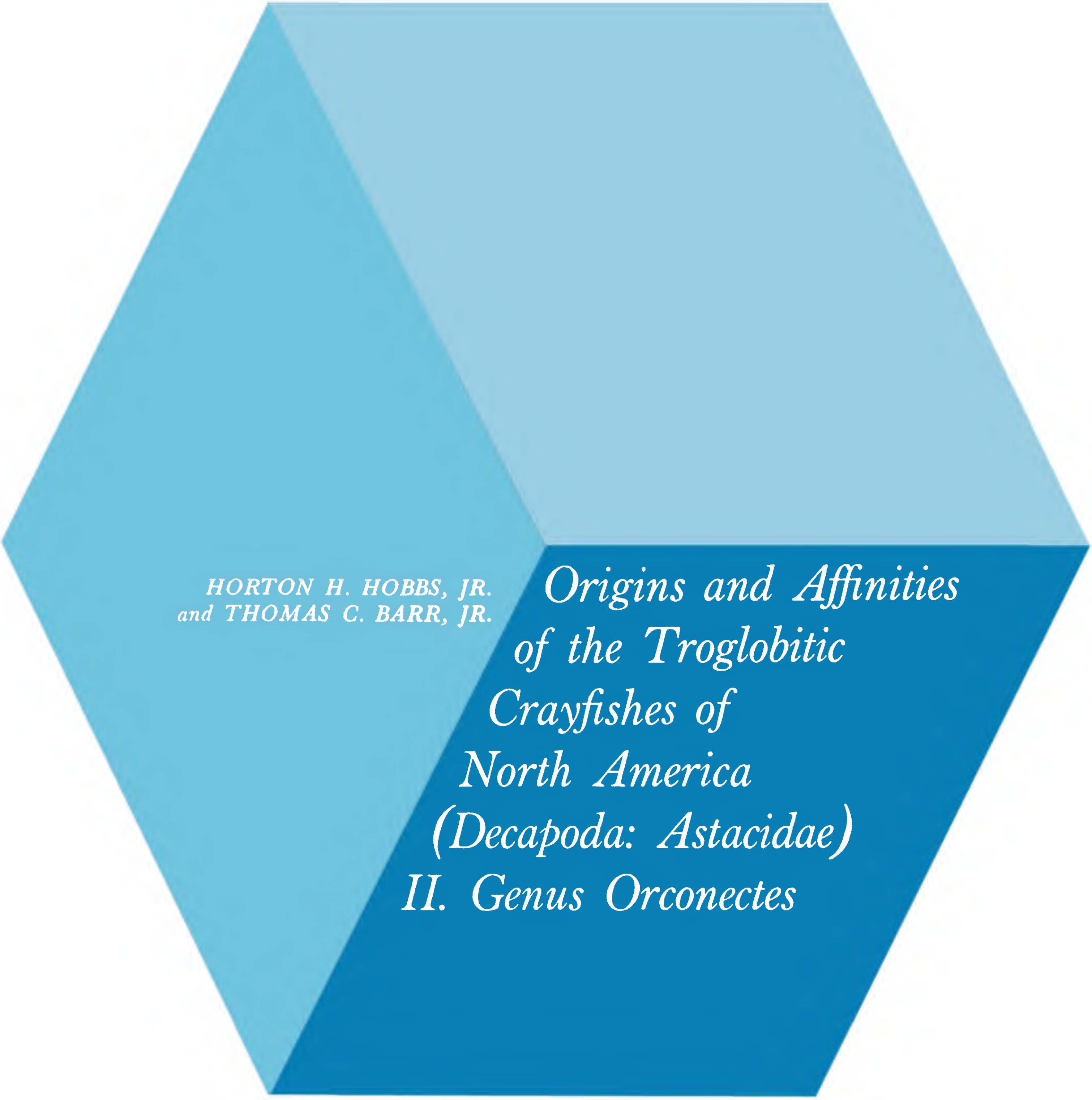


HORTON H. HOBBS, JR.
and THOMAS C. BARR, JR.

Origins and Affinities of the Troglobitic Crayfishes of North America (Decapoda: Astacidae)
II. Genus Orconectes

SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY NUMBER 105

SERIAL PUBLICATIONS OF THE SMITHSONIAN INSTITUTION

The emphasis upon publications as a means of diffusing knowledge was expressed by the first Secretary of the Smithsonian Institution. In his formal plan for the Institution, Joseph Henry articulated a program that included the following statement: "It is proposed to publish a series of reports, giving an account of the new discoveries in science, and of the changes made from year to year in all branches of knowledge." This keynote of basic research has been adhered to over the years in the issuance of thousands of titles in serial publications under the Smithsonian imprint, commencing with *Smithsonian Contributions to Knowledge* in 1848 and continuing with the following active series:

Smithsonian Annals of Flight
Smithsonian Contributions to Anthropology
Smithsonian Contributions to Astrophysics
Smithsonian Contributions to Botany
Smithsonian Contributions to the Earth Sciences
Smithsonian Contributions to Paleobiology
Smithsonian Contributions to Zoology
Smithsonian Studies in History and Technology

In these series, the Institution publishes original articles and monographs dealing with the research and collections of its several museums and offices and of professional colleagues at other institutions of learning. These papers report newly acquired facts, synoptic interpretations of data, or original theory in specialized fields. These publications are distributed by mailing lists to libraries, laboratories, and other interested institutions and specialists throughout the world. Individual copies may be obtained from the Smithsonian Institution Press as long as stocks are available.

S. Dillon Ripley
Secretary
Smithsonian Institution

SMITHSONIAN CONTRIBUTIONS TO
ZOOLOGY

NUMBER 105

Horton H. Hobbs, Jr.
and Thomas C. Barr, Jr.

Origins and Affinities of the Troglobitic Crayfishes of North America (Decapoda: Astacidae) II. Genus *Orconectes*

SMITHSONIAN INSTITUTION PRESS
CITY OF WASHINGTON
1972

ABSTRACT

Hobbs, Horton H., Jr., and Thomas C. Barr, Jr. Origins and Affinities of the Troglobitic Crayfishes of North America (Decapoda: Astacidae). II. Genus *Orconectes. Smithsonian Contributions to Zoology,* number 105, 84 pages, 1972.—The troglobitic members of the genus *Orconectes,* comprising six species and subspecies, are here assigned to the Pellucidus Section of the genus. *Orconectes australis australis* frequents spelean habitats along the eastern edge of the Cumberland Plateau from Alabama to Kentucky, where it intergrades with *Orconectes australis packardi,* which ranges as far north as Rockcastle County, Kentucky. *Orconectes incomptus,* new species, is known from only three localities at the base of the Highland Rim in Jackson County, Tennessee. *Orconectes pellucidus* ranges along the western flank of the Cincinnati Arch from Trigg County, Kentucky, and Montgomery County, Tennessee, northeastward to Hart County, Kentucky. The two subspecies of *O. inermis* occupy cave systems of the north Pennyroyal and Mitchell Plain in Kentucky and Indiana, the nominate subspecies occurring in the southern portion of the range and intergrading with the northern *O. inermis testii* from near the state line to Monroe County, Indiana. The four species are believed to have taken their origins from a wide-ranging, pre-Pleistocene, epigean stock which frequented streams of low gradient. With subsequent uplift of the area, the epigean derivatives of the stock for the most part became extinct, whereas the three or four derivatives that invaded subterranean habitats gave rise to the modern troglobites which occupy much of the original range of their ancestors. Complete bibliographic citations to these crayfishes and summaries of our present knowledge of them preceed a listing of all of the caves from which troglobitic *Orconectes* have been found, together with the identities of the crayfishes and previously reported epizootic ostracods.

Official publication date is handstamped in a limited number of initial copies and is recorded in the Institution's annual report, Smithsonian Year.

UNITED STATES GOVERNMENT PRINTING OFFICE
WASHINGTON : 1972

For sale by the Superintendent of Documents, U.S. Government Printing Office
Washington, D.C. 20402 - Price $1.25 (paper cover)
Stock Number 4700–0177

Contents

Horton H. Hobbs, Jr.
and Thomas C. Barr, Jr.

Origins and Affinities of the Troglobitic Crayfishes of North America (Decapoda: Astacidae)

II. Genus *Orconectes*

Introduction

The first mention of the existence of blind crayfishes seems to be a reference in the minutes of the "Stated Meeting of May 24, 1842" of the Academy of Natural Sciences at Philadelphia (Anonymous 1843), in which W. T. Craige, M.D., was credited with the donation of "A white eyeless crayfish (Astacus Bartoni?) and a small white fish, also eyeless (presumed to belong to a sub-genus of *Silurus*), both taken from a small stream called the 'River Styx' in the Mammoth Cave, Kentucky, about 2½ miles from the entrance." This crayfish occurring in Mammoth Cave was designated *Astacus pellucidus* by Tellkampf the following year.

Not until 1871 did Cope describe the second troglobitic species, *Orconectes inermis,* from Wyandotte Cave, Crawford County, Indiana, basing his new genus on the albinistic character of the species. The next troglobitic relative to be named was one supposedly collected from a cave in Jugoslavia and described in 1880 by Joseph as *Cambarus typhlobius.* In the following year he mentioned the same species under the names *Cambarus coecus* and *Cambarus stygius;* all three names are almost certainly based on a mislabeled specimen of *Orconectes pellucidus* (see Holthuis 1964). The type is no longer extant and repeated efforts to secure additional specimens from the type-locality have been unsuccessful; to cast further doubt on the existence of a member of the

Note and Acknowledgments

Part I of this series (Hobbs and Barr 1960) treated the genus *Cambarus,* and since its publication only one additional troglobite, *Cambarus zophonastes* Hobbs and Bedinger 1964, from Arkansas, has been added to the genus. No summary of the remaining troglobitic crayfishes is planned by us. A key to the seven Floridian species, together with summaries of their ranges, was recently prepared by Hobbs (1971b), and only three additional species are known: *Procambarus niveus* Hobbs and Villalobos 1964, from Pinar del Rio, Cuba; *Procambarus pecki* Hobbs 1967b, from northwestern Alabama; and *Procambarus rodriguezi* Hobbs 1943, from Veracruz, Mexico.

For their assistance in amassing most of the collection on which this study has been based, we express our appreciation to the many persons cited in the appropriate places. Particular thanks are due the following for the large number of specimens and data which they made available to us: Martha R. and John E. Cooper, H. H. Hobbs III, Thomas C. Jegla, Russell M. Norton, and Stewart B. Peck.

We should also like to thank Rendell Rhoades for calling to our attention the earliest reference of Tellkampf to *Orconectes pellucidus,* and we are indebted to Jack F. Marquardt for his patience and assistance in obtaining many of the references cited.

For assistance and suggestions during the preparation of the manuscript and for criticisms of the final draft, we are deeply grateful to Fenner A. Chace, Jr., Mr. and Mrs. John E. Cooper, Margaret A. Daniel, Joseph F. Fitzpatrick, Jr., Georgia B. Hobbs, and Mary H. Moulton.

Horton H Hobbs, Jr., Department of Invertebrate Zoology, Smithsonian Institution, Washington, D.C. 20560. Thomas C. Barr, Jr., Department of Zoology, University of Kentucky, Lexington, Kentucky 40506.

subfamily Cambarinae in Europe is the fact that the only other representative living on the continent is *Orconectes limosus* which was introduced from the United States.

Hay described *Cambarus pellucidus testii* from Mayfield's Cave in Monroe County, Indiana, in 1891, and not until 50 years later did Rhoades apply the name *Cambarus pellucidus australis* to a crayfish from caves in northern Alabama. In 1944, he named the subspecies *O. pellucidus packardi* from caves in the Cumberland watershed in Kentucky. An additional species, *Orconectes incomptus,* is described herein.

Generic stability for the American troglobitic crayfishes has existed since Hobbs (1942a), and since that time, all the forms mentioned above have been assigned to the genus *Orconectes* by all American crayfish systematists.

Thus, in the 100 years from 1844 to 1944, all except one of the presently recognized troglobitic crayfishes of the genus *Orconectes* had received names, and agreement had been reached on their generic designation. There were still some doubts on the part of some of us as to the affinities of these troglobites with each other and with epigean forms, so that an amassing of collections throughout the range of the complex had continued.

As a result of considerable field work by one of us, Barr (together with that of others interested in cave faunas), to determine the ranges and the limits of variation of the several populations, conclusions not in agreement with those of previous students of the complex have been reached concerning the relationships of these crayfishes. We are proposing the recognition of a Pellucidus Section of the genus, comprised of four species, two of them with geographic races (subspecies).

PELLUCIDUS SECTION

Diagnosis: Albinistic; areola 3.7 to 6.7 times longer than broad and constituting 34.0 to 46.0 percent of total length of carapace; terminal elements of first pleopod of first form male never constituting more than ⅛ total length of appendage; males with hooks on ischia of third or third and fourth pereiopods; females with small uniramous pleopods on first abdominal segment; annulus ventralis of female slightly movable, separated from sternum immediately cephalic to it by distinct sulcus.

The morphological bases for the above treatment, the ranges of each of the taxa, and postulates concerning their origins and relationships constitute the principal segment of this study.

The species and subspecies of the Pellucidus Section of the genus *Orconectes* are:

O. australis australis (Rhoades)
O. australis packardi Rhoades
O. incomptus, new species
O. inermis inermis Cope
O. inermis testii (Hay)
O. pellucidus (Tellkampf)

A discussion of the distribution and phylogeny of the newly erected Pellucidus Section is followed by a key to its six members. In the treatments of the individual species and subspecies, the synonymies are believed to be complete, and, excluding references to many newspaper articles, popular accounts, and brochures, the bibliographic citations have been searched and evaluated with reasonable thoroughness. Following these citations are chronologically arranged abstracts of the contributions made by each of the authors with emphasis being placed on systematics, distribution, ecology, and habits; comments, where appropriate, follow the summaries of previous contributions. Diagnosis of the taxon is amplified with full descriptions of type-specimens (or topotypes) and illustrations. The specimens examined are cited together with locality, collector, and date. We have not been consistent in presenting locality data, chiefly because we have attempted to follow the system of references utilized in the cave directories of the respective states (Barr 1961, Powell 1961, and Tarkington et al. 1965). For Alabama and Indiana, Public Land Survey coordinates are utilized; for Tennessee, latitude and longitude are employed; and for Kentucky for which no cave atlas exists, we have given simple directions for locating the caves. Lists are provided giving names of the collectors (page 83) and, by state and county, all the caves (page 81) in which the species treated here have been reported, with references to the crayfishes and the symbiotic ostracods which occur on them.

The troglobitic species which comprise the Pellucidus Section of *Orconectes* are most commonly found in larger, permanent underground streams. The largest populations occur in deep subterranean lakes, the bottoms of which are covered with fine silt, and through which water moves very slowly. When cave passages flood—a common phenomenon in late winter and early spring—the crayfishes quickly move into the flooded areas, where they are sometimes stranded in small pools as the flood waters recede. Although crayfishes are rarely observed moving overland, their occasional presence in isolated, upper level pools substantially above flood marks clearly indicates that they can and do migrate from pool to pool.

Sudden and sharp disturbances of the water results in rapid, backward darting of the cave *Orconectes,* but with a less pronounced disturbance they slowly crawl toward the deeper portions of the pools, sometimes disappearing beneath a ledge or pile of stones. If a crayfish is stranded in a small pool or on land, continued disturbance provokes a defensive stance, the animal rearing up on the ambulatory pereiopods and extending the open chelae. Some published statements to the contrary, troglobitic *Orconectes* definitely exhibit a negative phototaxis. Very dim, diffuse illumination, of an intensity comparable to the candlelight of the early cave explorers usually has little effect, which probably explains the older statements that these animals are insensitive to light. If a strong flashlight beam is focused on a crayfish, however, it invariably moves away, after an initial delay of about five to 10 seconds. The selective advantage of negative phototaxis is obvious.

An insect struggling on the surface of a quiet pool, or gentle disturbance of the surface with a stick or the fingers, soon attracts a nearby crayfish, which orients beneath the disturbance and slashes upward rapidly with the chelipeds. If a cave cricket or other insect is siezed in this manner it is immediately dragged beneath the surface and eaten. Crayfishes are also easily attracted by meat or fish baits, and can be caught readily in minnow traps.

Most of the available information on reproduction in troglobitic *Orconectes* is applicable only to *O. inermis* (Jegla 1966, Jegla and Poulson 1970). Although there is evidence that reproduction can occur at any time during the year, there are apparently definite seasonal peaks in the abundance of form I males, ovigerous females, and the hatching of juveniles.

