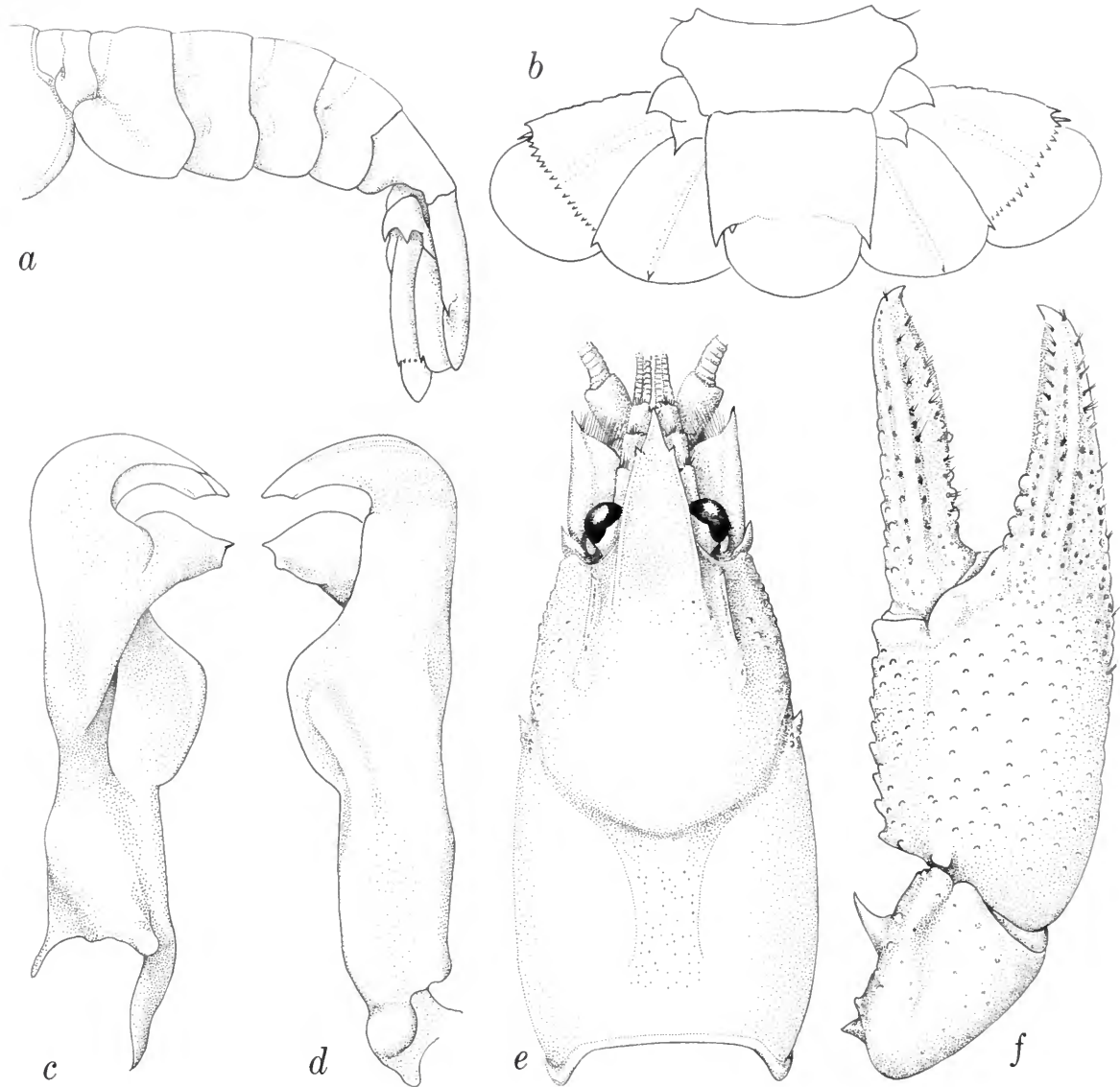


FIGURE 1.—*Cambarus (Exilicambarus) cracens*, new species (holotypic male, form I): *a*, lateral view of abdomen; *b*, dorsal view of caudal extremity of abdomen; *c*, mesial view of first pleopod; *d*, lateral view of first pleopod; *e*, dorsal view of carapace; *f*, dorsal view of distal podomeres of cheliped.

(Figure 1*b*) with 1 spine in caudodextral corner and 2 in caudosinistral, more mesial one movable. Proximal podomere of uropod with small distal spine on lateral lobe and larger one on mesial lobe; both rami with distinct median keel, that on mesial ramus with well-developed premarginal spine; lateral margin of lateral ramus subserrate with fixed and movable spines at extremity of proximal section; corresponding margin of mesial ramus with spine at distolateral angle.

Cephalic lobe of epistome (see Figure 2*i* of paratypic male, form I) apparently injured, rounded but with asymmetrical emargination cephalodextrally, margins only slightly thickened and marginal areas somewhat elevated, cephalomedian projection rather weak; main body of epistome with fovea represented by shallow depression not nearly so distinct as that illustrated, and arched epistomal zygoma flanked cephalolaterally by usual pair of slitlike fossae. Proximal segment of antennule with prominent spine on ventral surface at base of distal two-fifths. Antennal peduncle with lateral spine on basis and distal spine on ischium, flagellum extending caudally to third abdominal tergum. Antennal scale (see Figure 2*g* of paratypic male) rather broad, broadest distal to midlength, distomesial portion of lamellar area evenly rounded; distolateral spine strong, with long corneous tip, and reaching slightly beyond tip of rostrum. Postaxial surface of third maxilliped with stiff setae studding mesial half, row of submarginal shorter setae laterally, and with scattered setiferous punctations between submarginal row and clusters of stiff setae; distolateral extremity angular but not produced in spiniform projection.