Systematic Position

Although epigean crayfishes occur on all of the continental masses except Africa, only in North America are troglobitic species represented in the cave fauna. Furthermore, in only one subfamily, the Cambarinae, of the Holarctic Astacidae have some members become thoroughly adapted to a subterranean environment.

The taxonomic outline presented below indicates the relationships of the troglobitic *Orconectes* to other crayfishes occurring in the Northern Hemisphere. Those taxa with troglobitic representatives are indicated by an asterisk. Because no up-to-date list of these crayfishes is available, the described troglobitic species, together with original bibliographic citations, are listed under the appropriate genera.

Parastacidae.—Southern Hemisphere

*Astacidae.—Northern Hemisphere
  Astacinae.—Europe, western Asia, and western North America
  Cambaroidinae.—Eastern Asia and Japan
  Cambarellinae.—Gulf Coast and Mississippi Valley in the United States southward to the Cordillera Volcánica Transversal in Mexico
  *Cambarinae.—North America east of the Rocky Mountains, southward to Guatemala, Honduras, and Cuba
    **Cambarus.*—United States east of the Rocky Mountains and eastern Canada
      C. (Aviticambarus) hamulatus (Cope 1881: 879).—Alabama and Tennessee
      C. (Aviticambarus) jonesi Hobbs and Barr, 1960: 19.—Alabama
      C. (Erebicambarus) hubrichti Hobbs, 1952: 689.—Missouri
      C. (Jugicambarus) cryptodytes Hobbs, 1941: 110.—Florida and Georgia
      C. (Jugicambarus) setosus Faxon, 1889: 237.—Missouri
      C. (Jugicambarus) zophonastes Hobbs and Bedinger, 1964: 11.—Arkansas
      [*C. (Erebicambarus) cahni* Rhoades, 1941: 146, is not a troglobite.—Alabama]
    Fallicambarus.—Ontario, Michigan, and Illinois southward to Florida and Texas
    Faxonella.—Oklahoma and Texas eastward to South Carolina
    Hobbseus.—Alabama and Mississippi
    **Orconectes.*—East of the Rocky Mountains from southern Canada to Georgia and Texas
      O. australis australis (Rhoades, 1941: 142).—Alabama and Tennessee

  O. australis packardi (Rhoades, 1944a: 121).—Kentucky
  O. incomptus, new species.—Tennessee
  O. inermis inermis Cope, 1872a:419.—Indiana and Kentucky
  O. inermis testii (Hay, 1891:148).—Indiana
  O. pellucidus (Tellkampf, 1844b:383).—Kentucky and Tennessee
Paracambarus.—State of Puebla, Mexico
**Procambarus.*—Southern New England and Great Lakes southward to Honduras, Guatemala, and Cuba
  P. acherontis (Lönnberg, 1895:6).—Florida
  P. lucifugus lucifugus (Hobbs, 1940:398).—Florida
  P. lucifugus alachua (Hobbs, 1940:402).—Florida
  P. milleri Hobbs, 1971b:115.—Florida
  P. niveus Hobbs and Villalobos, 1964:342.—Cuba
  P. pallidus (Hobbs, 1940:394).—Florida
  P. pecki Hobbs, 1967b:2.—Alabama
  P. rodriguezi Hobbs, 1943:203.—Veracruz, Mexico
**Troglocambarus.*—Peninsular Florida
  T. maclanei Hobbs, 1942a:345.—Florida

Key to Genera of Troglobitic Crayfishes

1. Ischium of third maxilliped without teeth on opposable border. ***Troglocambarus*** Hobbs (1942b:345)
   Ischium of third maxilliped with teeth on opposable border 2
2. First pleopods of male terminating in two elements bent at no less than 90 degrees to principal axis of appendage .... ***Cambarus*** Erichson (1846:88)
   First pleopod of male terminating in two or more elements; if only two, then both never bent at angle as great as 90 degrees to principal axis of appendage 3
3. First pleopod terminating in two conspicuous elements, sometimes with minute rudiment of third (caudal process); cephalic surface of appendage either lacking shoulder or with shoulder adjacent to base of central projection .... ***Orconectes*** Cope (1872a:409)
   First pleopod terminating in two or more elements; if only two, then cephalic surface with strong, angular shoulder never contiguous with base of central projection. ***Procambarus*** Ortmann (1905b:437)

Distribution and Phylogeny

RANGE OF THE PELLUCIDUS SECTION.—As can be seen in Figures 1 and 2, the ranges of the troglobitic crayfishes of the genus *Orconectes* are allopatric and encompass, in three somewhat distinct geographic areas, much of the karst terrane from northern Alabama to southern Indiana. In caves in Mississippian limestone along the western margin of the Cumberland Plateau, *Orconectes australis* has been reported from 61 localities from Jackson and Madison counties in Alabama to Rockcastle County in Kentucky. Two geographic races of *australis* have been recognized, *O. a. australis* in the southern part of the range and *O. a. packardi* in the northern portion. A third member of the group, *O. incomptus,* is known from three caves in Ordovician limestones at the base of the Highland Rim in Jackson County, Tennessee.

Along the western flank of the Cincinnati Arch, in caves in Mississippian limestones of the Pennyroyal Plateau, *Orconectes pellucidus* has been found in 26 localities. Its range is a narrow one, apparently confined to the gently tilted outcrops extending from Trigg County, Kentucky, and Montgomery County, Tennessee, northeastward to Hart County, Kentucky. Within Hart County, apparently a barrier exists along an east-west sandstone ridge somewhat paralleling the Green River, which almost completely separates the range of *O. pellucidus* from that of *O. inermis inermis.* This ridge apparently resulted from deposition of sandstones in a pre-Pennsylvanian river channel (Burroughs 1923), and separates the Mammoth Cave fauna from that of the northern Pennyroyal (Barr 1967a).

Two subspecies of *Orconectes inermis,* together with intergrade populations, frequent the cave systems of the north Pennyroyal and Mitchell Plain between Hart County in Kentucky and Monroe County in Indiana, where they have been found in 44 localities. The nominate spiny race occupies the southern part of the range, with typical members occurring as far north as Crawford and Orange counties, Indiana. The spineless *O. inermis testii* is the troglobitic form found in the northernmost part of the range in Monroe County, Indiana; intergrading populations occur between Meade County in Kentucky and the southern counties in Indiana.

RELATIONSHIPS OF THE TROGLOBITIC ORCONECTES.—Hobbs (1969:119–126) has discussed the relationships of these troglobites to the members of other genera of the subfamily in which he cited several reasons for believing that the troglobitic *Orconectes,* which are here assigned to the Pellucidus Section, have retained some of the most primitive characteristics to be found among modern representatives of the genus. Whether some of these characteristics are fixed atavistic ones that reappeared when more recent ancestral forms "returned" to an environment resembling that of their ancestors or whether they represent primitive retentions cannot be properly assessed in the absence of a fossil record, but the fact that these appear in what are considered to be primitive members of several genera of epigean crayfishes suggests a primitive retention rather than products of convergent evolution.

One of the most regrettable facts related to the present study is that the primitive facies of the first pleopod and annulus ventralis of the Pellucidus Section have not been preserved in any of the epigean species of the genus; they are present with slight modification, however, in the not-too-distantly related *Cambarus (Veticambarus) pristinus* Hobbs, 1965, and to a lesser degree in *C. (V.) bouchardi* Hobbs, 1970, in which even the annulus ventralis bears a marked resemblance to those of the members of the Pellucidus Section. It can only be assumed that the pattern in the epigean stock of the genus *Orconectes* was destroyed during the Pleistocene and remains as a relict in the present members of the Pellucidus Section, the ancestors of which, having found refuge in subterranean waters, escaped the fate of their surface relatives.

THE ANCESTRAL STOCK.—Three of the more generalized members of the Pellucidus Section (*O. a. australis, O. i. inermis,* and *O. pellucidus*) seem to us to be remnants of an ancient, probably no younger than late Miocene, epigean stock which have undergone few modifications other than those channelized by the successful occupation of a spelean environment. To paraphrase Hobbs (1969:120), had these crayfishes retained a pigmented body, well developed eyes, a shorter areola, and a more robust body and appendages, they would exhibit essentially all of the characteristics attributed by him to the hypothetical "Adorconectid Stock," the supposed ancestral form of the genera *Orconectes, Hobbseus, Faxonella, Cambarus, Fallicambarus,* and of the graciloid and mexicanoid lines of *Procambarus.* Not only do these troglobites share more features in common with extra-generic members of the subfamily Cambarinae than do other members of the genus but also they are most similar to those species of *Orconectes* that are considered to be generalized.

ORIGIN OF THE PELLUCIDUS SECTION.—Postulates concerning the origin of the genus *Orconectes*—hence the Pellucidus Section—have been recently recounted and evaluated by Hobbs (1967b, 1969). It is indeed unfortunate that freshwater crayfishes have left so few fossils. To our knowledge, not a single Tertiary fossil of a member of the family Cambarinae has been discovered, and the few Quaternary fossils available are almost certainly members of extant species. Consequently, a reconstruction of the evolutionary history of any cambarine group must be based upon data derived from morphology, zoogeography, and upon what is known of the geological history of the area involved. Helpful, also, are data which permit inferences concerning availability of suitable ecological conditions in areas supposedly occupied by ancestral stocks.

In a reconstruction of evolution one of the most tantalizing factors is that of time. In this discussion, consideration is given to the time during which the ancestral stock invaded the subterranean waters, and further, to whether there was a single invasion or several of them. Obviously, in the absence of a fossil record, no absolute timetable can be established for the evolution of these crayfishes, but evidence exists that the general facies of the ancestral Adorconectoid Stock (Hobbs 1969:119, 1971a:11) had been established prior to the formation of the transverse volcanic ridge in Mexico. Only south of this ridge does the rather primitive Pilosimanus Group (Villalobos 1954:306) of the Mexicanus Section of the genus *Procambarus* occur, and there can be little doubt that the ancestors of this group were isolated from their northern relatives with the volcanic upheaval north of the Isthmus of Tehuantepec in early Pliocene times. If time can be allowed for the ancestral *pilosi-*

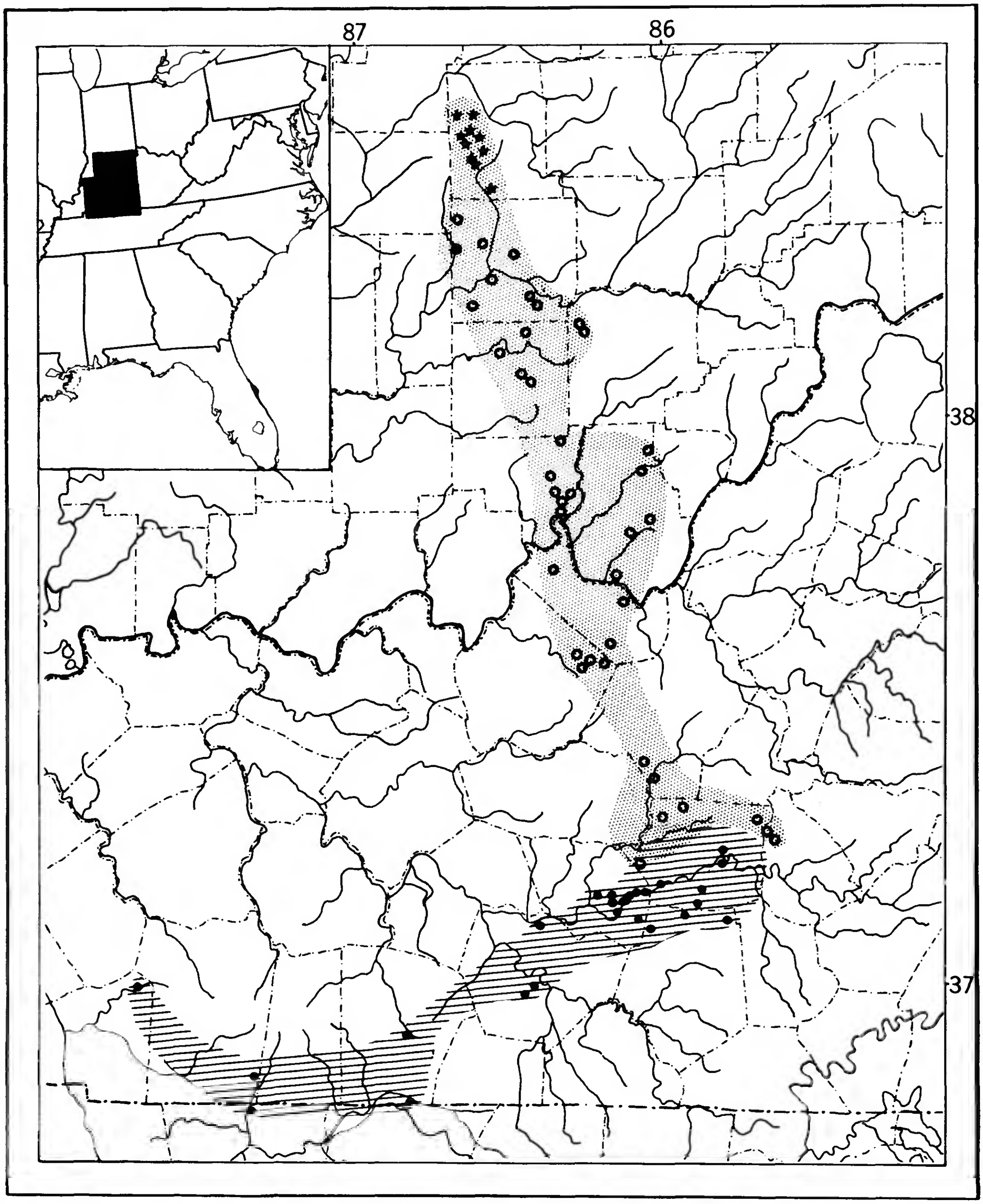


FIGURE 1.—Ranges of *Orconectes inermis inermis* and intergrades (open circles), *Orconectes inermis testii* (stars), and *Orconectes pellucidus* (closed circles).

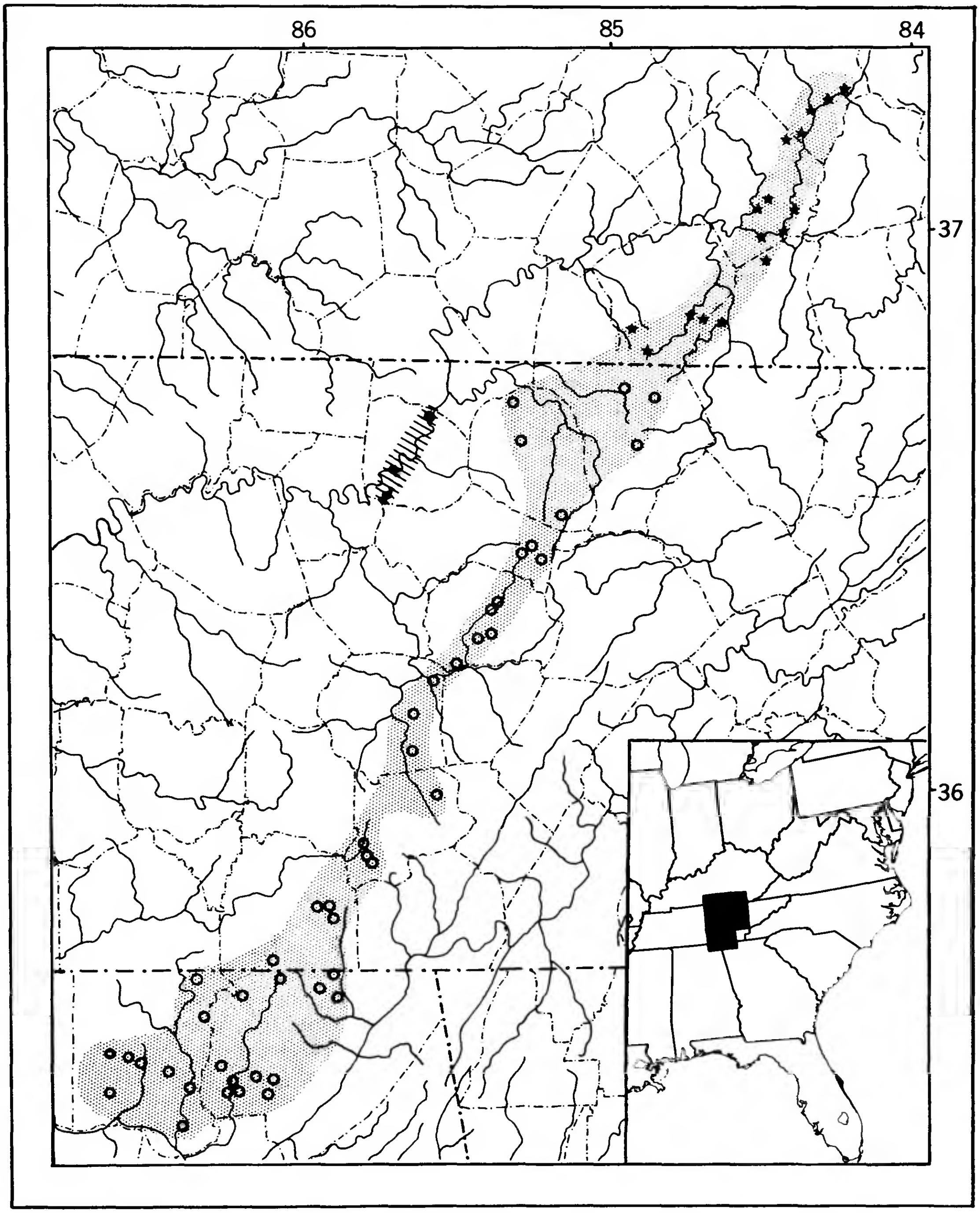


FIGURE 2.—Ranges of *Orconectes australis australis* and intergrades (open circles), *Orconectes australis packardi* (stars), and *Orconectes incomptus* (closed circles).

manus stock to have reached Veracruz in a southward migration from the central part of the United States, it is conceivable that the level of evolution represented by the *pilosimanus-pellucidus* ancestors (Adorconectoid Stock) had been accomplished not later than the middle Tertiary. If this dating is accepted, then in all probability the ancestral *pellucidus* or Archiorconectoid Stock (Hobbs 1969:119) was lurking in the area to the north and east of the Mississippi embayment at that time.

The Cincinnati Arch had its origin in the middle Ordovician and was uplifted several times during the Paleozoic and Mesozoic eras. As a result, considerable erosion must have been accomplished, so that by the middle of the Tertiary the development of a karst topography in the central Ordovician and flanking Mississippian sediments had progressed to a stage that invited the invasions of subterranean streams by a number of epigean stocks. Thus it seems entirely possible that as early as the Miocene the subterranean waters were available to the surface-dwelling Orconectoid Stock (Hobbs 1969:119). For the existence of a possible pre-Quaternary stock from which the cave fauna might have taken its origin, evidence may be had from an extrapolation of what must have occurred in the dispersal of the ancestors of *Orconectes limosus,* one of the closest extant relatives of the troglobitic forms and one which is restricted to the Atlantic slope east of the Appalachian Mountains. This spiny crayfish is apparently most at home in streams with a gentle gradient and has never been found in cascading streams or in those with a rapidly shifting bottom; furthermore, all its closer relatives occur in similar habitats west of the Allegheny Mountains and none to the south of the Mountains. These facts strongly suggest that the ancestors of *O. limosus* reached the Atlantic seaboard through migrations to the east across and/or north of the region presently occupied by the Alleghenies. Although Rhoades (1962) proposed that it was the Illinoian glacier that was responsible for impounding the Ohio River and for reversing the flow of the segment east of Cincinnati to the Chesapeake Bay, carrying with it the *limosus* ancestors, an earlier arrival of this stock seems far more likely to us. This conclusion is based on the fact that (1) the isolated range of *limosus,* which abuts the Atlantic Ocean, is otherwise surrounded by that of more progressive members of the genus, and (2) *limosus* shares only the upland streams (marginal in respect to its range) with these more divergent forms (members of the Propinquus Group; for ranges see Crocker and Barr 1968, Fitzpatrick 1967, Meredith and Schwartz 1960, and Ortmann 1906). As to how early in the Tertiary the migration eastward occurred cannot be determined on the basis of available data, but it must have been at a time that a low-lying stream flowed from the West Virginia-Ohio region into the Atlantic, or involved stream piracy in low gradient headwaters. Either might well have existed in pre-Pleistocene times, for there existed eastward flowing rivers (for example, the old Erigan River), and the Alleghenies were peneplained several times during the Tertiary. Perhaps there was a deflection of a segment of the upper Teays River during one of the periods of peneplanation. If it could be tentatively assumed that the *limosus* ancestors reached the east coastal waters in the Tertiary, then the relationship of its range to those of the eastern members of the Propinquus Section could be explained by the latter having reached their present ranges after *limosus* had arrived, perhaps during the Illinoian and Wisconsin glacial periods as proposed by Fitzpatrick (1967:166).

In attempting to determine the place of origin of the Pellucidus Section, consideration has been given to the intra-group relationships in order to ascertain which assemblage within the Section is probably the most generalized. On the basis of the pleopod of the male, it is obvious that two types are represented: (1) that found in *O. pellucidus,* which in lateral view exhibits a slender distal portion, with the distally directed mesial process distinctly longer than the central element, a feature that seems to be unique in the genus; and (2) the type found in *O. australis, O. incomptus,* and *O. inermis,* in which the distal portion of the appendage is comparatively broader and the two terminal elements are of approximately the same length, usually with the mesial process directed caudodistad. In the conformation of the pleopod, the *australis-inermis* type is more like those of the epigean forms than is the *pellucidus* type. Also, it is in *O. a. australis* and *O. incomptus* that the primitive caudal element of the pleopod is present; furthermore, the only indication of a cephalic process in the entire genus is the reduced one observed on both appendages of a single male of *O. a. packardi* from Hydens Cave, Pulaski County, Kentucky. Many populations of *australis* are quite spiny, as strongly so as typical forms of *pellucidus* and *inermis,* and like them, either occasionally (in *a. australis*) or typically (in *a. packardi*), possess hooks on the ischia of the third and fourth pereiopods. Except for the absence of the caudal process on the first pleopod of *inermis* and no indication of a cephalic one, *O. i. inermis* is apparently equally as primitive as *O. australis*. Therefore, we have concluded that the subspecies of *O. australis,* inhabiting subterranean streams of the Cumberland Plateau, approaches more nearly the hypothetical adorconectoid stock than do any of the others, and that *incomptus* and *inermis* are more closely allied to *australis* than is *pellucidus*.

Hobbs (1967b, 1969) postulated that the ancestral genus *Procambarus* had its center of distribution in the southeastern part of the United States and that the adorconectid segment became differentiated in pre-Pliocene times. It spread through "an area extending from Alabama northward to Kentucky, on and near the Cumberland plateau." This stock was believed to have been a pioneering one, inhabiting small to large streams flowing over a gentle to moderate gradient, and, although able to negotiate riffle areas, was not able to become established in them. Whereas the most primitive *Orconectes* and some of the more generalized members of the genera *Cambarus* and *Procambarus* are still largely restricted to such habitats, other stocks invaded the sluggish areas of streams, lakes, ponds, swamps, and subterranean waters, and some eventually sought groundwater by burrowing. Puzzling is the fact that even though the early Orconectoid stock gave rise to several lines that resulted in comparatively broad adaptive radiations (Hobbs, 1969), the *Orconectes* line has, in general although not without exception, remained more conservative in maintaining its adaptations to a lotic environment. Perhaps this apparent conservatism, particularly from Tennessee and Missouri northward, was not actually real, for radiation which might have occurred in the north could well have been terminated during the Pleistocene; however, the fact remains that *Cambarus diogenes* and *Fallicambarus fodiens* are burrowing species throughout an area which might well have been taken over by burrowing species of the genus *Orconectes*. Regardless of what might have occurred prior to the Pleistocene, no primary or secondary burrowing (sensu Hobbs 1942b:20) *Orconectes* is known to exist today, and there are fewer than a dozen of the approximately 70 described species and subspecies which typically frequent lentic habitats. Thus we visualize the early *Orconectes* stock as resembling in most of its facies a combination of the characteristics exhibited by *O. limosus* and the troglobitic *O. a. australis,* and differing only slightly, if at all, from the former in its ecological requirements. By the Mid-Cenozoic, the most primitive segment probably inhabited streams in the gently rolling terrane of a broad belt extending from Alabama northward to the east of the old Mississippi embayment to, and perhaps beyond, the present Ohio River. More progressive segments had, by this time, migrated around the northern end of the embayment occupying other virginal, in respect to crayfish habitation, streams to the west.

Because of the marked similarities between *O. inermis* and *O. australis* as compared with the striking differences which exist between closely related epigean allies having no more distant ranges, it is perhaps difficult to conceive of the current troglobitic fauna representing products of parallel development in three segments of a primitive, wide-ranging surface species. Equally incredible, however, would be an assumption of the existence of east-west subterranean aquatic corridors across the Cincinnati arch in Kentucky; even the supposition of a temporal continuity is beset with difficulties in the region of the now barren (in respect to troglobitic crayfishes) axis of the Cincinnati Arch.

Should one be reasonably confident (which we are not) of the previous existence of an aquatic corridor through the dome of the Arch connecting the spelean waters of the eastern edge of the Cumberland Plateau with those of the Pennyroyal Plateau, this would allow the hypothesis that the Adorconectoid ancestor invaded the subterranean water system of the Cumberland Plateau in Tennessee during the Middle or Late Tertiary. From this center it could have migrated along underground channels to the northwest and south, gradually spreading throughout an area that cumulatively is even larger than that frequented by the extant descendants. The stock would have had to cross the dome of the Cincinnati Arch, cross the Pennyroyal Plateau, and ultimately colonize the Mitchell Plain. Subsequent degradation of the dome of the Arch, destroying the continuous subterranean passageways in it, would account for the isolation of the ancestors of *australis-incomptus* from those of *inermis-pellucidus;* likewise, the previously mentioned sandstone ridge along the Green River could well have disrupted communicating channels along it, thus segregating the ancestors of *inermis* from those of *pellucidus*. Further erosion of the underground passages of the Cumberland Plateau probably would account for the segregation of *incomptus* as a relic along the base of the Eastern Highland Rim from ancestral *australis* at the edge of the Plateau.

An alternative hypothesis (which we consider more probable) involves multiple colonizations of the subterranean waters by populations of a single widely ranging ancestral epigean species: one on the Cumberland Plateau, ancestral to *O. australis* and *O. incomptus*; a second on the Pennyroyal Plateau, precursor of *O. pellucidus*; and a third on the Mitchell Plain, the antecedent of *O. inermis*. The close morphological resemblance between *inermis* and *australis* could be accounted for by postulating a dual invasion of the Teays and upper Cumberland drainages by a common epigean ancestor. The barriers mentioned above would have been equally effective should this hypothesis prove to be more consistent with data obtained in the future.

As has been pointed out above, and indirectly by Barr (1968:85), there are no epigean remnants of the Section present in the area occupied by these troglobites. An explanation for their absence, according to Barr, lies in the fact that with the regional uplift at the end of the Pliocene or beginning of the Pleistocene, the low-gradient streams in which the ancestral stock lived were transformed to rapidly-flowing ones with steeper gradients, thus destroying the habitat of this stock and thereby bringing about its extinction at the surface. It seems at least possible, if not probable, that one or more of the colonizations of the subterranean waters coincided with the extinction of the ancestral stock.

Subspeciation in both *O. australis* and *O. inermis* has probably been a product of Pleistocene and post-Pleistocene evolution with greater diversity in body proportions and spination in *inermis* and in spination and pleopodial diversity in *australis*. Morphologically, *incomptus* bears the same relationship to *O. a. australis* as does *O. i. testii* to the nominate subspecies; however, the ranges of *australis* and *incomptus,* while being nearly contiguous, seem to be completely isolated.

To recapitulate the major features of the hypotheses proposed to account for some of the factors involved in the origin and evolution of the troglobitic crayfishes of the genus *Orconectes,* it has been postulated that the ancestral stock of the Pellucidus Section was derived from a primitive *Procambarus* stock in the early or middle Tertiary; that it occupied streams of low gradient in the area of the dome of the Cincinnati Arch; that in the late Tertiary, three segments invaded subterranean channels of the Cumberland Plateau, Pennyroyal Plateau, and Mitchell Plain where they were isolated from one another, respectively, by the belt of Middle Ordovician shales along the crest of the Cincinnati Arch and by a sandstone ridge which parallels the Green River in Hart County, Kentucky; and finally, that subspeciation in *O. australis* and *O. inermis* and the isolation of *incomptus* from *australis* occurred in Pleistocene or Recent times. To account for the apparent closer affinities between *australis* and *inermis* than of either to *pellucidus,* the range of which is somewhat interposed between their respective ones, it is suggested that the ancestral *pellucidus* stock, located in the western part of the area, became differentiated from the common stem first. Later, stream piracy between the Cumberland and Teays systems resulted in there being dispersed in the two basins a more recent common stock from which on the Cumberland Plateau arose *australis,* and from which on the Mitchell Plain was derived *inermis*. The ancestral surface stock, unlike that of the Floridian troglobitic members of the Pictus Group of the genus *Procambarus* (see Hobbs 1958), did not survive to the present but was destroyed with the destruction of their habitat—the result of a regional uplift at the close of the Pliocene.

FAUNISTIC ASSOCIATIONS.—Barr (1967a:184) presented a sketch of the regional cave faunas of the Interior Low plateaus. Within these faunal groups associations of the troglobitic *Orconectes* are as follows:

O. i. testii.—Northern Bedford fauna (I-A)
O. i. inermis.—Southern Bedford, Corydon, and Breckenridge faunas (I-A,B,C)
O. pellucidus.—Mammoth Cave and Hopkinsville faunas (I-D,E)
O. a. packardi.—Rockcastle fauna (V-C)
O. a. australis.—Caney Fork and Huntsville faunas (V-D,E)
O. incomptus.—Not characteristic of any regional fauna, but in the northeast corner of the Central Basin faunal region

Troglobitic crayfishes appear to be absent from regions II (Bluegrass), III (Cumberland Saddle), IV (Central Basin) except for *O. incomptus,* and V-F (Guntersville).

Key to Troglobitic Species of the Genus *Orconectes*

(Based on First Form Male)

1. First pleopod without shoulder at cephalic base of central projection (Figures 10*a*, 11*a*), or distal portion of appendage much slenderer than that proximal to it (Figure 14*a*) 2
First pleopod with shoulder at cephalic base of central projection (Figures 3*a*, 4*a*, 9*a*) 4
2. Cephalo-caudal thickness of first pleopod immediately proximal to base of central projection less than half maximum cephalo-caudal thickness (Figure 14*a*). ***Orconectes pellucidus*** (Tellkampf)
Cephalo-caudal thickness of first pleopod immediately proximal to base of central projection more than half maximum cephalo-caudal thickness (Figures 10*a*, 11*a*) 3
3. Rostrum usually without marginal spines or tubercles, and areola constituting at least 43 percent of entire length of carapace (Figure 11*c*) .... ***Orconectes inermis testii*** (Hay)
Rostrum with marginal spines and areola constituting less than 43 percent of entire length of carapace (Figure 10*c*) .... ***Orconectes inermis inermis*** Cope
4. Rostrum without marginal spines or tubercles (Figure 9*c*); mesial process of first pleopod comparatively heavy (Figure 9*a*, *e*) .... ***Orconectes incomptus***, new species
Rostrum with marginal spines or tubercles (Figures 3*c*, 4*c*); mesial process of first pleopod slender or not so heavy as in *O. incomptus* (Figures 3*a*, 4*a*) 5
5. Hooks usually present on ischiopodites of fourth pereiopods; shoulder at cephalic base of central projection of first pleopod angular; caudal process of first pleopod absent but caudal element prominently inflated (Figure 4*e*). ***Orconectes australis packardi*** Rhoades
Hooks usually absent on ischiopodites of fourth pereiopods; shoulder at cephalic base of central projection of first pleopod rounded; caudal process usually present as fine spiniform tubercle, remainder of caudal element not inflated (Figure 3*e*). ***Orconectes australis australis*** (Rhoades)

Orconectes australis australis (Rhoades)

FIGURES 2, 3, 5*o–v*, 6, 7, 8*i–cc*

Cambarus (Faxonius) pellucidus australis Rhoades, 1941: 141–148, fig. 35 [Type-locality: Shelta Cave*, Madison County, Alabama].
Cambarus pellucidus australis.—Hobbs, 1942a:353.—Jeannel and Henrot, 1949:84.—Rhoades, 1959:399.
Orconectes pellucidus australis.—Hobbs, 1942a:353.—Rhoades, 1944:117, 121.—Hobbs, 1948a:16, 19, 20, figs. 6, 13,; 1948b:85.—Eberly, 1958:3.—Nicholas, 1960:133.—Eberly, 1960:30.—Fingerman and Mobberly, 1960:44, 45.—Barr, 1961:32, 33, fig. 10.—Hart and Hobbs, 1961: 175, 176, 178.— Rhoades, 1962:65, 69, 79, 92.—Jegla et al., 1965:639.—Larimer et al., 1966:409–413.—Hart and Hart, 1966:8.—Hobbs, 1967b:8, 9, 12, 15.—Cooper, 1967:14.—Jones and Varnedoe, 1968:2, fig. 1.—Cooper, M., 1969:203, 204.—Cooper and Cooper, 1969a:28; 1969b:22–23.—Nicholas, 1969:14.—Hobbs, 1969:120, 121.
Orconectes (Orconectes) pellucidus australis.—Hobbs, 1942b:154 [by implication].
Cambarus.—Jeannel and Henrot, 1949:24.
Orconectes pellucidus.—Pennak, 1953:458 [in part].—Hobbs, 1967b:12 [in part].—Poulson, 1964:757.—Cooper, 1966:97.
Orconectes (Orconectes) pellucidus.—Hobbs, 1959:890 [in part].
Orconectes pellucidus pellucidus.—Hart and Hobbs, 1961: 176, 178, 180, 184.—Hart and Hart, 1966:9.
Orconectes australis australis.—Barr, 1967a:161 [by implication].
Colorless crayfish.—Tarkington et al., 1965, map 6.
Orconectes.—Barr, 1968:85 [in part].
Blind crayfish.—Jones and Varnedoe, 1968:11, 18, 31.—Nicholas, 1970:22, illus.
White crayfish.—Jones and Varnedoe, 1968:45, 79.—Graham, 1969:4.
Cave crayfish.—Cooper, 1968:34.
Orconectes Pellucidus.—Cooper and Poulson, 1968:30, fig. 8.
Crayfish.—Torode, 1968:152; 1969:16.