Right chela (Figure 1*f*; see also Figure 2*l*) 3.7 times as long as broad (28.1 and 10.7 mm), subovate, slightly depressed; mesial margin of palm with irregular row of 8 tubercles, 2 immediately ventral to row and irregular row of 8 immediately dorsolaterally; remainder of palm studded with squamous tubercles, although few present ventromesially; distoventral surface of palm with usual prominent tubercle at base of dactyl and several somewhat larger than neighboring ones extending proximomesially from submedian ridge on fixed finger. Lateral surface of propodus costate with row of punctations causing irregular appearance of proximolateral margin on fixed finger and disto-

lateral part of palm. Both fingers with well-defined submedian ridges flanked by setiferous punctations dorsally and ventrally; opposable surface of fixed finger with row of 5 rounded tubercles, fourth from base largest, along proximal two-fifths of fingers, and broad band of minute denticles (between, ventral to, and beyond tubercles) reaching base of corneous tip of finger; usual large, single, more ventral tubercle lacking. Opposable margin of dactyl with row of 5 tubercles along proximal three-fifths; proximal 3 tubercles subequal in size and much larger than distal 2, distal-most somewhat removed from more proximal 4, and additional large tubercle present more ventrally between distal 2 tubercles of row; minute denticles dispersed very similarly to those on fixed finger; lateral surface of dactyl tuberculate along proximal half and punctate distally.

Carpus longer than broad (10.3 and 6.9 mm) with moderately deep oblique furrow dorsally; mesial surface with prominent procurved spine near midlength and very small tubercle proximally (carpus of left chela with two procurved spines); distoventral margin with strong submedian spiniform tubercle, another on ventrolateral articular knob, and 2 smaller tubercles proximomesial to submedian one; podomere otherwise sparsely punctate.

Dorsal surface of merus with irregular row of small tubercles and 2 subdistal spines; mesial and lateral surfaces with scattered punctations; ventral surface with mesial row of 10 (8 on left cheliped), mostly spiniform, tubercles, and 2 (4 on left) strong ones representing lateral row; also spine present on ventral margin of distolateral articular knob. Ischium with row of 5 small tubercles ventromesially.

Hook on ischium of third pereopod only (see Figure 2*h* of paratypic male, form I); hook simple, overreaching basioischial articulation and not opposed by tubercle on basis. Coxa of fourth pereopod with moderately prominent caudomesial boss, that of fifth well developed but much less conspicuous than that on fourth. (See "Measurements.")

First pleopods (Figure 1*c,d*; see also Figure 2*b,f*) reaching coxae of third pereopods when abdomen flexed. See "Diagnosis" for description. (The almost straight distal half of the pleopod directed at about 135 degrees to the main shaft

of the appendage is a unique feature of this crayfish.)

ALLOTYPIC FEMALE.—Excluding secondary sexual features, differing from holotype in following respects: epistome symmetrical, more nearly subtriangular and fovea slightly deeper; cephalic section of telson with 2 spines in each caudolateral corner; more lateral row of tubercles on dorsomesial surface of palm of chela consisting of 6 or 7 tubercles; ventral surface of palm with fewer and smaller tubercles, row extending proximomesially from submedian ridge on fixed finger in holotype not recognizable; opposable margin of fixed finger with row of 10 tubercles, that of dactyl with 9 on right and 11 on left chela; carpus of both chelipeds with 2 procurved tubercles mesially but lacking small tubercle on proximomesial surface; only 1 small tubercle proximomesial to median ventromarginal tubercle; merus with 3 subdistal acute tubercles dorsally on left cheliped, ventral surface with 10 tubercles in mesial row and 4 in lateral, right cheliped with 12 and 3 respectively; ischium with 4 tubercles on right and 3 on left cheliped. (See "Measurements.")

Annulus ventralis (Figure 2*k*) distinctly asymmetrical and cephalic region not nearly so strongly calcified as caudal; cephalic half with shallow, submedian, longitudinal trough; sinus originating at sinistrocandal end of latter and extending sinistrally, making hairpin turn, returning almost to median line before forming broad arc over caudal wall, there crossing median line and ending very slightly dextral to it; tongue directed sinistrally into fossa. Postannular sclerite 2.5 times as broad as long and half as wide as annulus. First pleopod almost reaching midlength of annulus when abdomen flexed.

MORPHOTYPIC MALE, FORM II.—Differing from holotype in following respects: epistome resembling that of allotype; tubercles flanking cervical spine on holotype and allotype not evident; cephalic section of telson with 2 spines in each caudolateral corner; opposable margin of fixed finger of right cheliped with 3 (4 on left) tubercles (third from base largest) along proximal third of finger, and large, more ventrally placed tubercle at base of distal two-fifths (absent on left); opposable margin of dactyl of right chela with 3 (5 on left) tubercles along proximal fourth and more ventrally placed one (absent on left) at end of

proximal third; mesial surface of carpus of left cheliped with 2 procurved spines and smaller proximal tubercle; 3 subdistal spines dorsally on merus of right cheliped, ventral surface with mesial row of 9 and lateral one of 3 tubercles on both chelipeds; ischia of both with row of 3 tubercles; hook on ischium of third pereopod much reduced, not overreaching basioischial articulation; bosses on coxae of fourth and fifth pereopods also greatly reduced. (See "Measurements".) First pleopods (Figure 2*c,e*) with mesial process lacking acute extension; central projection noncorneous, more massive, not so strongly recurved, with subacute apex directed caudally at approximately 90 degrees; only trace of caudal element evident.

COLOR NOTES.—Carapace olive tan with irregular cream tan mottlings dorsally and dorsolaterally, fading ventrally; rostral margins, suffused with red, flanking olive brown dorsum; hepatic region largely mustard yellow with prominent olive brown spot. Area over and between attachments of mandibular muscles dark olive, and median part of cervical groove flanked cephalically by broad dark brown band paralleling contour of groove. First through sixth abdominal terga olive tan with paired, pale to dark brown markings dorsolaterally (larger, although less intensely colored on first and second segments); terga with or without narrow, almost linear, scarlet band on caudal margin; if present, band continuing ventrally along cephalic and cephaloventral margins of pleuron of next segment, becoming reddish brown on pleuron and fading before reaching caudoventral extremity; first abdominal pleuron cream to white, succeeding ones with conspicuous similarly colored spot; bases of second through fifth pleura with oblique reddish brown bar subparallel to ventral margin. Margins of telson, as well as keels, lateral margins, and proximal borders of transverse articulations of uropods reddish brown. Remaining pereopods largely cream to white with olive suffusion dorsally on distal part of merus, carpus, and proximal part of propodus. Peduncle of antennule, antenna, and antennal scale brown mottled with olive cream; flagella olive brown. Dorsal surface of cheliped distal to midlength of merus olive tan, fingers fading to base of distal third where becoming vermilion to scarlet; tubercles and articular knobs olive cream to almost white.