REVIEW OF LITERATURE.—*Cambarus pellucidus australis* was described by Rhoades (1941:141) from Shelta Cave, SE ¼ NE ¼ sec. 27, T.3S, R.1W, north of Huntsville, Madison County, Alabama. He also recorded its presence in five additional caves in Madison and Jackson counties, Alabama. While his description of the subspecies is brief, he emphasized its important features, pointed out the principal variations, and contrasted it with the typical subspecies. Included were brief notes on the caves from which the crayfish was reported.

Hobbs (1942a) added no new data but in his

---

*This cave has been purchased by the National Speleological Society and has been designated a Nature Preserve (NSS News, 26(2):28, 1968).

generic revision of the Cambarinae referred Rhoades' subspecies to the genus *Orconectes.* Hobbs (1942b), by recognizing the subgenus *Faxonella,* implied that this subspecies was a member of the typical subgenus.

Rhoades (1944) assigned the subspecies of *O. pellucidus* to his new "Group rafinesquei" and contrasted his new subspecies, *O. p. packardi,* with the previously described ones stating that it "differs from *O. pellucidus australis* (Rhoades) (1941) in having a much shorter areola and thicker, longer tips on the gonopods. Also *O. p. australis* has hooks only on the third walking legs."

Hobbs (1948a) figured the first pleopods of each of the described subspecies of *O. pellucidus* except *O. p. testii,* questioned the propriety of referring them to Rhoades' Group rafinesquei, and indicated that "if any division of the Limosus section is made then it would seem that *O. inermis* and the various subspecies of *O. pellucidus* would constitute a natural group that should receive a status equivalent to that of the other subdivisions." He also included a key for the separation of the species and subspecies belonging to the Limosus Section of the genus.

Hobbs (1948b), in remarking on the range of his new *Orconectes wrighti,* indicated that "Among the members of the Limosus Section only the cavernicolous *Orconectes pellucidus australis* . . . has been collected farther south—in several caves in northern Alabama—and no species belonging to this section has been taken farther southwest."

Jeannel and Henrot (1949) reported this crayfish from Shelta Cave and, as "*Cambarus,*" from Crystal Cave. Pennak (1953) simply listed *O. pellucidus* from Alabama caves. Eberly (1958 and 1960) reiterated the presence of this subspecies in northern Alabama.

Rhoades (1959) in discussing the status of *Orconectes inermis* indicated that "With the description of *Cambarus pellucidus australis* Rhoades (1941) from Alabama caves, it became evident that the hooks on the fourth walking legs represent a significant character for generic determination. In light of this new evidence, Hobbs (1942a) redefined the genus." Hobbs (1959) included the subspecies of *O. (O.) pellucidus* in his key to the North American crayfishes.

Nicholas (1960) included this subspecies in his checklist of macroscopic troglobitic organisms but erred in indicating that it was known only from the type-locality.

Fingerman and Mobberly (1960) found that the "eyestalks, supraesophageal ganglia, and circumesophageal connectives of this subspecies contain a red pigment-concentrating substance and a distal retinal pigment light adapting one." This is cited by Poulson (1964).

Barr (1961) stated that "Two species of white, eyeless crayfishes inhabit Tennessee caves. *Orconectes pellucidus australis* (Rhoades) is found along the western margin of the Cumberland plateau from Kentucky into Alabama." He also included a photograph of this crayfish.

Hart and Hobbs (1961), in describing new entocytherid ostracods, listed this subspecies as a host of *Entocythere barri (=Sagittocythere barri)* in Cave Spring Cave and Shelta Cave, Madison County, Alabama, and Blind Fish Cave, Putnam County, Tennessee. *Entocythere ungulata (=Dactylocythere ungulata)* was found on *O. p. australis* in Big Mouth Cave, Grundy County, Tennessee, and in Blind Fish Cave, Putnam County, Tennessee. *Entocythere steevesi (=Dactylocythere steevesi)* and *Entocythere tuberosa (=Donnaldsoncythere tuberosa)* were also found to be infesting this crayfish in Blind Fish Cave. The crayfish in Blind Fish Cave was mistakenly identified as *O. p. pellucidus* by them.

Rhoades (1962) had the following to say about *O. p. australis:* "The armature of the carapace and chelae much reduced from that of typical *O. pellucidus.* Areola the longest of all the *O. pellucidus* subspecies. Hooks on the third walking legs only. Gonopods with very short tips and the outer ramus tends to clasp the inner ramus. Annulus ventralis with high hemispherical area close to the anterior margin.

"This blind cave subspecies appears to be widely distributed and in considerable abundance in the large underground drainage of the Mussel Shoals region." Later, he cited Jackson and Madison counties, Alabama.

Rhoades maintained the assignment of the *pellucidus* subspecies to his Group rafinesquei, discussed the origins of the four subspecies recognized by him, and concluded his treatment of *O. p. australis* with "The southern subspecies of the blind crayfish seems rather abundant in the well developed subterranean drainage of northern Alabama. Dr. Walter B. Jones, in outlining the ecology of Alabama caves (Rhoades, 1941), mentions that the presence of blind crayfishes is associated with the presence of cave fishes and aquatic insects. Individuals seem to be most numerous where surface water enters caves during the wet season. Debris washed in tends to initiate the food chains. Once begun, food chains may continue among animals present. Bat guano and the molds that grow from these deposits are important sources of food for cave species."

Jegla et al. (1965) indicated that *O. p. australis* in two Alabama caves [Shelta Cave and Sauta Cave, personal communication, M. R. Cooper] "differ by 20 mm in maximum length attained, by 20 mm in length at maturity, and in inflection point for cheliped allometric growth" and stated that "these variations may be a result of different levels of food supply and interspecific competition."

Tarkington et al. (1965) simply noted having observed both green and colorless crayfishes in Hering Cave, Madison County, Alabama. All colorless ones from this locality observed by us were *O. a. australis*.

Cooper (1966) indicated that this crayfish is the largest "and by far the most numerous macroscopic organism in the aquatic community" of Shelta Cave.

Hart and Hart (1966), in citing locality records for entocytherid ostracods which had been garnered from the national crayfish collection, cited new locality records for this crayfish as host to the ostracods.

Larimer et al. (1966), investigating the caudal photoreceptors of this crayfish from Shelta Cave, found that while sensitivity to variations in wave length is not markedly different from that of certain epigean species, "there is a uniform shift of the spectral sensitivity toward shorter wavelengths, placing the peak at about 497 mμ as compared to 502 mμ for the epigean species."

Barr (1967a:161) utilized the combination *Orconectes australis packardi*, thus implying that Rhoades' *Orconectes pellucidus australis* was the nominate subspecies, *Orconectes australis australis*. (See review of literature for *O. australis packardi*.) Hobbs (1967b) discussed the affinities of this crayfish with allies in other genera. Cooper (1967 and 1968) contributed no new information.

Barr (1968:85) discussed the range of the troglobitic *Orconectes*, commenting on their possible origins.

Jones and Varnedoe (1968) listed this crayfish from several caves in Madison County, Alabama, and included a photograph of a specimen from Shelta Cave. Cooper and Poulson (1968) illustrated a crayfish from the same cave. Torode (1968:152) reported the observation of two ovigerous females in Canyon Cave; the same data were reprinted in 1969.

M. Cooper (1969), in comparing this crayfish with the related epigean *O. limosus*, found that not only does it possess chelae of greater relative length than does the epigean species but also exhibits "an increased rate of elongation" in development. Furthermore, the remaining pereiopods are comparatively longer and narrower. Whereas the total length of the antennule is no greater than that of the epigean species, the flagella are proportionately longer, and the external flagellum bears "a greater number of segments, greater number of asthetasc-bearing segments, and . . . a strikingly greater length of the chemoreceptive asthetascs." The internal flagellum of the antennule and the antenna, which bear mechanoreceptors only, "are considerably longer" in the troglobite.

Cooper and Cooper (1969a) indicated that this crayfish occurs in many caves in Madison and Jackson counties, Alabama. Cooper and Cooper (1969b) noted the association of this crayfish with the salamander *Gyrinophilus palleucus* in Alabama. Nicholas (1969) added no original data.

Hobbs (1969:120), in discussing the origins of the genera *Orconectes, Hobbseus, Faxonella, Fallicambarus,* and *Cambarus,* pointed out the primitive characteristics of *O. a. australis*.

Graham (1969:4) reported having collected two white crayfish from Indian Rock Cave, Jackson County, Alabama.

Nicholas (1970:22) included a color photograph of this crayfish from Turkey Scratch Cave, Warren County, Tennessee.

COMMENTS ON PREVIOUSLY RECORDED DATA.—(See also comments on *O. australis packardi* and *O. pellucidus*.) Of Rhoades' (1941) remarks concerning this subspecies, only a few of them need to be modified in light of specimens that have been subsequently acquired. Some first-form males do have rudimentary hooks on the ischiopodites of the fourth pereiopods. He did not mention, nor did he figure, the short, very slender caudal process that is present on the pleopods of all of the first form males we have seen from the type-locality as well as on those from several other localities. The inner and outer rami (=mesial process and central projection) of the first pleopod of the first form male are as widely separated in *australis* as in any of the other species. Thus Rhoades' statement that "Outer ramus with corneous tip, curved tightly around the inner ramus" (1941:142) and "outer ramus tends to clasp the inner ramus" (1962:

69) probably refers to the more laterally directed central projection in *australis*. Among our specimens from Shelta Cave, the length of the areola ranges from 36.9 to 40.5 percent of the entire length of the carapace; from the nearby Hering Cave, also in Madison County, 34.0 to 38.8 percent; and specimens from other caves within the range of the subspecies have areolae that constitute percentages within these extremes (34.0 to 40.5 percent).

In his 1962 account, Rhoades indicated that the areola of *australis* is "the longest of all the *O. pellucidus* subspecies" (page 69). While in some individuals this is true (because individuals of the subspecies are larger), the ratio of the areola length to carapace length is not. That it is longer than that of *O. a. packardi* was claimed earlier by Rhoades (1944:121). Remeasurements of the types of the latter indicate areolae constituting 42.4, 41.3, and 41.7 percent of the respective carapaces—percentages exceeding that of most specimens of *O. a. australis* examined by us. Rhoades (1941:144) cited a range of 33.3 to 39.5 percent for *australis* and indicated that in *O. pellucidus* the range was 36 to 41 percent. Furthermore, the areolae of *O. inermis testii* sometimes constitute as much as 45.0 percent of the carapace length.

Hobbs (1948b:85) indicated that the range of *australis* was situated farther south than that of any other member of the Limosus Section, to which *australis* and its allies were assigned and which embraces its closest epigean *Orconectes* relatives. In 1952, however, Penn described *Orconectes hathawayi* (now considered to be a member of the Section) from Rapides Parish, Louisiana (and it, or a closely allied species, has been collected subsequently in Clarke County, Alabama), thus extending the known range of the Section more than 300 miles to the southwest. And if *O. lancifer* (Hagen) should be assigned to the Limosus Section as suggested by Fitzpatrick in Fitzpatrick and Prins (1965:146), then the range of the section extends some 600 miles to the southwest in eastern Texas.

Rhoades' (1959:399) statement concerning Hobbs' basis for redefining the genus is not clear to us; the hooks on the fourth walking legs have generic significance only to the extent that a crayfish with such hooks might belong to any of the cambarine genera except *Cambarus, Faxonella,* and *Hobbseus;* even various combinations of hooks on the ischia of the second, third, and fourth pereiopods are not really diagnostic for any of the crayfish genera (Hobbs 1962:274).

DIAGNOSIS.—Albinistic; eyes reduced and without pigment; rostrum with marginal spines or tubercles delimiting base of acumen, margins subparallel, convex or converging, upper surface concave and without median carina; postorbital ridges terminating cephalically in spines or tubercles; hepatic area often with number of spines; at least one, often several, cervical spines present; areola 3.9 to 6.0 times longer than broad and constituting 34.1 to 41.9 percent of entire length of carapace; chelae not conspicuously setose but with ciliated tubercles, mesiodorsal surface of palm with several irregular rows of tubercles; hooks on ischiopodites of third, and sometimes fourth, pereiopods. First pleopod of first-form male with greatest cephalocaudal axis of pleopod less than twice that immediately proximal to base of central projection, always terminating in two elements, and frequently bearing vestigial spinelike caudal process; non-corneous mesial process moderately narrow, subacute, directed caudomesially, and reaching distally approximately same level as central projection, partially obscuring latter in caudal aspect; central projection corneous, flattened in cephalocaudal plane and directed somewhat laterally; shoulder at cephalic base of central projection rounded. Annulus ventralis only slightly broader than long, and as illustrated in Figure 3*l*.

Holotypic Male, Form I: Body (Figure 3*c, i*) subovate, depressed. Abdomen narrower than thorax (14.7 and 19.7 mm in widest parts, respectively). Width of carapace greater than depth in region of caudodorsal margin of cervical groove (19.7 and 15.0 mm). Areola moderately broad (5.1 times longer than wide), with 6 minute punctations across narrowest part. Cephalic section of carapace 1.5 times as long as areola; length of areola 40 percent of entire length of carapace. Rostrum almost twice as long as broad, excavate, and with acumen 5/6 as long as width of rostrum at base; cephalic extremity reaching distal end of antennular peduncle; margins not swollen, only slightly elevated, and with small, acute, corneous marginal spines at base of acumen; upper surface with evenly spaced minute setiferous punctations; subrostral ridges very weak and evident for only short distance along basal rostral margins.

Postorbital ridges poorly developed, short, with shallow dorsolateral grooves, and terminating cephalically in small corneous acute tubercles. Suborbital angle lacking. Branchiostegal spines represented by small acute tubercles. Seven or eight small cervical spines or tubercles present on each side of carapace immediately caudal to cervical groove. Carapace punctate dorsally and granulate laterally; hepatic area with few small acute tubercles but without spines. Abdomen shorter than carapace (41.5 and 44.2 mm). Cephalic section of telson with 2 strong spines in each caudolateral corner, mesial ones movable.

Projecting portion of epistome (Figure 3*h*) subtriangular, with rounded basal extremities and with small cephalomedian extension; concave surface with crowded setae. Eyes much reduced, completely hidden beneath rostrum in dorsal aspect and extending cephalically only halfway between margin of orbit and marginal spines of rostrum. Antennules of usual form, with small spine on ventral surface of basal segment. Antennae broken but probably extending beyond caudal margin of telson. Antennal scale (Figure 3*g*) broadest distal to midlength, distinctly less than half as broad as long; outer thickened portion narrower than lamellar area and terminating in prominent corneous-tipped spine. Third maxillipeds extending almost to distal end of peduncle of antenna.

Chela (Figure 3*f*) slender and only slightly inflated; mesial margin of palm 1.5 times longer than width of palm; dorsal surface of palmar area largely tuberculate in mesial half and punctate in lateral half, both punctations and distal bases of tubercles with fine setae; ventral surface of palm entirely tuberculate, with prominent corneous-tipped spine opposite base of articulation of dactyl; tubercles along mesial portion arranged in irregular longitudinal series, innermost row of about 14 tubercles; lateral margin of propodus costate along almost its entire length. Fingers not gaping; dorsal and ventral surfaces of both with longitudinal ridges flanked by setiferous punctations; opposable margin of immovable finger with row of 17 rounded, corneous tubercles, sixth from base largest; at lower level of same margin, larger tubercle present between eleventh and twelfth tubercles of upper row; single row of minute denticles between fifth and eleventh tubercles and similar denticles crowded distally to base of broken tip; opposable margin of dactyl with 19 tubercles, seventh from base largest, single row of minute denticles between first and fourteenth tubercle, distally minute denticles becoming crowded and extending to base of broken tip of finger; mesial surface of dactyl with tubercles along proximal half and punctations along distal. Carpus longer than broad, with proximal two-thirds of mesial, dorsal, and lateral surfaces tuberculate; ventral surface punctate; mesial surface with 2 large corneous-tipped spines, smaller one ventral to larger; similar spine at mesioventral distal angle, another adjacent to boss of ventrolateral articulation with propodus. Merus mostly tuberculate except ventrolaterally; tubercles present along almost entire dorsal surface, and 2 corneous-tipped, subapical ones; ventrolateral margin with row of 12 spikelike tubercles and ventromesial margin with approximately 16; scattered tubercles closely flanking these rows, a contributing cause of inexact counts. Ischium with rows of tubercles along outer and opposable margins, row of 7 on opposable margin, with additional ones flanking it.

Ischia of third pereiopods (Figure 3*k*) with strong simple hooks broadly rounded apically and projecting proximad beyond distal margin of basis. Coxae of fourth pereiopods with caudomesially projecting prominences; coxae of fifth pereiopods without prominences except for small mesioventral projections at bases of phallic papillae.

First pleopod (Figure 3*a, e, j, k*) symmetrical, reaching bases of third pereiopods when abdomen is flexed and only shallowly situated in sternal groove; tip ending in two or three parts as described in Diagnosis.

Allotypic Female: Differs from holotype in following respects (acumen broken so that some proportions and other details cannot be determined): cervical tubercles and spines small but 9 on one side and 11 on other; cephalic section of telson with 3 spines in caudodextral corner; third maxillipeds extending cephalically to distal end of penultimate segment of peduncle of antenna; mesial row of 12 tubercles on palm of chela, opposable margin of fixed finger with row of 16 (fifth from base largest), and opposable margin of dactyl with row of 21 (sixth from base largest); mesial surface of carpus of cheliped with 2 corneous-tipped tubercles, smaller situated proximoventral to larger; upper distal margin of merus with 1 spiniform tubercle, others as in holotype, lower surface with lateral row of 9 tubercles and mesial row of 17. (See measurements.)

Annulus ventralis (Figure 3*l*) rather shallowly situ-

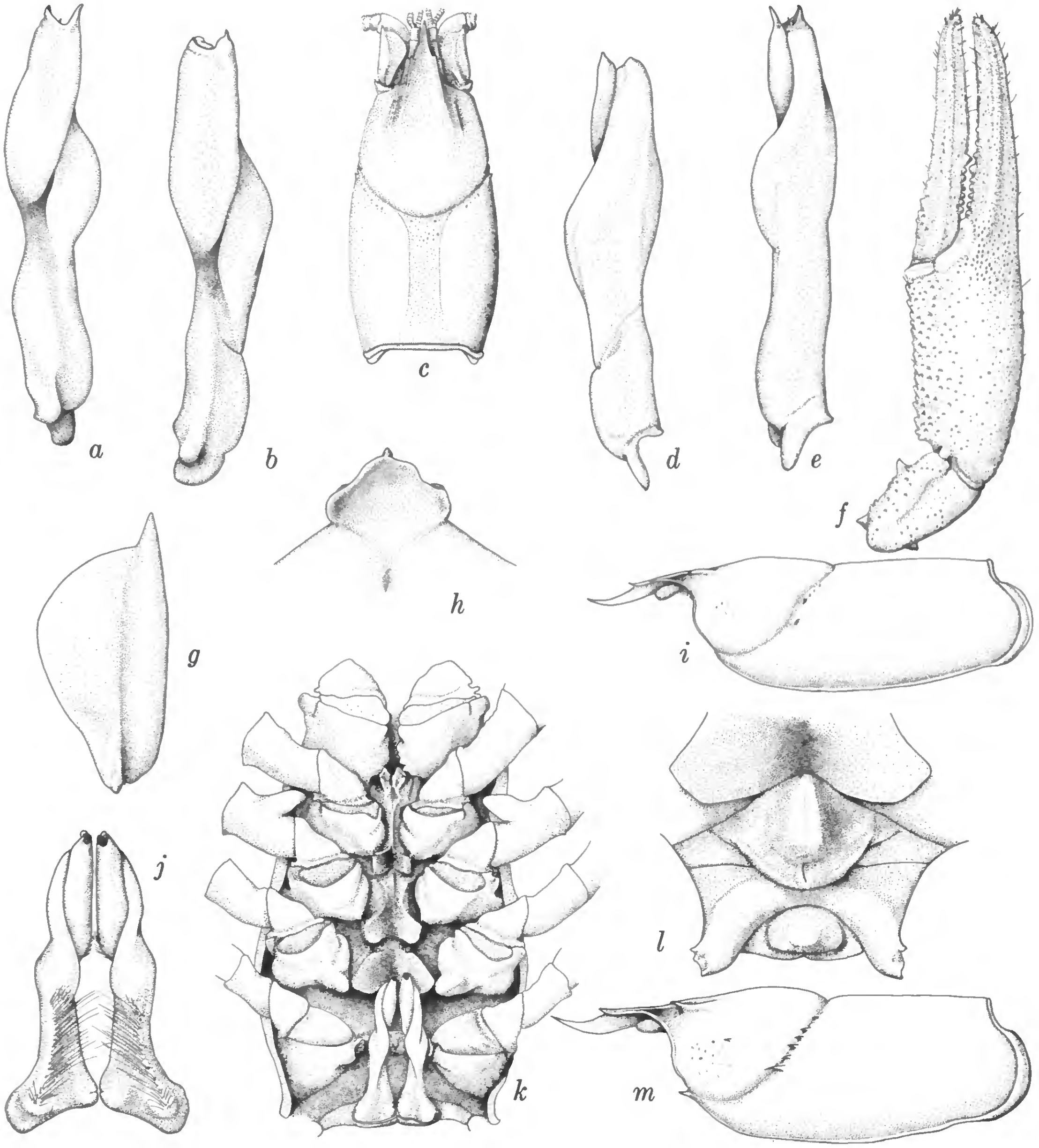


FIGURE 3.—*Orconectes australis australis:* ***a,*** mesial view of first pleopod of holotypic male, form I; ***b,*** mesial view of first pleopod of morphotypic male, form II; ***c,*** dorsal view of carapace of holotypic male, form I; ***d,*** lateral view of first pleopod of morphotypic male, form II; ***e,*** lateral view of first pleopod of holotypic male, form I; ***f,*** dorsal view of distal podomeres of cheliped of holotypic male, form I; ***g,*** antennal scale of holotypic male, form I; ***h,*** epistome of holotypic male, form I; ***i,*** lateral view of carapace of holotypic male, form I; ***j,*** caudal view of first pleopods of holotypic male, form I; ***k,*** ventral view of caudal thoracic region of holotypic male, form I; ***l,*** annulus ventralis and portion of sternum of allotypic female; ***m,*** lateral view of carapace of male from Blind Fish Cave, Putnam County, Tennessee.

ated in sternum and not firmly fused to sternal plate immediately cephalic to it; outline subovate, 1.2 times broader than long with median portion elevated ventrally and forming broad arc having its highest segment slightly cephalic to midlength; arched portion, bearing shallow longitudinal groove, ending caudally on gently sloping plateau-like rim about one-fourth length of annulus from caudal margin; sinus originating at caudal base of arch sinistral to median line, and after extending dextrally to median line, turning suddenly caudally and ending on caudal margin of annulus.

Morphotypic* Male, Form II: Differs from holotype in following respects: acumen, slightly longer than width of rostrum at base, extending beyond distal end of peduncle of antennule; third maxillipeds extending cephalically slightly beyond base of ultimate segment of peduncle of antenna. Hooks on ischia of third pereiopods unusually prominent for second-form male, but boss on coxa of fourth pereiopod not so well developed.

First pleopod (Figure 3*b, d*) with no trace of caudal process and mesial process extending slightly beyond tip of central projection, latter especially reduced and less well defined than in holotype.

Chelae lacking in morphotype but in second form paratype differs from holotype as follows: mesial row of only 10 or 11 tubercles on inner margin of palm; opposable margin of fixed finger with row of 15 small rounded tubercles, progressively smaller distally, with 3 somewhat larger ones forming row below level of long row, 2 of them situated between ninth and tenth tubercles of upper row and 1 between tenth and eleventh; carpus as in allotype; merus with 1 spiniform tubercle near upper distal end and with lower mesial row of 17 tubercles and lateral one of 13.

MEASUREMENTS (in millimeters).—*Orconectes australis australis:*

	Holotype	*Allotype*	*Morphotype*
Carapace:			
Height	15.0	12.7	10.8
Width	19.7	16.6	13.6
Length	44.2	—	31.2
Rostrum:			
Width	6.0	5.5	4.4
Length	11.4	acumen broken	8.9
Areola:			
Width	3.5	3.3	2.3
Length	17.7	15.0	12.5
Chela:			
Length of mesial margin of palm	15.9	11.0	no chela
Width of palm	10.3	7.3	
Length of lateral margin of chela	41.4	28.3	–
Length of dactyl	22.5	15.1	–

TYPES.—Holotype, allotype, and morphotype, USNM 79363, 79364, 79365 (♂I, ♀, ♂II); Paratypes, Academy of Natural Sciences, Alabama Museum of Natural History, collections of Leslie Hubricht and Rendell Rhoades.

TYPE-LOCALITY.—Shelta Cave (SE ¼, NE ¼, sec. 27, T.3S, R.1W), Huntsville, Madison County, Alabama.

SPECIMENS EXAMINED.—Specimens from Alabama and Tennessee were examined as follows:

ALABAMA: *Jackson County:* (1) Limrock Blowing Cave, SW ¼, NW ¼, sec. 11, T.4S, R.4E, 3♂II, 2♀, S. B. Peck, XII/29/65. (2) Doodlebug Hole (=Blowing Cave), NW ¼, NE ¼, sec. 30, T.1S, R.4E, 1♂I, John Stade, II/14/60. (3) Saltpeter Cave, SW ¼, SW ¼, sec. 16, T.3S, R.3E, 1♂I, 1♂II, 1♀, W. B. Jones, VI/9/40. (4) Kennamer Cave, NW ¼, SE ¼, sec. 27, R.4S, T.3E, 1♀, Bret Blosser, X/20/63. (5) Salt River Cave, NW ¼, NW ¼, sec. 2, R.1S, T.6E, 1♀, T. C. Barr, Jr., X/17/54. (6) McFarland Cave, SW ¼, NW ¼, sec. 22, T.3S, R.3E, 2♂I, 1j♂, W.B.J., II/29/40; 1♂I, 2♂II, S.B.P., XII/29/65. (7) Paint Rock Cave, SE ¼, SW ¼, sec. 29, R.4S, T.3E, 1♀, S.B.P., IX/6/65; 1♀, S.B.P., XII/20/65. (8) Guess Creek Cave, SW ¼, SE ¼, sec. 22, T.3S, R.4E, 2♂I, 2♂II, 3♀, T.C.B. and S.B.P., IX/5/65. (9) Jess Elliott Cave, NW ¼, NE ¼, sec. 31, T.1S, R.6E, 1♂I, 1♀ with eggs, S.B.P., IX/3/65. (10) Doug Green Cave, SW ¼, SW ¼, sec. 9, T.2S, R.4E, 1♀, S.B.P., III/14/66. (11) Bell Spring Cave, NW ¼, NE ¼, sec. 9, T.2S, R.6E, 1♂II, J. E. and M. R. Cooper, IV/9/66. (12) Fern Cave, SE ¼, SE ¼, sec. 21, T.4S, R.3E, 2♂I, 4♀, J.E.C. and M.R.C., VIII/26/63; 1♀, H.H.H. III, VI/6/70. (13) Borderline Cave, NE ¼, NW ¼, sec. 17, T.2S, R.3E, 1♀, William Torode, XI/7/67. (14) Larkins Cave, NW ¼, NE ¼, sec. 27, T.4S, R.4E, 1j♂, 1j♀, S.B.P., IX/14/68. (15) Sauta Cave (=Blowing Cave), SE ¼, SE ¼, sec. 7, T.5S, R.5E, 1♂I, 1♂II, L. G. Conrad, VI/18/63. (16)

---

*Rhoades did not specifically designate a morphotype but labeled one of the second form males as "allotype," as he also designated the allotypic female. This "allotypic male" is considered equivalent to the morphotypic male of other authors.

Canyon Cave, NE ¼, NE ¼, Sec. 36, T.4S, R.3E, 1♀ with eggs and young, Richard Graham and W.T., XI/29/68. *Madison County:* (1) Shelta Cave (=Shelta Cavern), SE ¼, NE ¼, sec. 27, T.3S, R.1W, 1♂I, 1♂II, 1♀ (holotype, allotype, morphotype), A. R. Cahn, III/1/38; 1♂II, 2♀, A.R.C., VI/1936; 1♂II, 1♀, Leslie Hubricht, VIII/5/39; 1♂II, H. Henrot, VIII/16/46; 1♂I, 1♂II, 1♀, Donald Blair, VI/15/57; 2♂I, 1♂II, 4♀, T.C.B. and W.B.J., V/3/59; 1♂I, 2♂II, L.G.Co., VI/19/63; 2♂II, 2♀, S.B.P., 1965. (2) Sadler Spring Cave, SE ¼, NE ¼, sec. 3, T.4S, R.1E, 1♂II, 1j♀, W.B.J., VI/14/40. (3) Hering Cave (=Cave Spring Cave), NE ¼, NE ¼, sec. 10, T.5S, R.2E, 2♀, 1j♂, W.B.J., IX/26/39; 3♂II, 3♀, 1j♂, 3j♀, W.B.J., XII/1/39; 1♂I, 4♂II, 7♀, 4j♂, 4j♀, B. D. Valentine, X/14/48; 2♂II, 3♀, 3j♀, B.D.V., X/21/48; 1♂I, S.B.P., VIII/24/68. (4) Aladdin Cave, NE ¼, SW ¼, sec. 30, T.2S, R.3E, 1♀, L.H., VI/18/57. (5) Burwell Cave, SW ¼, NW ¼, sec. 36, T.2S, R.2W, 1♂I, S.B.P., III/13/66; 6♂I, 6♂II, 4♀, Arthur W. Dobson, Jr., II/10–11/68. (6) Huntsville Spring Cave (=Big Spring Cave), SE ¼, SW ¼, sec. 36, T.3S, R.1W, 1♀, W.B.J., X/6/39. (7) Fuqua Spring Cave, NE ¼, NW ¼, sec. 15, T.1S, R.2E, 2j♂, 2j♀, S.B.P. and A. Fiske, VI/25/67. (8) Byrd Spring Cave, SW ¼, NE ¼, sec. 25, T.4S, R.1W, 2♀, S.B.P., and A.F., VII/5/67. (9) Matthews Cave, SE ¼, SE ¼, sec. 12, T.4S, R.2W, 7♂I, 2♂II, 11♀, 2j♂, S.B.P., VIII/26/68. (10) Cold Spring Cave, NE ¼, SW ¼, sec. 28, T.3S, R.1E, 1j♂, 1j♀, S.B.P., VIII/20/68.