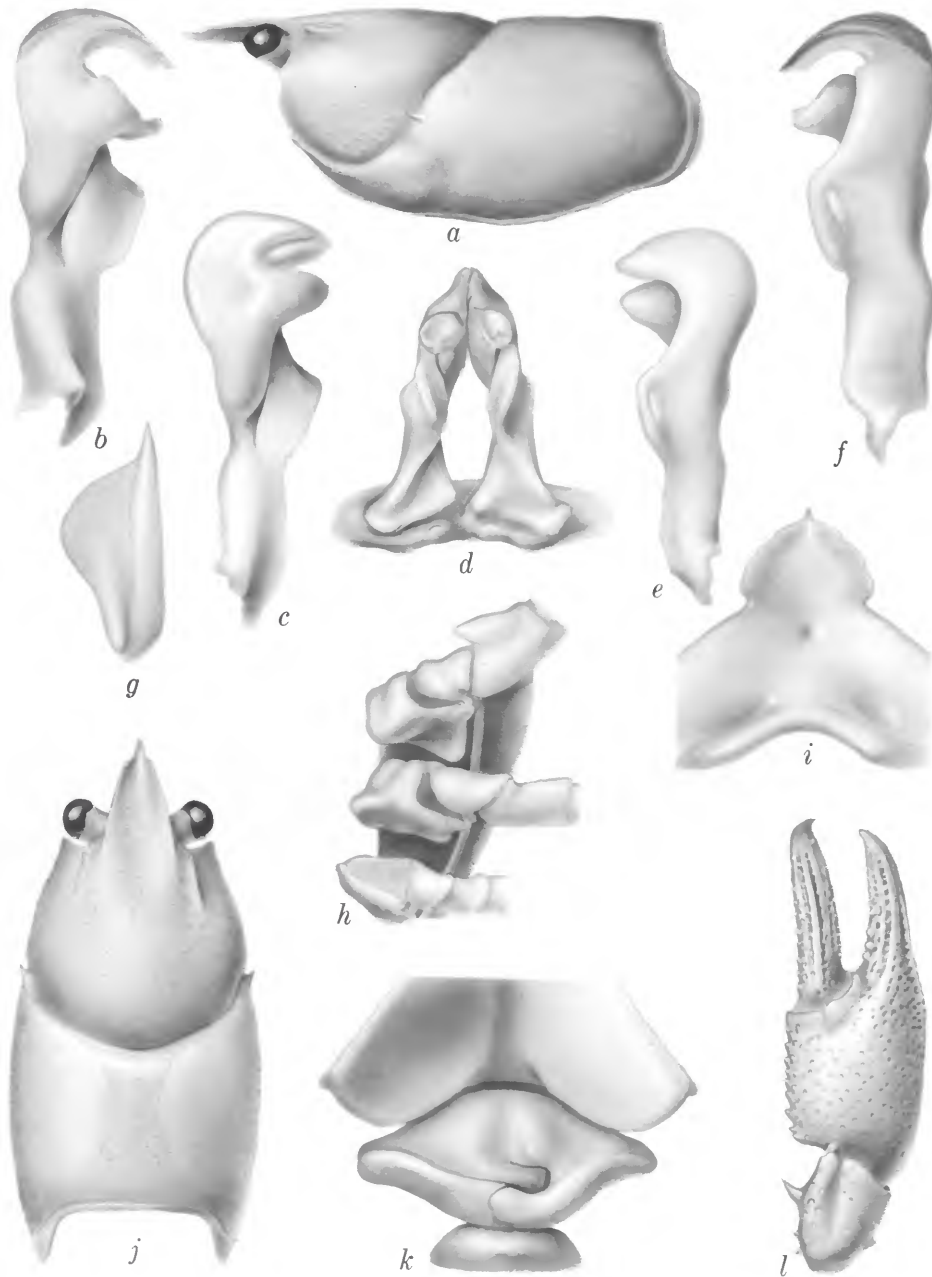


FIGURE 2.—*Cambarus (Exilicambarus) cracens*, new species (all depicting paratypic male, form I, except *c* and *e* of morphotypic male, form II, and *k* of allotype): *a*, lateral view of carapace; *b, c*, mesial view of first pleopod; *d*, caudal view of first pleopods; *e, f*, lateral view of first pleopod; *g*, antennal scale; *h*, basal podomeres of third, fourth, and fifth pereopods; *i*, epistome; *j*, dorsal view of carapace; *k*, annulus ventralis; *l*, dorsal view of distal podomeres of cheliped.

MEASUREMENTS (in mm).—

Characters	Holotype	Allotype	Morphotype
Carapace:			
Total length of carapace	35.4	39.7	24.8
Postorbital carapace length	27.0	30.7	19.2
Width	17.6	19.9	12.0
Height	13.6	17.1	10.0
Areola:			
Width	3.3	4.1	2.3
Length	11.3	13.4	8.1
Rostrum:			
Width	4.9	6.0	4.0
Length	9.7	11.1	7.2
Chela:			
Length, mesial margin of palm	10.4	10.3	5.2
Width, palm	10.7	10.9	6.5
Length, lateral margin	28.1	28.1	15.1
Length, dactyl	15.5	15.6	9.0
Abdomen:			
Width	14.8	18.4	10.9
Length	35.0	42.5	27.0

TYPE-LOCALITY.—Short Creek at State Route 75, 1.1 miles southwest of the junction with State Route 68 (T.8S, R.4E, Sec. 36), Marshall County, Alabama. There the clear stream, some 35 to 40 feet wide and mostly less than one foot deep, flows rather sluggishly over a bed-rock and sandy bottom littered with large rocks. Shading the shore line are *Platanus occidentalis*, *Liriodendron tulipifera*, *Quercus* sp., and *Pinus* sp. Only two other crayfishes, *Cambarus (Depressicambarus) striatus* Hay (1902:437) and *C. (Jugicambarus) distans* Rhoades (1944:136), share this locality with *C. (E.) cracens*.

DISPOSITION OF TYPES.—The holotypic male, form I (no. 146082), the allotype (no. 146083), and the morphotypic male, form II (no. 146084), are deposited in the National Museum of Natural History (NMNH), Smithsonian Institution. Paratypes consisting of 10 ♂ I, 1 ♂ II, 9 ♀, 28j ♂, and 19j ♀ are also in NMNH, and 9 ♂ I, 1 ♂ II, 2 ♀, 2j ♂, and 6j ♀ are in the collection of the senior author.