TENNESSEE: *Fentress County:* (1) Buffalo Cave, lat. 36°22′35″N, long. 84°57′36″W, 1♀, R. M. Norton, IX/30/63. (2) Sells Cave, Lat. 36°33′25″N, long. 85°00′24″W, 1♀, T.C.B., III/7/59. (3) Wolf River Cave, lat. 36°31′58″N, long. 84°56′38″W, 1♀ with eggs, J. E. Crouch and T.C.B., VII/27/54. *Franklin County:* (1) Wet Cave, Rowark Cove, lat. 35°13′47″N, long. 85°55′13″W, 1♂I, T.C.B., VII/15/54; 1♂II, T.C.B., X/14/56. (2) Walker Spring Cave, lat. 35°13′36″N, long. 85°54′57″W, 1♀, T.C.B., X/10/55; 1♂II, T.C.B., X/15/55. (3) Partin Spring Cave, lat. 35°15′56″N, long. 85°52′51″W, 1♂II, S.B.P. and A.F., VII/19/67. (4) Caroline Cove Cave, lat. 35°03′54″N, long. 86°07′41″W, 1♂I, 1♂II, 4♀, 3j♀; S.B.P. and A.F., VII/11/67. *Grundy County:* (1) Big Mouth Cave, lat. 35°19′58″N, long. 85°34′48″W, 1♀, J. N. Dent, VIII/2/55; 2♂I, 6♂II, 7♀, 1j♂, 5j♀, 1♀ with eggs, R. B. Cumming, VIII/23/52. (2) Wonder Cave, lat. 35°16′24″N, long. 85°50′59″W, 2♂I, 1♀, J. M. Valentine, III/17/31; 2♂I, J.M.V. and J. C. Beakley, IV/19/35; 3♂I, 1♂II, 2♀, Charles E. Mohr, VI/30/37; 1♂I, Nat. Spel. Soc., VIII/30/41; 1♀, 2j♂, H.H., VIII/13/46. (3) Bear Cave, lat. 35°27′07″N, long. 85°34′48″W, 1♂I, C. E. McCary, X/12/55. (4) Crystal Cave, lat. 35°15′25″N. long. 85°51′15″, 1♀, H.H., VIII/13/46. *Overton County:* (1) Raven Bluff Cave, lat. 36°29′33″N, long. 85°21′36″W, 1♀ with eggs, S. R. Gorin, VI/7/48; 1♂II, 1♀, T.C.B., II/28/59; 1♂I, 1♂II, T.C.B., III/19/61. (2) Sheep Cave, lat. 36°12′41″N, long. 85°11′38″W, 1♀, T.C.B., VII/23/55. *Putnam County:* (1) Bridge Creek Cave, lat. 36°02′12″N, long. 85°37′55″W, 1♂II, T.C.B., VIII/4/54; 2♂I, 4♂II, T.C.B., III/15/59. (2) Blind Fish Cave, lat. 36°03′19″N, long. 85°20′31″W, 11♂I, 2♂II, 2♀, T.C.B., C. E. Bush, and J. Harris, X/16/58; 1♂I, T.C.B., IX/24/60; 7♂I, 2♂II, T.C.B., H. R. Steeves, Jr. and H. R. Steeves III, XI/8/59. (3) Johnson Saltpeter Cave, lat. 36°04′19″N, long. 85°47′38″W, 1♂I, T.C.B., XI/5/55. *Warren County:* (1) Cumberland Caverns, lat. 35°40′09″N, long. 85°40′51″W, 1♀, D. Egbert, VI/10/55; 1♂I, Bert Denton, II/7/54. (2) Turkeyscratch Cave, lat. 35°44′23″N, long. 85°36′00″W, 1♀, T. C. B., I/1/58. *White County:* (1) Indian Cave, lat. 35°49′01″N, long. 85°31′14″W, 1j♀, T.C.B., VI/19/55. (2) Wildcat Cove Cave, lat. 35°56′38″N, long. 85°25′25″W, 2♀, 1j♂, T.C.B. and L.H., XII/24/56. (3) Ward Cave (=Dairy House Cave), lat. 35°56′32″N, long. 85°27′03″W, 2♂I, 3♂II, 2♀, T.C.B., X/14/58; 1♂II, 1♀, R. Baroody and J. R. Holsinger, X/28/69. (4) Ross Cave (exact location not known), 1♀, T. E. Simpson, 1966.

RANGE.—*Orconectes a. australis* has a comparatively large range extending from the northern tributaries of the Tennessee River in Jackson and Madison counties, Alabama, north-northeastward on the Cumberland Plateau to the area of Fentress County, Tennessee, and adjacent Wayne County, Kentucky, where it intergrades with *O. a. packardi.*

VARIATIONS.—While no significance is attached to political boundaries, they do furnish a convenient means of associating variations in populations from differing caves throughout the range of the subspecies with readily identifiable geographic regions. For this reason, and the fact that the type-locality is situated in the southernmost portion of the range, the treatment is arranged by counties from the southwest to the northeast.

Not discussed below are the variations that occur in the mesial process and central projection of the first pleopod of the male, but some of them, including the extremes, are illustrated in Figure 8.

Madison County, Alabama: Specimens from the type-locality (Shelta Cave) (Figure 7*j*) possess rostra the margins of which may be subparallel, convex, or convergent, and which, except in length, encompass the limits of variation observed in the subspecies. The marginal spines may be reduced to tubercles, but the acumen is usually moderately long. The postorbital spines are quite variable in length, usually moderately long but occasionally reduced to tubercles. The number of cervical spines, or tubercles, varies from 7 to 9, and those on the hepatic region from 2 to 5 (spines are usually rather heavy and short but more spinelike in smaller individuals). The areola ranges from 4.2 to 5.5 times longer than broad and constitutes 37.5 to 40.5 percent of the entire length of the carapace. Hooks are invariably present on the ischia of the third pair of pereiopods in males but may be present, but never well developed, or absent on the fourth pair. The caudal process of the first pleopod of first-form males is always small, and in some specimens is minute. The relative height of the median longitudinal elevation of the annulus ventralis is rather uniform, but the median furrow on it may be very shallow or deep; the characteristic caudal shelf is constant although it may be sloping or gently curved.

In specimens from Hering Cave, the rostrum is provided with longer marginal spines and acumen; the cervical and hepatic spines are conspicuously long and slender, and in number vary, respectively, from 4 to 8 and 0 to 7. The areola varies from 4.9 to 5.9 times longer than wide and comprises 34.6 to 38.8 percent of the length of the carapace. Hooks are lacking on the fourth pair of pereiopods in the second-form males (no first-form males are available). The median longitudinal elevation of the annulus is somewhat depressed and its longitudinal furrow almost obsolete. The spines on the cheliped are comparatively more prominent than in specimens from the type-locality.

In representatives of the populations in Aladdin (Figure 7*e*) and Fuqua Springs (Figure 7*g*) caves, the marginal spines on the rostrum are reduced to tubercles and the acumen is only moderately long. The number of cervical tubercles varies from 3 to 5, and the hepatic spines are represented by low tubercles. The dimensions of the areola are within the range of variation noted in topotypic specimens, and the annulus ventralis is similar to that occurring in specimens from Cave Spring Cave.

Specimens from Burwell (Figure 7*i*) and Matthews caves are quite similar and comparatively large, and an individual from Burwell Cave is the largest specimen of the species available to us. Its rostrum has very short, heavy tubercles and the acumen is short. The cervical spines are reduced in size and in number (1 to 3), and there are no hepatic spines. The areola varies from 4.1 to 6.6 times longer than broad and comprises 38.5 to 42.7 percent of the carapace length. All traces of hooks on the fourth pereiopod in males from Burwell Cave are lacking, but in those from Matthews Cave they are vestigial or well developed. The caudal process of the first pleopod is well developed, and the annulus ventralis resembles that in specimens from Shelta Cave.

The single female from Big Spring Cave (Figure 7*d*) has a unique rostrum (probably resulting from an injury) in that the sinistral border bears 2 marginal spines and the dextral none. There are 6 cervical spines and 1 or 2 very small hepatic spines; otherwise, the specimen is much like those from the type-locality. In the Byrd Spring specimens (Figure 7*k*) most spines are long but there are fewer cervical (4 to 6) and hepatic (0 to 1) spines than in topotypes.

Jackson County, Alabama: Two of the most distinctive populations of this subspecies occur in Fern (Figure 6*p*) and Saltpeter caves (Figure 6*w*). In them, all the pereiopods seem to be more robust than in specimens from elsewhere; the tubercles on the chelipeds are heavy and short, and those on the opposable margins of the fingers of the chela are conspicuously strong. The marginal spines on the rostrum are reduced to tubercles, and in one female, almost obsolete; the cervical tubercles (occasionally one spine) are quite small as are those on the hepatic region, the latter tubercles sometimes lacking. The areola is 4.2 to 5.3 times longer than broad and comprises 38.5 to 39.6 percent of the carapace length. Hooks are present only on the third pair of pereiopods in the male.

Similar to the specimens from Fern and Saltpeter caves are the two crayfish from Jess Elliot Cave (Figure 6*v*), but in them the pereiopods are not so robust, and the tubercles on the opposable margins of the fingers of the chelae are not nearly so strong. Their areolae are 4.0 and 4.4 times longer than broad and constitute 37.8 and 39.6 percent of the entire length of the carapace. The first pleopod lacks a caudal process, and the median longitudinal elevation of the annulus is somewhat depressed but has a deep longitudinal furrow.

In sharp contrast to the populations just discussed, those in Guess Creek Cave (Figure 6*u*) and Sauta Cave (Figure 6*r*) have strong marginal spines on the rostrum, a long acumen, as many as 8 slender, long cervical spines and 7 hepatic spines. The pereiopods are more like those in specimens from the type-locality, but the spines on the chelipeds are also long and slender. The areola varies from 4.1 to 5.3 times longer than broad and, reflecting the long rostra, constitutes 36.2 to 39.3 percent of the total length of the carapace (the three males, no more than 37.5 percent). In the specimens from Guess Creek Cave, hooks are present on only the third pair of pereiopods, but in the male from Sauta Cave, rudimentary hooks are also borne on the fourth. The first pleopods of the males lack the caudal process.

Somewhat intermediate in spination between the Fern and Guess Creek specimens are those from McFarland (Figure 6*s*) and Doug Green (Figure 6*q*) caves, but considerable variation exists in those from the former; some have a few (one with 5) long cervical spines and others have none—all reduced to tubercles. The areolae are approximately 4.5 times longer than wide and comprise 37.6 to 38.7 percent of the carapace length. Hooks are present on only the third pereiopods in the male and the first pleopods lack or have very small caudal processes.

In addition to being almost aspinous (the rostrum has been broken and partially regenerated), our specimen from Doodlebug Hole (Figure 7*c*) has an unusual mesial process on the first pleopod of the male (Figure 8*w*); its laterodistal margin is emarginate, rendering the impression of a subterminal tooth on that margin. The pleopod is devoid of a caudal process, and hooks are restricted to the third pair of pereiopods. Also almost spineless are the two females from Paint Rock Cave (Figure 7*a*) and the single females from Borderline, Kennamer (Figure 7*b*), and Salt River (Figure 6*t*) caves. The areolae vary from 4.4 to 5.8 times longer than broad and constitute 37.0 to 37.7 percent of the carapace length.

Specimens from Limrock Blowing Cave (Figure 6*o*) are moderately spiny to smooth. Only second-form males and females are available, but the males have no hooks on the fourth pereiopod. The areolae are 3.9 to 5.0 times longer than broad and comprise 37.7 to 39.0 percent of the length of the carapace.

Franklin County, Tennessee: Specimens from the four localities in Franklin County (Figure 6*j-n*) are rather uniform. All are comparatively aspinous, possessing short marginal spines on the rostrum and postorbital ridges, and having reduced cervical and hepatic spines. The areolae range from 3.7 to 5.0 times longer than broad and constitute 36.4 to 41.0 (average 38.3) percent of the entire length of the carapace. Hooks are present on only the third pereiopods, and the pleopods of the male lack a caudal process. The annuli ventrales are typical of specimens from the type-locality.

Grundy County, Tennessee: Three of the four populations known to occur in Grundy County exhibit considerable variation. From Bear Cave (Figure 6*g*), Caney Fork drainage, the single specimen has few and small spines. The areola is 4.3 times longer than broad and constitutes 38.7 percent of the carapace length. It has hooks on only the third pair of pereiopods, and the first pleopod is provided with a caudal process.

In contrast, the population in Wonder Cave (Figure 6*i*), Elk River drainage, has both spiny and aspinous members. Cervical spines are usually few in number but are very prominent; hepatic spines may or may not be present, but, if evident, are usually small. The areola is 4.2 to 5.7 times longer than broad and comprises 36.0 to 37.8 percent of the total length of the carapace. Hooks are present only on the third pereiopods of the male, and the first pleopod may or may not bear a caudal process. One specimen has a single cervical tubercle, no hepatic spines, and the marginal spines on the rostrum are reduced.

In Big Mouth Cave (Figure 6*h*), Elk River drainage, most of the individuals have few, poorly developed spines, although one specimen could be described as very spiny. The areola is 4.7 to 5.7 times longer than broad and occupies 36.8 to 39.8 percent of the carapace length. In the males, hooks are present only on the third pair of pereiopods, and the caudal process is absent.

Warren County, Tennessee: Only three specimens from two localities are available from Warren County, and the two from Cumberland Caverns (Figure 6*e*) are similar to those from Bear Cave, Grundy County, as would be expected, since both caves are close together in the head of the Caney Fork basin. The areolae are 4.7 and 4.8 times longer than broad, and constitute 39.0 and 41.8 percent of the carapace length. The single female from Turkey Scratch Cave (Figure 6*f*), however, has few, but more strongly developed, cervical spines; moreover, almost no trace of hepatic spines is evident. The areola is proportionately broader and shorter than in those specimens from Cumberland caverns—4.5 times longer than broad and constituting 37.5 percent of the carapace length. This specimen is morphologically and geographically intermediate between the other Warren County specimens and those from White County.

White County, Tennessee: White County is represented in collections from four localities (Figures

6*a-d*), in three of which the specimens possess very small rostral and cervical tubercles and the hepatic ones are obsolete. The areola ranges from 3.5 to 5.0 times longer than broad and comprises 36.9 to 39.8 (average 37.8) percent of the carapace length. Well-developed hooks are present on the third pair of pereiopods of the males, rudimentary ones occur on the fourth, and the first pleopod bears a small caudal process. In the single female from Ross Cave (Figure 6*b*), the rostral spines are long, as are the postorbitals, two cervicals, and one hepatic. The longitudinal elevation of the annulus ventralis is somewhat depressed.

Putnam County, Tennessee: With a single exception, the Putnam County populations typically have long rostra. This is reflected in the fact that, omitting two specimens, the areolae constitute from 35.7 to 38.5 percent (average 36.6) of the carapace length, and are 3.8 to 5.0 times longer than broad. In the two exceptions, one from Blind Fish Cave (Figure 5*t*) and the other from Johnson Saltpeter Cave (Figure 5*v*), the percentages are 39.6 and 39.3, respectively. Much greater variation is apparent in the relative development of the cervical and hepatic spines. In Bridge Creek (Figure 5*u*) and Johnson Saltpeter caves, they are characteristically small, as they are in a few specimens from Blind Fish Cave, but most of the latter have very long spines. Although all these caves are rather close together in the Calfkiller Valley and its tributaries, Blind Fish Cave differs markedly in the sort of habitat provided. The crayfish occur in a wide, deep, and slowly moving stream, rather than a small underground brook of the type found in the other caves. Conceivably the development of spininess is partly ecophenotypic, so that individuals from deep lakes and pools are likely to have longer spines than those from brook habitats. In the males, there are hooks on the third pereiopods, and in a few, rudiments on the fourth. In one second-form male, a hook is also present on one of the second pereiopods. The caudal process of the first pleopod may or may not be present.

Overton County, Tennessee: Only six specimens from two rather widely separated localities are available from Overton County (Figure 5*r, s*) in the Obey River drainage. These crayfish have very weak or obsolete postorbital and hepatic spines, and the cervical spines are reduced to 1 to 3 small tubercles. The areolae range from 3.7 to 4.9 times longer than broad and comprise 38.7 to 41.9 (average 40.1) percent of the carapace length. In the single first-form male, the hooks on the third pereiopods are well developed and very weak ones are present on the fourth; in the second-form males, there is no trace of them on the fourth. The first pleopods possess a minute caudal process, and, in the females, the longitudinal elevation of the annulus is somewhat depressed.

Fentress County, Tennessee: A single female from each of three caves (Figure 5*o, p, q*) are the only specimens available to us. Like the specimens from Overton County, they have very reduced spiny elements. The areola constitutes 40.2 to 42.7 percent of the carapace length, actually reflecting the short rostrum, and is 4.1 to 4.8 times longer than wide. The annulus ventralis also resembles that of specimens from Overton County.

Insofar as we have been able to determine, none of the variations indicated are clinal; rather, they occur in a mosaic pattern and, with few exceptions, most are encompassed in the range of variations observed in the comparatively large series of specimens from the type-locality. Were larger series available throughout the range of the subspecies, certain combinations of characters might prove to be preponderant in some local populations. The only somewhat distinctive ones recognized by us, however, are those from Jackson County, Alabama, with robust pereiopods, and those from White County, with long rostra.