RANGE AND SPECIMENS EXAMINED.—This crayfish is known only from the localities cited here, all in the southeastern tributaries of Guntersville Lake (impounded Tennessee River) in DeKalb and Marshall counties, Alabama.

DEKALB COUNTY: Scarham Creek at State Route 20, 1 mile west of Skirum (T.2S, R.6E, Sec. 23), 1 ♂ I, 1 ♂ II, 1 ♀, IV/29/70, P. L. Holcomb and H. H. H., Jr., coll.; 2 ♂ I, 3 ♀, 9j ♂, 7j ♀, XI/11/73, T. A. English, Jr., and H. H. H., Jr., coll.; 8 ♂ I, 1 ♂ II, 2j ♂, 2j ♀, III/26/74, J. W. Bouchard and R. W. B., coll. Scarham Creek at State Route 277, 1.4 miles north of Crossville (T.8S, R.6E, Sec. 27), 4 ♂ I, 2 ♀, 10j ♂, 7j ♀, XI/12/73, T. A. E., Jr. and H. H. H., Jr., coll. Bengis Creek at County Road 116 (T.5S, R.8E, Sec. 25), 1 ♂ II (morphotype), X/31/74, J. W. B. and R. W. B., coll. MARSHALL COUNTY: Type-locality, 4 ♂ I, 4 ♀, 9j ♂, 5j ♀, XI/12/73, T. A. E., Jr., and H. H. H., Jr., coll. Shoal Creek at unpaved road off County Road 60 (T.8S, R.5E, Sec. 4), 1 ♂ I, 2 ♀, 4j ♀, VIII/21/73, J. W. B. and R. W. B., coll.

VARIATIONS.—Among the variations noted, only one seems to be restricted to some degree to a part of the range. The spination of the carapace (marginal spines of the rostrum, postorbital tubercles or spines, and cervical spines) is more pronounced in most of the specimens from the type-locality than from elsewhere. In many of the crayfish from the other localities, the marginal spines on the rostrum are reduced to small tubercles and in one or two are reduced to the extent that while the rostral margins at the base of the acumen are angular they are not produced in spines or tubercles. The postorbital tubercles are frequently markedly reduced or they may be well developed and spiniform; the cervical spines, always present, may be long and very sharp, or somewhat tuberculiform, although always bearing an acute tip. Frequently, one (sometimes two) spiniform tubercle flanking the cervical spine dorsally is somewhat larger than others in the vicinity. The chelipeds are rather uniform in general contour, and the numbers of tubercles pointed out on the cheliped vary little from the ranges indicated in the descriptions of the three specimens above. The first pleopod of the male, form I, exhibits few variations, the only conspicuous one being in the mesial process—in two specimens the distal extremity is rounded instead of possessing a short, apical, spiniform process on the margin adjacent to the central projection. The concavity of that margin, illustrated in Figure 2*b* and *f*, is present in only one other specimen, and both are probable artifacts of preservation.

SIZE.—The largest specimen available is a female having a carapace length of 39.7 mm (postorbital carapace length 30.7 mm). The corresponding measurements of the largest first form

male are 37.3 and 28.6 mm, and of the smallest first form male, 24.7 and 18.7 mm.

LIFE HISTORY NOTES.—First form males have been collected in March, August, and November, and the exoskeletons of most are encrusted. No large second form males are available, so there is no direct evidence as to the probable molting seasons in the adult male population. Neither ovigerous females nor those carrying young have been found, although well-developed cement glands were observed on two females collected in November. Judging by the sizes of the limited number of specimens at hand, three generations are present in the populations sampled. The smallest individual is a juvenile male, collected on 11 November 1974, having a carapace length of 12.2 mm.

ECOLOGICAL NOTES.—All of our collections were made in rock-littered areas of the streams. The first lot was obtained from Scarham Creek in April 1970 when the stream was at flood stage, some four feet above usual water level, and so swift that one could not stand in it except in lee and shallow marginal areas.

In November 1973, the stream was quite sluggish. At that season, the rock-littered areas were so choked with leaves that it is possible the crayfish were among the latter rather than having sought cover beneath the rocks. All of the specimens collected by the senior author were taken from under rocks. In none of the localities was the water swift except during the period of flood mentioned above.

RELATIONSHIPS.—Our assessment of the affinities of this crayfish is to some degree based on negative conclusions. Most of the characteristics of the carapace, except the comparatively small number of punctations in the areola in most of the specimens, are those usually associated with members of the subgenus *Puncticambarus*. The rather long, strongly recurved, central projection of the first pleopod of the first form male, the few punctations in the areola of most of the specimens, and the slightly downcurved fingers of the cheliped are suggestive of crayfishes comprising the subgenus *Jugicambarus*. The elongate chela resembles that of the monotypic subgenus *Veticambarus*, and to a lesser degree that of *C. (Puncticambarus) reburus* Prins (1968:458). In few species of the genus is the palm of the chela so nearly completely covered with tubercles; only in some members of the

subgenus *Depressicambarus* is such a tuberculate condition approximated.

The tapering central projection of the first pleopod of the first form male, although strongly recurved, is unique in that the morphologically cephalodistal margin is almost straight.

For the following reasons, it does not seem appropriate to assign this crayfish to any of these subgenera. The usually limited number of punctations in the areola, the strongly recurved central projection of the first pleopod of the male, and the absence of a tubercle on the basis of the third pereopod opposing the hook on the ischium constitute a combination of features that does not occur elsewhere in members of the subgenus *Puncticambarus*. The long rostrum with marginal tubercles or spines, the strongly developed cervical spine, and the elongate chela studded with tubercles, distinguish it from all known epigeal members of the subgenus *Jugicambarus*. From the monotypic *Cambarus (Veticambarus) pristinus* Hobbs (1965:268) it differs in possessing marginal spines on the rostrum, lacking an acute suborbital angle, a tubercle on the basis of the third pereopod that opposes the hook on the ischium, and a cephalic excavation on the boss on the coxa of the fourth pereopod. In addition, the following differences exist in the first pleopod of the first form male: the central projection is more strongly recurved; the mesial process is bent caudally at at least 90 degrees to the main shaft of appendage; and the caudal process is not nearly so well developed. The shape and armature of the chela and the nature of the first pleopod of the first form male isolate this crayfish from members of the subgenus *Depressicambarus*. Accordingly, it has been assigned to the new monotypic subgenus *Exilicambarus*.

ETYMOLOGY.—The name *cracens* (L., = slender) was chosen because of the elongate, comparatively slender chela.

Cambarus (Jugicambarus) nodosus, new species

FIGURE 3a-1

Cambarus carolinus.—Holt, 1968:32.

DIAGNOSIS.—Body and eyes with pigment, latter small. Rostrum without marginal spines or tubercles. Areola 5.0 to 13.6 times as long as broad and

constituting 33.9 to 41.4 percent of total length of carapace (38.2 to 46.5 percent of postorbital carapace length) with 2 to 4 punctations across narrowest part. Cervical spine lacking, although small rounded tubercle present. Hepatic spines absent; branchiostegal tubercle small and rounded; suborbital angle moderately to well developed. Postorbital ridge rather well developed without cephalic tubercle. Antennal scale longer than broad, broadest slightly distal to midlength. Chela with 2 rows of tubercles along mesial margin of palm, mesialmost subserrate, secondary row uneven; scattered tubercles over dorsomesial half of palm; well-defined longitudinal ridges on dorsal surface of fingers, less obvious ones on ventral side; lateral surface of fixed finger weakly costate. Hook on ischium of third pereopod of first form male overreaching basioischial articulation and not opposed by tubercle on basis. First pleopod of first form male with central projection corneous, blade-like, tapering, bearing distinct, small subapical notch, and recurved at angle of approximately 90 degrees to shaft of appendage; mesial process tumescent, tapering to acute tip and directed caudally at angle of approximately 90 degrees. Both elements of first pleopod appreciably longer than cephalocaudal diameter of shaft of appendage. Annulus ventralis asymmetrical, subcylindrical and movable; cephalic half bearing longitudinal median trough between anteriorly converging ridges, and caudal half with sinuate dextral or sinistral sinus. Caudal wall of annulus elevated. First pleopod of female uniramous and reaching at least midlength of annulus when abdomen flexed.

HOLOTYPE MALE, FORM I.—Body subovate, depressed (Figure 3*a,f*). Abdomen narrower than thorax (12.9 and 14.9 mm). Greatest width of carapace greater than height at caudodorsal margin of cervical groove (14.9 and 12.0 mm). Areola 7.1 times as long as wide with 3 punctations across narrowest part; length of areola 37 percent of entire length of carapace (42.3 percent of postorbital carapace length). Rostrum with thickened, slightly concave, subparallel margins devoid of marginal spines or tubercles. Acumen set off from basal portion of rostrum, with concave, oblique, slender margins, and terminating in small upturned tubercle. Rostrum excavate dorsally, especially deep anteriorly, with submarginal punctations and few scattered ones basally. Ventrolateral

margin of rostrum with long, thick setae except at apex of acumen. Postorbital ridges moderately well developed, shallowly grooved dorsolaterally and lacking cephalic tubercle. Suborbital angle moderately strong, lacking corneous tip; branchiostegal spine represented by small tubercle. Cervical spine absent although represented by very small rounded tubercle. Hepatic area and lateral portion of branchiostegite tuberculate; dorsal surface of carapace punctate.

Abdomen longer than carapace (29.3 and 28.9 mm); pleura of moderate length with caudoverentral extremities subangular. Cephalic section of telson with marginal spine and submarginal movable spine in each caudolateral corner and partially delimited from caudal section by paired oblique incisions. Basal podomere of uropod with spine extending over mesial ramus; lateral ramus with median and submedian ridges, former terminating in acute spine at transverse flexure. Proximal portion of lateral ramus with row of small spines distally and large, submarginal movable spine at caudolateral corner. Mesial ramus of uropod with median ridge terminating distally in pre-marginal acute spine; lateral margin with distolateral acute spine. Dorsal surface of telson and uropod lightly setiferous and fringed caudally.

Cephalic lobe of epistome (Figure 3*g*) rounded with small cephalomedian projection and slightly irregular, thickened cephalolateral margins. Main body of epistome with very shallow median fovea and pair of obliquely disposed slitlike fossae immediately cephalic and subparallel to thickened, slightly arched epistomal zygotha; lateral extremities with several small tubercles. Proximal segment of antennule with small spine on ventral surface near midlength. Antennae broken. Antennal scale (Figure 3*i*) broadly declivous, broadest distal to midlength; thickened lateral portion terminating in prominent, acute, corneous-tipped spine projecting anteriorly beyond tip of rostrum.

Right chela (Figure 3*l*) about 2 times as long as broad (21.9 and 11.0 mm), inflated, especially proximolaterally; mesial margin of palm with primary subserrate row of 7 tubercles and uneven secondary row of slightly smaller tubercles dorsolateral to primary row; scattered tubercles over dorsomesial half of palm; distoventral surface of palm with 2 large, swollen tubercles at base of dactyl, mesial one with small, corneous, rounded