Populations which are interpreted to represent intergrades between *O. australis packardi* and the nominate subspecies are discussed under the treatment of the former.

SIZE.—The largest specimen available is a second form male, collected in Burwell Cave, Madison County, Alabama, which has a carapace length of 48.0 mm. The largest first-form male (46.2 mm) was found in the same cave, and the smallest first-form male was collected in Wonder Cave, Grundy County, Tennessee (17.8 mm).

LIFE HISTORY NOTE.—First-form males have been found during every month of the year except January, and a lack of collections made during that month (only one specimen) is undoubtedly responsible for this gap. Our records fail to indicate a distinct preponderance of males of the first form during any season. Ovigerous females were taken in June, July, August, September, and November. William Torode (1968:152; 1969:16) reported that on 29 November 1968 he and members of his party, in exploring Canyon Cave, "found two female crayfish carrying eggs, one of which was collected for John Cooper. We watched the other one while little crayfish were crawling out of the eggs attached under the abdomen." The preserved specimen has 66 first-instar young and 14 eggs that had not hatched.

SEASONAL COLLECTIONS OF SPECIMENS EXAMINED

Sex	*Jan.*	*Feb.*	*Mar.*	*Apr.*	*May*	*June*	*July*	*Aug.*	*Sept.*	*Oct.*	*Nov.*	*Dec.*	*Not known*	*Total*
♂I	–	10	7	2	2	7	2	13	11	17	1	1	–	73
♂II	–	7	6	1	1	8	2	11	4	15	–	8	2	65
♀	1	5	4	–	4	8	8	26	6	18	2	8	4	94
juv. ♂	–	1	–	–	–	2	–	5	2	4	–	2	–	16
juv. ♀	–	–	–	–	–	4	3	6	1	7	–	3	–	24
ovig. ♀ ..	–	–	–	–	–	1	1	1	1	–	1	–	–	5
Totals	1	23	17	3	7	30	18	63	25	61	4	19	6	277

Orconectes australis packardi Rhoades

FIGURES 2, 4, 5*a–n*, 8*a–h*

Orconectes pellucidus packardi Rhoades, 1944:113, 115, 117, 118, 121–122, figs. 3a–f [Type-locality: Cumberland Crystal Cave (=Sloans Valley Cave) at Alpine, Pulaski County, Kentucky].—Hobbs, 1948a:16, 19, 21, figs. 8, 11. —Eberly, 1958:3.—Cole, 1959:81.—Eberly, 1960:30.—Hart and Hobbs, 1961:180.—Rhoades, 1962:65, 68, 79, 90.—Hart and Hart, 1966:8, 9.

Cambarus pellucidus.—Jillson, 1954:23.

Orconectes pellucidus.—Eberly, 1958:1–6 [in part].

Orconectes (Orconectes) pellucidus.—Hobbs, 1959:890 [in part].

Orconectes pellucidus packardii.—Nicholas, 1960:133.

Orconectes australis packardi.—Barr, 1967a:161, 190.

Orconectes.—Barr, 1968:85 [in part].

REVIEW OF LITERATURE.—*Orconectes australis packardi* was described by Rhoades (1944:121). His description, consisting of comparisons with *O. pellucidus* and *O. australis australis* together with six figures and measurements of the primary types, is quoted in full: "*O. pellucidus packardi* differs from *O. pellucidus pellucidus* by having a shorter acumen, smoother carapace, longer areola, more ovate antennal scale, and more strongly curved tips of the gonopod. *O. p. pellucidus* always has hooks on both the third and fourth walking legs but they are not always present on the fourth walking legs of *O. p. packardi.*

"*O. p. packardi* differs from *O. pellucidus australis* (Rhoades) (1941) in having a much shorter areola and thicker, longer tips on the gonopods. Also *O. p. australis* has hooks only on the third walking legs." He also assigned the subspecies of *O. pellucidus* to his new "Group rafinesquei." In addition to the type-locality, Rhoades listed a sight record for Eureka Cave, six miles west of Parker Lake, McCreary County, Kentucky.

Hobbs (1948a) presented a key to the species belonging to the Limosus Section of the genus *Orconectes,* depicted certain diagnostic features, and questioned the advisability of recognizing the subdivision of the Limosus Section into the Limosus and Rafinesquei groups as proposed by Rhoades (1944:113).

Jillson (1954) reported the presence of this crayfish in the type-locality.

Eberly (1958 and 1960), primarily concerned with competition between *O. inermis (*=his *O. pellucidus)* and *Cambarus laevis (*=*C. bartonii laevis),* presented speculations concerning the relationships and origins of the troglobitic members of the genus but presented no additional information concerning *O. australis packardi.*

Hobbs (1959), in his key to the crayfishes, referred to this subspecies as one of four of *Orconectes (O.) pellucidus* occurring between southern Indiana and northern Alabama.

Nicholas (1960) included this crayfish in his checklist of macroscopic troglobitic organisms of the United States and indicated that its range included "Caves of Pulaski Co., Kentucky."

Hart and Hobbs (1961) indicated that *Orconectes pellucidus packardi* serves as host for *Dactylocythere prionata (*=*Entocythere prionata)* which they described from Wind Cave, Pulaski County, Kentucky.

Rhoades (1962) presented a short diagnosis of this subspecies and offered a postulate concerning its origin, essentially assuming that it was derived by a "separation of a segment of *O. pellucidus* in the caves of southeastern Kentucky. . . ."

Hart and Hart (1966) cited three new locality records in reporting the hosts of the entocytherid *Sagittocythere barri* which were obtained from the national collection of crayfishes.

Barr (1967a) utilized the new combination *O. australis packardi,* anticipating the completion of the present study prior to that of his ecological treatment of Mammoth Cave. In 1968, he indicated that "Three or four separate colonizations are postulated to account for the known troglobitic species of *Orconectes* and their present distribution."

COMMENTS ON PREVIOUSLY RECORDED DATA.—As is obvious from the above summary of our previous knowledge of this subspecies, almost nothing was known about it, and the available descriptions and figures are brief and incomplete. Except for confusion that might arise from the statement that the areola of this subspecies is shorter than that of *O. a. australis,* Rhoades' list of differential characters are clear and concise. Whereas most populations of *O. a. australis* attain a greater length than *O. a. packardi,* and the absolute length of the areola is therefore greater, there is an overlap in the range of variation in respect to the ratio of the areola length to carapace length. Most members of *O. a. packardi,* however, exhibit a proportionately longer areola than do most *O. a. australis,* the former ranging from 37.1 to 43.8 percent, and the latter from 34.1 to 41.9 percent of the entire length of the carapace. As pointed out above, usually this difference is a reflection of rostral length rather than one in the length of the areola.

DIAGNOSIS.—Albinistic; eyes reduced and without pigment; rostrum with marginal spines or tubercles delimiting base of usually short acumen, margins converging, its upper surface concave and lacking median carina; postorbital ridges terminating cephalically in small spines or tubercles; hepatic area with or without small spiniform tubercles; at least one cervical spine or tubercle present, occasionally as many as five; areola 4.2 to 5.9 times longer than broad and constituting 37.1 to 43.8 percent of total length of carapace; mesial surface of palm of chela with several irregular rows of tubercles; well-developed hooks on ischiopodites of third pereiopods and small or rudimentary ones often on those of fourth. First pleopod of first-form male with length of greatest cephalocaudal diameter of pleopod less than twice that immediately proximal to base of central projection, and always terminating in two terminal elements, caudal process absent or extremely vestigial; broad, non-corneous mesial process directed somewhat caudally and distolaterally so that corneous central projection, extending distally only slightly beyond mesial process, almost completely visible in caudal aspect; cephalodistal margin with distinct angle at base of central projection. Annulus ventralis approximately 1.7 times broader than long, and as illustrated in Figure 4*k*.

Holotypic Male, Form I: Body (Figure 4*c, l*) subovate, depressed. Abdomen narrower than thorax (9.8 and 11.1 mm in widest parts, respectively). Width of carapace greater than depth in region of caudodorsal margin of cervical groove (11.1 and 9.2 mm). Areola broad (about 4 times longer than wide), with widely scattered minute punctations, only 3 or 4 across narrowest part. Cephalic section of carapace about 1.5 times as long as areola; length of areola 42.4 percent of length of carapace. Rostrum approximately 1.6 times as long as broad, excavate, and with acumen (although broken) slightly more than 3/5 as long as width of rostrum at base; cephalic extremity reaching almost to distal end of peduncle of antennule; margins not swollen, only slightly elevated, and with small corneous tubercles at base of acumen; upper surface with widely spaced minute setiferous punctations; subrostral ridges moderately strong and, in dorsal aspect, evident to almost midway between caudal margin of orbit and marginal tubercles.

Postorbital ridges rather weak, short, with shallow dorsolateral grooves, and terminating cephalically in minute tubercles. Suborbital angle lacking. Branchiostegal spines acute. Five or six small, spiniform cervical tubercles present on each side of carapace immediately caudal to cervical groove. Carapace punctate dorsally and granulate laterally; hepatic area with few very small acute tubercles but lacking spines. Abdomen longer than carapace (29.0 and 26.2 mm). Cephalic section of telson with 2 strong spines in each caudolateral corner, mesial ones movable.

Epistome (Figure 4*j*) broadly rounded cephalically, with prominent subacute cephalomedian extension, surface concave (dorsally), with crowded setae. Eyes much reduced, completely hidden beneath rostrum in dorsal aspect and extending cephalically slightly less than halfway between caudodorsal margin of orbit and marginal tubercles of rostrum. Antennules of usual form with prominent spine near distal end of ventral surface of basal segment. Antennae extending caudally almost to caudal margin of telson.

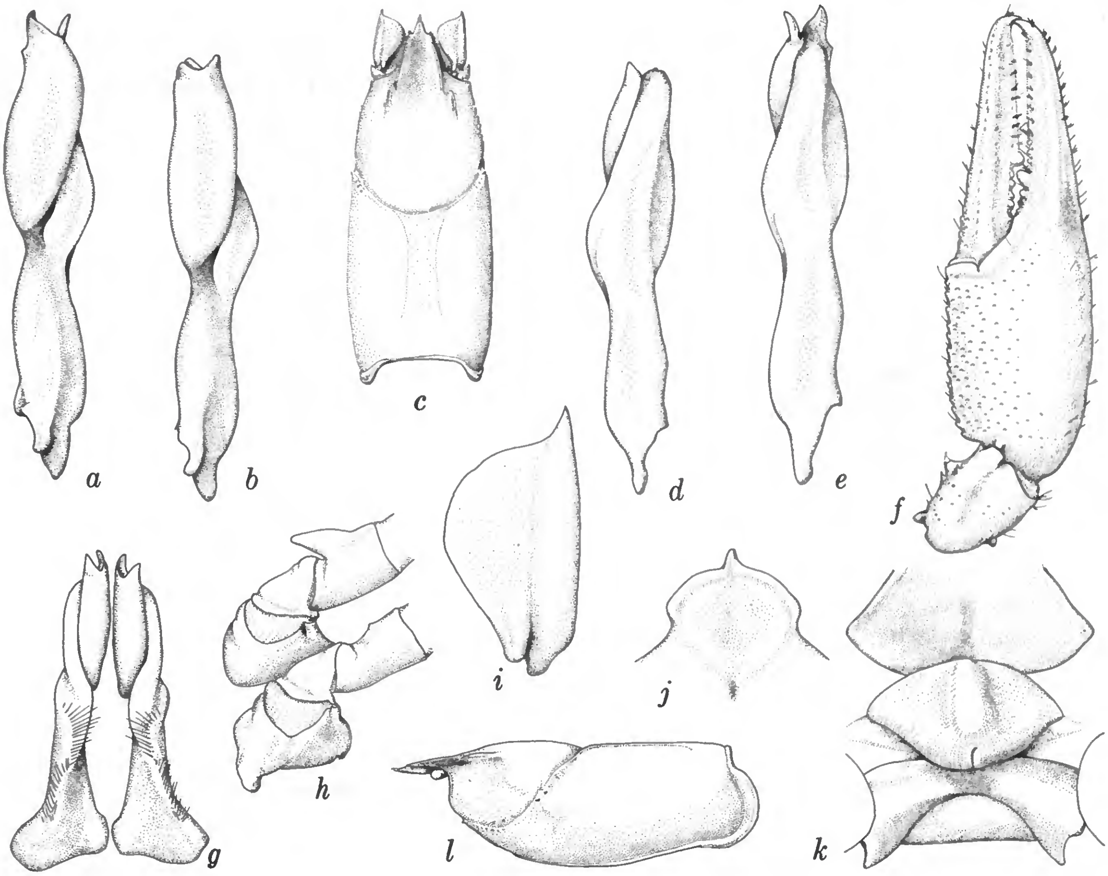


FIGURE 4.—*Orconectes australis packardi:* ***a***, mesial view of first pleopod of holotypic male, form I; *b*, mesial view of first pleopod of morphotypic male, form II; *c*, dorsal view of carapace of holotypic male, form I; *d*, lateral view of first pleopod of morphotypic male, form II; *e*, lateral view of first pleopod of holotypic male, form I; *f*, dorsal view of distal podomeres of cheliped of holotypic male, form I; *g*, caudal view of first pleopod of holotypic male, form I; *h*, basal podomeres of third and fourth pereiopods of holotypic male, form I; *i*, antennal scale of holotypic male, form I; *j*, epistome of holotypic male, form I; *k*, annulus ventralis and portion of sternum of allotype; *l*, lateral view of carapace of holotypic male, form I.

Antennal scale (Figure 4*i*) broadest near midlength, almost half as broad as long; outer thickened portion much narrower than lamellar area and terminating distally in prominent corneous-tipped spine. Third maxillipeds extending slightly beyond proximal end of distal segment of peduncle of antenna.

Chela (Figure 4*f*) moderately heavy and somewhat inflated; mesial margin of palm about 1.2 times longer than width of palm; dorsal surface of palmar area tuberculate mesially and proximally, otherwise punctate, both tubercles and punctations with fine setae; ventral surface of palm heavily tuberculate mesially and punctate laterally, and without spine at base of articulation with dactyl; tubercles along mesial portion of palm arranged in irregular longitudinal series, innermost row of about 14 tubercles. Fingers not gaping; dorsal and ventral surfaces of both with rounded longitudinal ridges flanked by setiferous punctations; opposable margin of immovable finger with row of 7 rounded corneous tubercles, fourth from base largest, and several minute ones continuing row distally; at lower level of same margin, large tubercle present just distal to seventh tubercle of upper row; several rows of minute denticles extending distally from seventh tubercle in upper row to corneous tip of finger; lateral margin of finger subcostate; opposable margin of dactyl with row of 16 tubercles, sixth from base largest, those beyond eighth exceedingly small; two or three rows of minute denticles extending distally from eighth tubercle to corneous tip of finger; mesial surface of dactyl with small tubercles proximally and punctations distally. Carpus longer than broad, with proximal two-thirds of mesial, dorsal, and lateral surfaces tuberculate; ventral surface tuberculate proximally and mesially, otherwise punctate; mesial surface with 3 prominent corneous-tipped spines, largest near midlength, another proximal to it, and third immediately ventral to largest; ventrodistal margin with prominent spine mesially and conspicuous tubercle laterally, latter articulating with socket on proximoventral surface of propodus. Merus mostly tuberculate except ventrolaterally; tubercles along entire dorsal surface generally increasing in size distally, but none corneous-tipped; ventrolateral margin with somewhat irregular row of 11 spikelike tubercles and ventromesial margin with approximately 12; scattered tubercles closely flanking both rows. Ischium with tubercles along outer and opposable margins, opposable margin with row of 7 flanked by additional ones.

Ischia of third pereiopods only (Figure 4*h*) with strong, simple, tapering hooks projecting proximally beyond distal margin of basis. Coxae of fourth pereiopods with caudomesially projecting prominences; coxae of fifth pereiopods without prominences except for small mesioventral projections at base of phallic papillae.

First pleopods (Figure 4*a, e, g*) symmetrical, barely reaching level of caudal margins of coxae of third pereiopods when abdomen is flexed, and shallowly situated in sternal groove; tip ending in two parts as described in Diagnosis.

Allotypic Female: Differs from holotype in following respects: tip of rostrum extending slightly beyond peduncle of antennule; cervical tubercles smaller; epistome, injured in previous instar, with distinct subangular emargination on cephalodextral border; chela with 10 tubercles along inner margin of palm, tubercles more conspicuous and more linearly arranged on dorsomesial surface of palm, ventral surface of palm less tuberculate, most setae on chela longer, single row of minute denticles along almost entire opposable margin of immovable finger interrupted by row of 18 very small corneous tubercles along proximal three-fourths, opposable margin of dactyl similar but with 21 small tubercles; carpus of cheliped with large mesial spine bifurcate; spine ventral to it not conspicuously larger than other adjacent ones. (See measurements.)