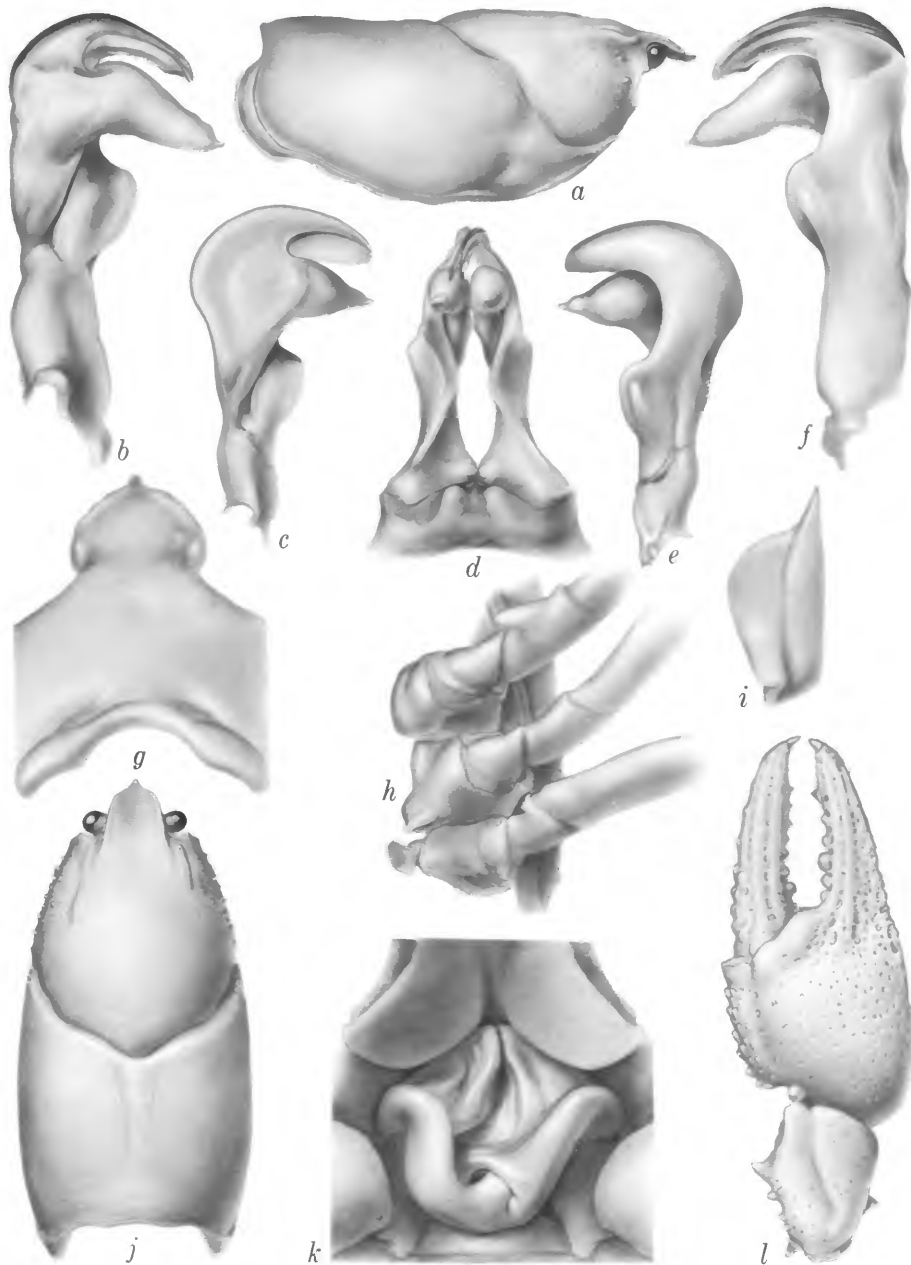


FIGURE 3.—*Cambarus (Jugicambarus) nodosus*, new species (all depicting holotypic male, form I, except *b* and *f* of paratypic male, form I (Union County, Georgia), *c* and *e* of morphotypic male, form II, and *k* of allotype): *a*, lateral view of carapace; *b,c*, mesial view of first pleopod; *d*, caudal view of first pleopods; *e,f*, lateral view of first pleopod; *g*, epistome; *h*, basal podomeres of third, fourth, and fifth pereopods; *i*, antennal scale; *j*, dorsal view of carapace; *k*, annulus ventralis; *l*, dorsal view of distal podomeres of cheliped.

tip. Lateral surface of propodus weakly costate with row of punctations rendering proximolateral base slightly impressed dorsally, less so ventrally; dorsal and ventral surfaces of fixed finger with distinct submedian ridges flanked by setiferous punctations; opposable surface with row of 5 tubercles along proximal half, third from base largest; distal tubercle moderately acute, others knoblike; additional acute tubercle present on lower level near base of distal fourth; opposable surface also with row of minute denticles extending distally from fourth tubercle from base, row interrupted only by fifth. Dorsal and ventral surfaces of dactyl with median longitudinal ridges flanked by setiferous punctations; opposable margin with row of 7 tubercles situated in slight excavation, proximal 3 rounded (basalmost largest), followed by 2 moderately acute and 2 acute distal ones; row of denticles, broken by tubercles, extending from third tubercle to distal end of finger. Fingers terminating in large, acute, corneous spines.

Carpus longer than broad (9.2 and 6.0 mm) with deep oblique furrow dorsally; mesial surface with large spine near midlength and small tubercle near proximal base of latter; 3 rounded tubercles on dorsomesial surface; distoventral margin with 3 rounded tubercles; podomere otherwise punctate.

Upper surface of merus with 3 rounded subdistal tubercles and 11 along crest of podomere; ventral surface with lateral row of 5 subacute spines, and mesial row of 11 subacute ones, both rows decreasing in size proximally. Ischium with row of 3 small tubercles on ventromesial margin.

Hook on ischium of third pereopod only (Figure 3*h*); hook simple, overreaching basioischial articulation and not opposed by tubercle on basis. Coxa of fourth pereopod with prominent caudomesial boss, that of fifth without prominence. (See "Measurements".)

First pleopods (Figure 3*b,d,f*) reaching caudal portion of coxae of third pereopods when abdomen flexed. (See "Diagnosis" for description.)

ALLOTYPIC FEMALE.—Differing from holotype in following respects: areola constituting 37.7 percent of entire length of carapace (43.1 percent of postorbital carapace length) and 5.8 times as long as broad. Cephalic lobe of epistome triangular. Palm of right chela with primary row of 8 tubercles.

Mesial surface of carpus with horizontal row of 3 tubercles proximal to large spine; dorsomesial surface with 3 very small tubercles (6 on left cheliped); distoventral surface with cluster of 5 tubercles. Upper surface of merus of right cheliped with 2 subdistal rounded tubercles and 10 (8 on left) along crest of podomere; ventrolateral margin with row of 7 spines on both chelipeds; ventral surface with more acute spines. (See "Measurements".)

Sternum between third and fourth pereopods broadly V-shaped and moderately deep. Annulus ventralis (Figure 3*k*) with cephalic half bearing median longitudinal trough flanked by ridges converging anteriorly; caudal half with sinistral sinus. Caudal wall of annulus elevated, especially caudolaterally. First pleopod uniramous and reaching at least midlength of annulus when abdomen flexed.

MORPHOTYPIC MALE, FORM II.—Differing from holotype in following respects: rostrum less excavate anteriorly; ventral margin with setae sparse on sides of rostrum and lacking on most of acumen; cephalic tubercle more spiniform. Areola constituting 37.9 percent of entire length of carapace (43.8 percent of postorbital carapace length) and 7.1 times as long as broad with 2 punctations across narrowest part. Palm on left chela with primary row of 6 tubercles. Mesial surface of carpus of both left and right chelipeds with horizontal row of 3 tubercles proximal to large spine; dorsomesial surface of both with 2 tubercles. Upper surface of merus of right cheliped with 2 rounded subdistal tubercles and 11 along crest of both right and left, latter with additional laterally disposed tubercle; ventrolateral margin of merus of left cheliped with row of 6 spines, and ventromesial margin of left and right with row of 10 and 9, respectively. Caudolateral corners of epistome especially elevated. Propodus of chela with third and fourth tubercles from proximal end more acute.

Hook on ischium of third pereopod much reduced, not reaching basioischial articulation. Boss on coxa of fourth pereopod somewhat smaller and less sharply defined. (See "Measurements".)

First pleopods (Figure 3*c,e*) of uniform texture, neither element corneous, central projection heavier, rounded caudally, and recurved at angle of approximately 90 degrees to shaft of appendage; mesial process tumescent, terminating ce-

phalically in acute tip and directed caudally at angle of approximately 90 degrees. Both elements of first pleopod appreciably longer than cephalo-caudal diameter of shaft of appendage.

COLOR NOTES.—Based on specimens from the type-locality. Cephalothorax and abdomen concolorous blue gray, blue green to brown dorsally with pair of submedian broken, dark brown stripes on abdomen. Stripes evident in younger individuals and less apparent, or faded, in adults. Branchiostegites and hepatic region light brown. Chela blue gray, blue green to brown dorsally with lighter proximolateral area. Distal half or less of fingers orange to yellow. Pereiopods brown dorsolaterally; distal podomeres darker dorsally than proximal ones.

Rostral margins and postorbital ridges light brown. Lateral margin of antennal scale dark brown. Color of antenna and antennule like that of dorsal surface of body. Tubercles on dorsal surface of chela, carpus, merus, and lateral surface of cephalothorax (especially cephalic region of carapace) cream to yellow. Large swollen tubercle at base of dactyl and articular knob on dorsal surface at base of palm yellow.

The following color notes are based on specimens from Towns and Union counties, Georgia. Dorsum of carapace 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 peduncles 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, 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 dactyl. Ventral surface of third maxilliped, sternum, and ventral surface of proximal podomeres of pereiopods pinkish cream.

The orange coloration on the ventral surface of *C. nodosus* is shared by certain other close relatives belonging to the subgenus *Jugicambarus*: *C. as-*

perimanus Faxon (1914:391) (Blue Ridge province of North Carolina, Tennessee, Georgia, and South Carolina), *C. conasaugaensis* Hobbs and Hobbs (1962:41) (Blue Ridge province of Tennessee and Georgia), and *C. parvoculus* Hobbs and Shoup (1947:142) (Cumberland Plateau and Cumberland Mountains, descending to western edge of Ridge and Valley province in Virginia, Kentucky, Tennessee, and probably Georgia). (See Bouchard, in press.)

MEASUREMENTS (in mm).—

Characters	Holotype	Allotype	Morphotype
Carapace:			
Total length of carapace	28.9	30.8	31.7
Postorbital carapace length	25.3	26.9	27.4
Width	14.9	15.1	16.4
Height	12.0	12.8	12.6
Areola:			
Width	1.5	2.0	1.7
Length	10.7	11.6	12.0
Rostrum:			
Width	3.8	4.2	4.2
Length	3.6	3.9	4.3
Chela:			
Length, mesial margin of palm	7.8	7.4	8.2
Width, palm	11.0	10.4	10.5
Length, lateral margin	21.9	21.2	23.0
Length, dactyl	13.1	12.2	13.2
Abdomen:			
Width	12.9	14.6	14.0
Length	29.3	29.6	31.6

TYPE-LOCALITY.—A small unnamed tributary of North Potato Creek (Hiwassee River system via Ocoee River) between 0.7 and 0.9 mile west of the Tennessee-North Carolina border on U.S. Highway 64, Polk County, Tennessee. During the autumn, the water level was low, and the depth varied from several inches in the riffles to less than 15 inches in the pools. The stream is approximately 2 to 6 feet wide and flows over a substrate of sand and mica with stretches of bedrock and scattered small to large rocks. The banks consist of sand with scattered embedded rocks. At this locality the stream is bordered with grasses and a dense growth of *Bidens* sp.

DISPOSITION OF TYPES.—The holotypic male, form I (no. 146756), the allotype (no. 146757), and the morphotypic male, form II (no. 146758) are deposited in the National Museum of Natural

History, Smithsonian Institution. Paratypes consisting of 5 ♂ I, 8 ♂ II, 20 ♀, 11 ♂ ♂, 7 ♀ ♀, 4 ♀ with eggs and 2 ♀ with young are also in NMNH, and 4 ♂ II, 4 ♀, 1 ♂ ♂ and 1 ♀ ♀ are in the collection of the senior author.

RANGE AND SPECIMENS EXAMINED.—The crayfish is known from the Hiwassee (Ocoee, Nottely, and Toccoa river basins), Savannah (Chatooga and Tugaloo river basins) and Chattahoochee river systems in Tennessee, North Carolina, and Georgia. It seems possible that it also may be found in South Carolina. The presence of an additional member of the subgenus *Jugicambarus* in the Blue Ridge province lends countenance to the hypothesis that the subgenus used this province as a path of migration and radiation.

GEORGIA. LUMPKIN COUNTY: (1) 3.6 miles south of Union County line on U.S. Highway 19 and 0.4 mile west of Highway in DeSota Falls camping area, 1 ♂ II, 3 ♀ ♀, 2 ♀ ♀, VI/17/75, D. J. Peters, J. E. Pugh, and H. H. H., Jr., coll. **RABUN COUNTY:** (2) County Road just south of U.S. Highway 76, 2 miles east of Clayton, 1 ♀, IV/25/67, Torgny Unestam and H. H. H., Jr., coll. **TOWNS COUNTY:** (3) Bog in headwaters of Tallulah River north of Tate City, 2 ♂ I, 2 ♀, IV/11/67, C. H. Wharton and F. K. Parrish, coll.; 1 ♂ I, VI/7/67, C. H. W., coll.; 1 ♀, VI/23/67, C. H. W., coll.; 1 ♂ II, 1 ♀, VII/6/67, C. H. W., coll. (4) Along roadside seepage area on Forest Road 70 at edge of Tate City, 2 ♀, 1 ♂ ♂, 2 ovigerous ♀, 1 ♀ with young, VI/16/75; D. J. P., J. E. P., and H. H. H., Jr., coll. (5) Roadside ditch 5 miles south of junction of U.S. Highway 76 on State Route 17, 2 ♀, 1 ovigerous ♀, 1 ♀ with young, VI/17/75, D. J. P., J. E. P., and H. H. H., Jr., coll. **UNION COUNTY:** (6) Seepage area 3.6 miles west of U.S. Highway 19 on State Route 180 (top of mountain west of Vogel State Park), 1 ♀ ♀, IV/27/67, T. U. and H. H. H., Jr., coll.; 1 ♂ II, 3 ♀, 1 ♂ ♂, VI/17/75, D. J. P., J. E. P., H. H. H., Jr., coll. (7) Stream 0.5 mile north of Vogel State Park on U.S. Highway 19, 1 ♂ I, XI/5/58, K. W. Simonds, coll. **WHITE COUNTY:** (8) Seepage area across road from Spoil Cane Creek, 9.1 miles south of Towns County line on State Route 17, 2 ♂ II, 3 ♀, 2 ♂ ♂, 2 ♀ ♀, 1 ovigerous ♀, VI/17/75, D. J. P., J. E. P., and H. H. H., Jr., coll.

NORTH CAROLINA. CHEROKEE COUNTY: (1) 1.6 miles west of junction U.S. Highway 64 and North Carolina State Route 60 on latter, 1 ♀, VI/12/60, K. W. S., coll. (2) 6.9 miles east of Tennessee-North Carolina state line on U.S. Highway 64, 1 ♀, IV/15/62, K. W. S., coll.

TENNESSEE. POLK COUNTY: (1) Type-locality, 4 ♂ II, 4 ♀, 1 ♂ ♂, 1 ♀ ♀, XI/5/72, F. L. Oakberg, B. E. Oakberg, J. W. Bouchard and R. W. B., coll.; 1 ♂ I, 1 ♂ II, 1 ♀, X/23/71, J. W. B. and R. W. B., coll.; 1 ♂ I, 1 ♂ II, XII/9/59, K. W. S., coll.; 1 ♂ II, 1 ♀, 1 ♂ ♂, VI/8/59, K. W. S., coll. (2) Tennessee Route 68 in Harbuck, 1 ♂ II, VI/8/59, K. W. S., coll. (3) Public picnic area 0.9 mile west of Turtletown on Tennessee Route 68, 2 ♀, 3 ♂ ♂, 2 ♀ ♀, VI/12/59, K. W. S., coll.

VARIATIONS.—The most evident variations in this species are found in the chela, suborbital angle, rostrum, and areola. The tubercles on the dorsal surface of the chela vary in size and area of dispersal. The suborbital angle varies from subacute to broadly rounded, while the rostrum on the Georgia material often possesses a distinct carina at the tip. The areola of specimens from the headwaters of the Hiwassee and Savannah rivers in Georgia is narrower, ranging from 8.5 to 13.6 times as long as broad. None of the other specimens available possess such a narrow areola.

Other than an expected range in meristic and mensural characters, as well as in density of setae, there exist few notable variations. (See "Diagnosis.")

LIFE HISTORY NOTES.—First form males have been collected in April, June, and from October to December. Females carrying eggs or young were collected during the month of June.

ECOLOGICAL NOTES.—*Cambarus (J.) nodosus* has been collected from burrows in the stream bank and in seepage areas, under rocks on shore or at the shoreline, and under rocks in midstream of pools and slow runs. Despite this broad array of habitats, the reduced size of the eyes and the relatively narrow areola indicate that *C. (J.) nodosus* is primarily a burrowing species. Most of our specimens were dug from complex burrows consisting of branching galleries with two or more openings to the surface. Several were taken from a sphagnum bog in pit traps set to catch small mammals.

Collected with *Cambarus (J.) nodosus* in one or more localities were *Cambarus (C.) bartonii* (Fabricius, 1798:407), *C. (Hiaticambarus) longirostris* Faxon (1885:64), and two undescribed congeners, one each of the subgenera *Puncticambarus* and *Lacunicambarus*. *Cambarus (Lacunicambarus)* sp. was collected only from burrows in the stream bank, and *C. (C.) bartonii* was taken in the stream as well as under rocks at or on the shore. *Cambarus (H.) longirostris* was found primarily in runs and *C. (Puncticambarus)* sp. in pools and riffle areas of streams.

RELATIONSHIPS.—*Cambarus (J.) nodosus* has its closest affinities with *C. (J.) carolinus*, sharing with it a similar first form male gonopod and general mien. It differs from *C. (J.) carolinus* primarily in exhibiting the following characters: the chela of *C. (J.) nodosus* possesses two well-defined

rows of tubercles along the mesial surface of the palm with additional smaller ones dispersed over the dorsal surface; the central projection of the first form male gonopod bears a distinct, small subapical notch; and the suborbital angle is moderately to well developed. An additional character that will serve to separate *C. (J.) nodosus* from *C. (J.) carolinus* is exhibited in the areola width, the former possessing an areola 5.0 to 13.6 times as long as broad compared to a range of 13.7 to 39.3 in the latter (data from Hobbs and Bouchard, 1973).

The more subdued coloration of *C. (J.) nodosus* is in sharp contrast to the bright red to red orange colors exhibited by *C. (J.) carolinus*. Only a single individual of the latter is known to have

exhibited a different color after molting—from red to blue gray in captivity.

SIZE.—The largest specimen available is a female from Polk County, Tennessee, with a carapace length of 36.5 mm (postorbital carapace length 32.4 mm). The smallest first form male is from Towns County, Georgia, and has corresponding lengths of 26.8 and 23.9 mm. The smallest female with eggs or young is also from Towns County and has comparable lengths of 26.5 and 23.4 mm.

ETYMOLOGY.—The name *nodosus* (L., = knotty) was chosen because of the large number of well-developed tubercles on the dorsomesial half of the palm of the chela and on the hepatic region of the carapace.

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