Annulus ventralis (Figure 4*k*) roughly subovate in outline, with high, longitudinal, median elevation devoid of shallow longitudinal trough; elevation highest (ventrally) along caudal half; subangular sinus low on midcaudal face.

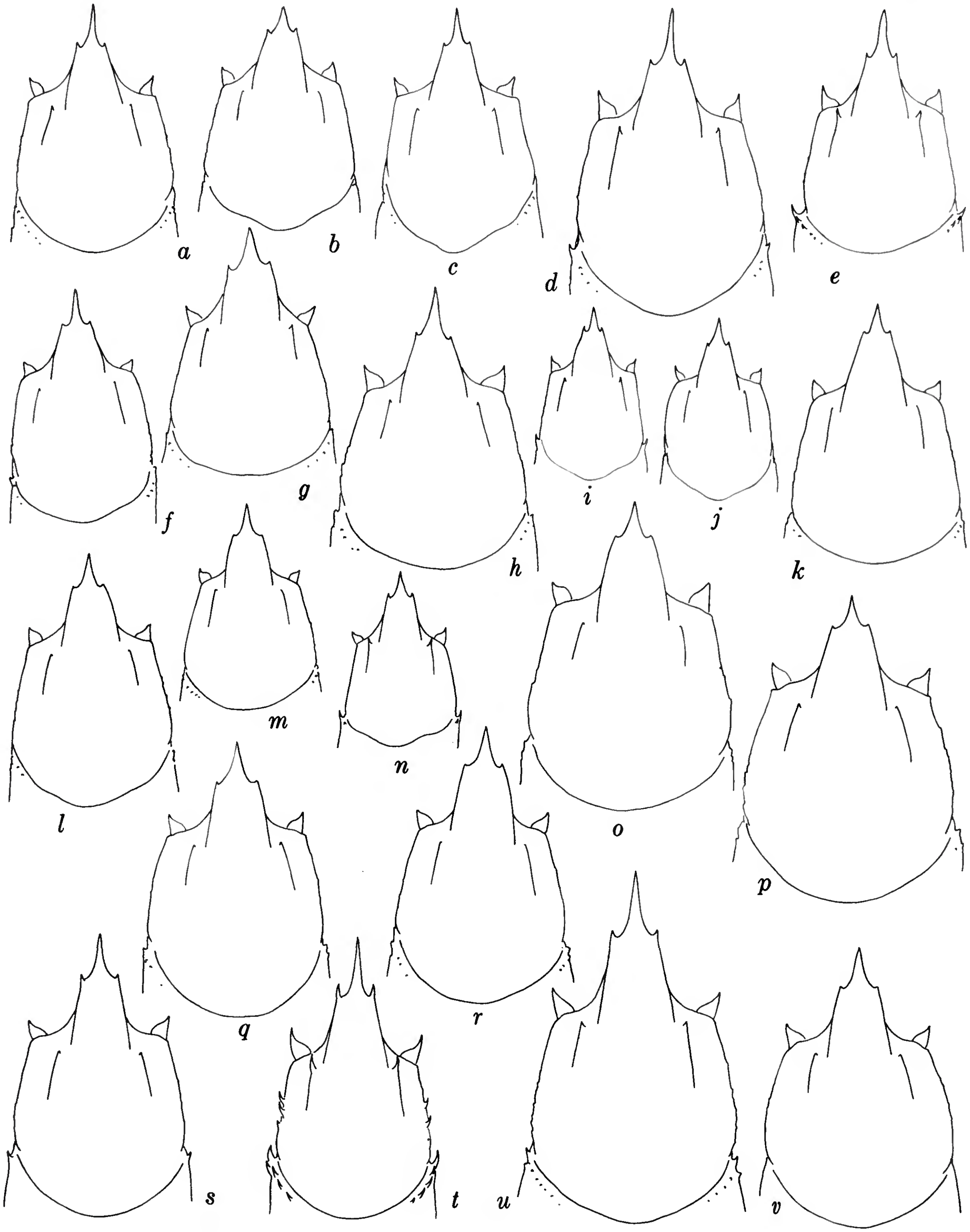
Morphotypic Male, Form II: Differs from holotype in following respects: rostral margins convex laterally; only single cervical tubercle present; cephalic section of telson with three spines in caudodextral corner; chela closely resembling that of allotype but much smaller and slenderer.

First pleopods (Figure 4*b, d*) essentially similar to that of holotype but terminal elements shorter with central projection more rounded and non-corneous; cephalic surface lacking angle at base of central projection.

MEASUREMENTS (in millimeters).—*Orconectes australis packardi*:

	Holotype	*Allotype*	*Morphotype*
Carapace:			
Height	9.2	10.5	7.8
Width	11.1	12.6	9.1
Length	26.2	30.0	22.3
Rostrum:			
Width	3.6	4.3	3.3
Length	5.7	7.4	5.7
Areola:			
Width	2.5	2.7	1.9
Length	11.1	12.4	9.4
Right Chela:			
Length of inner margin of palm	9.9	8.3	4.6
Width of palm	8.1	6.4	3.1
Length of outer margin of chela	25.5	24.0	14.9
Length of dactyl	14.1	14.0	8.2

TYPES.—Holotype, allotype, and morphotype, USNM 81310, 81312, 81331 (♂I, ♀, ♂II); Paratypes, Museum of Comparative Zoology, USNM, and collection of Rendell Rhoades.


a
b
c
d
e
f
g
h
i
j
k
l
m
n
o
p
q
r
s
t
u
v

TYPE-LOCALITY.—Cumberland Crystal Cave (Sloans Valley Cave) at Sloans Valley, Pulaski County, Kentucky.

SPECIMENS EXAMINED.—Specimens from Kentucky were examined as follows:

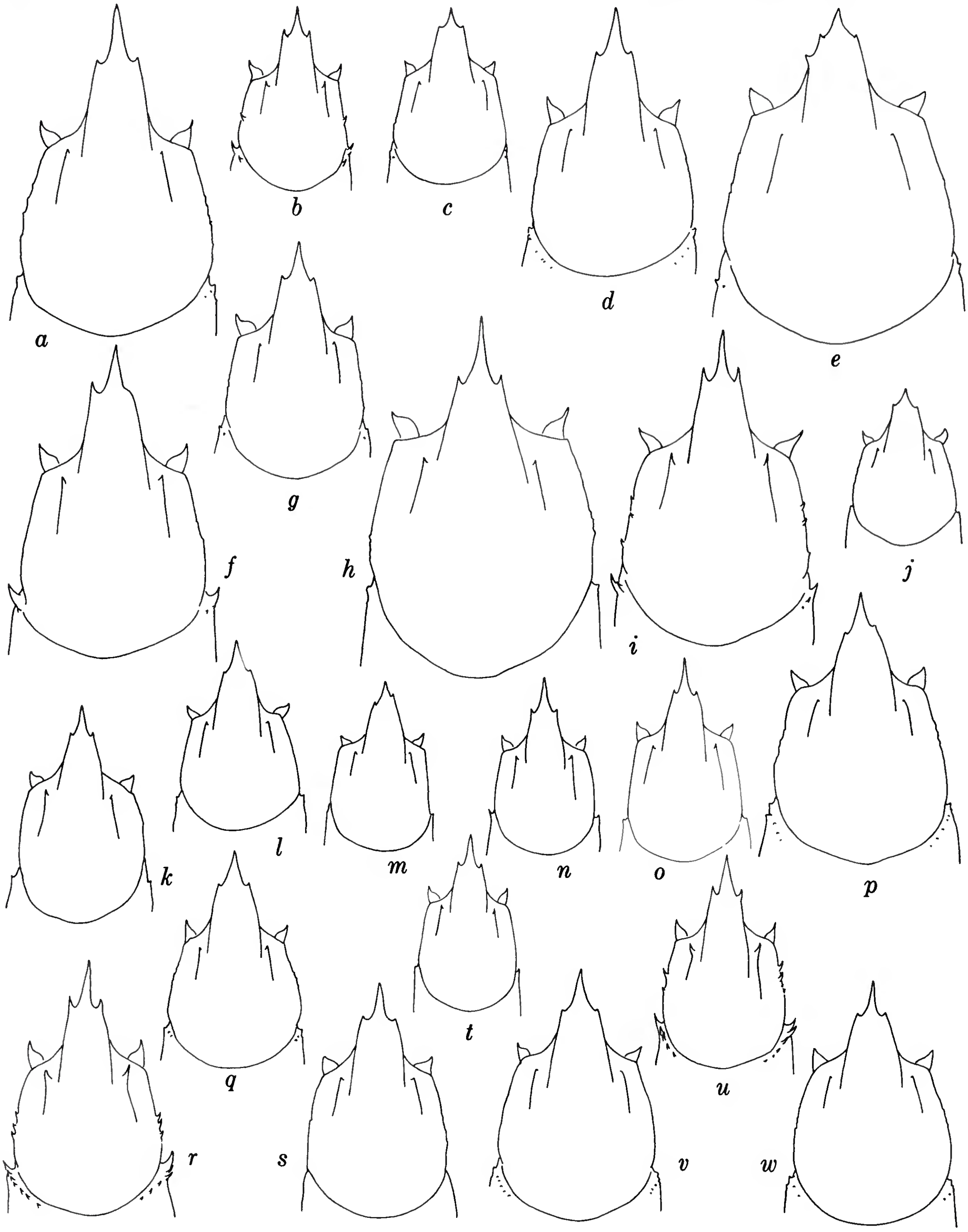
McCreary County: (1) Eureka Cave, 0.6 mile NNW of Nevelsville, 1♂I, 1♀, T.C.B., II/14/59. (2) Steele Hollow Cave, 1.7 miles WNW of Bell Farm, 1♂I, T.C.B. and Russell M. Norton, IX/26/64. *Pulaski County:* (1) type-locality, 1♂I, 1♀, G. H. Ehlers, X/8/41; 2♂II, G.H.E., date unknown; 1♂I, 1♀, R. Rhoades, X/7/41; 1♂II, 1♀, G.H.E., I/25/42; 2♂I, 1♂II, 1♀, T.C.B., VIII/9/63; 4♂I, 3♂II, 4♀, 1j♂, 1j♀, S.B.P., W. M. Andrews, and R.M.N., XI/5/64; 1♂I, R. Walker, J. Purcell, and C. Harrell, II/20/65. (2) Hydens Cave, 1.3 mi. NE of Blue John, about 6 miles from Sloans Valley, 2♂I, 2♂II, 3♀, T.C.B., S.B.P., and W.M.A., VI/10/64. (3) Old Kentucky Cave, 6 miles S of Somerset, 2♂I, 1♂II, 8♀, 1j♀, 1♀ with young, James R. Reddell and T.C.B., I/29/67; 1♂I, 1♂II, 2♀, 1j♂, Terrence G. Marsh, R.M.N., and L. Merkle, III/4/67. (4) Pourover Cave, 0.8 mile ENE of Colo in Happy Hollow, 4♀, T.C.B. and W.M.A., VI/2/65. (5) Wind Cave, 5.0 miles SE of Somerset, 1♀, T.C.B., XII/16/56; 2♂II, 1♀, T.C.B., IX/3/59; 1♂II, Jerry H. Carpenter and T.G.M., II/8/69. (6) Baker Cave, near Plato, 1♂I, David P. Beiter and T.G.M., III/2/68; numerous small specimens stranded on gravel after flood [sight record], T.C.B., II/1962. *Rockcastle County:* (1) Duvalt Cave, 3 miles SE of Mt. Vernon, near head of East Fork, 1♂II, 1♀, S.B.P., VIII/30/64. (2) Fletchers Spring Cave, 1.0 mile N of Sand Springs on Dry Fork, 2♂II, T.C.B. and R. A. Kuehne, VI/14/62; 1♂I, 1♀, T.G.M., II/20/68. (3) Pine Hill Cave, at Pine Hill on U.S. hwy. 25, 1♂I, S.B.P., IX/7/64; 4♀, J.R.R., IV/7/67; 1♂II, J. P. Voigt, IX/9/65; 1♀, L. G. Carr, date unknown. (4) Teamers Cave, 1.2 miles NE of Mullins, 1♀, T.C.B., V/11/63; 1♀, T.C.B., VI/18/63. *Wayne County:* (1) Blowing Cave, 0.75 mile SE of Sunnybrook at head of Carpenters Fork, 1♂I, T.G.M. and Andrew R. Boone, VIII/21/67; 2♀, R.A.K., VII/25/65. (2) Horse Hollow Cave, 0.75 mile NW of Parmleysville in Horse Hollow, 1♂II, 6♀, 1j♀, S.B.P., VII/15/64. (3) Kogers Cave, 2.0 miles N of Hidalgo on west side of Shearer Valley, 1♂I, T.C.B. and W.M.A., II/5/67; 1♂II, J.H.C. and T.G.M., VII/13/68. (4) Johnson Fork Cave, 0.4 mile E of Burfield on north side of Johnson Fork, 1♀, T.C.B., VII/10/64.

Two females of this species in the Muséum d'Histoire Naturelle in Genéve bear the label "grottee des montagnes de Cumberland"; paratypes are in the collection of the Museum of Comparative Zoology, Harvard University, and that of Rendell Rhoades. The latter paratypes have not been examined by us.

RANGE.—This subspecies seems to be confined to subterranean passages in the upper Cumberland drainage system in southeastern Kentucky. In the southernmost localities in the State and in those in the northern part of Tennessee, the characteristics indicate that *packardi* intergrades with the nominate subspecies.

A geographic parallel exists between the *australis australis–australis packardi* contact zone and the peripheral distribution of certain troglobitic beetles (Carabidae, Trechini) which one of us (Barr) is currently investigating. The comparatively large (6-7 mm), eyeless beetles of the genus *Nelsonites* Valentine (1952) occur in many of the same caves. *Nelsonites jonesi* Valentine and *Darlingtonea kentuckensis* Valentine occupy roughly the same range as *O. a. packardi* in the Kentucky Cumberland Plateau, extending a little farther north in the Kentucky River drainage into a few caves which *packardi* has not attained. *Nelsonites walteri* Valentine, on the other hand, occurs in Tennessee from Fentress to Van Buren County, thus coexisting with *O. a. australis* throughout the northern half of its range. The range of the large (7–8 mm) and very abundant *Darlingtonea kentuckensis* stops with a single Tennessee cave record just south of the Kentucky border. The Tennessee-Kentucky boundary is the approximate dividing line separating still other elements of the regional trechine fauna. To the north (Wayne, Clinton, and McCreary counties, Kentucky) are *Ameroduvalius jeanneli* Valentine and a series of undescribed species of the *robustus* and *pubescens* groups of *Pseudanophthalmus*

FIGURE 5.—*Orconectes australis packardi (a–n), O. australis australis (o–v),* and intergrades between them illustrating variation in spination: *a,* Duvalt Cave, Rockcastle Co., Ky. (♀); *b,* Teamers Cave, Rockcastle Co., Ky. (♀); *c,* Pine Hill Cave, Rockcastle Co., Ky. (♀); *d,e,* Cumberland Crystal Cave, Pulaski Co., Ky. (♂I, ♂II); *f,* Wind Cave, Pulaski Co., Ky. (♂II); *g,* Pourover Cave, Pulaski Co., Ky. (♀); *h,* Hydens Cave, Pulaski Co., Ky. (♂I); *i,* Eureka Cave, McCreary Co., Ky. (♂I); *j,* Steele Hollow Cave, McCreary Co., Ky. (♂I); *k,* Horse Hollow Cave, Wayne Co., Ky. (♀); *l,* Kogers Cave, Wayne Co., Ky. (♂I); *m,* Blowing Cave, Wayne Co., Ky. (♂I); *n,* Johnson Fork Cave, Wayne Co., Ky. (♀); *o,* Sells Cave, Fentress Co., Tenn. (♀); *p,* Wolf River Cave, Fentress Co., Tenn. (♀); *q,* Buffalo Cave, Fentress Co., Tenn. (♀); *r,* Raven Bluff Cave, Overton Co., Tenn. (♂II); *s,* Sheep Cave, Overton Co., Tenn. (♀); *t,* Blind Fish Cave, Putnam Co., Tenn. (♂I); *u,* Bridge Creek Cave, Putnam Co., Tenn. (♂I); *v,* Johnson Saltpeter Cave, Putnam Co., Tenn. (♂I).


a
b
c
d
e
f
g
h
i
j
k
l
m
n
o
p
q
r
s
t
u
v
w

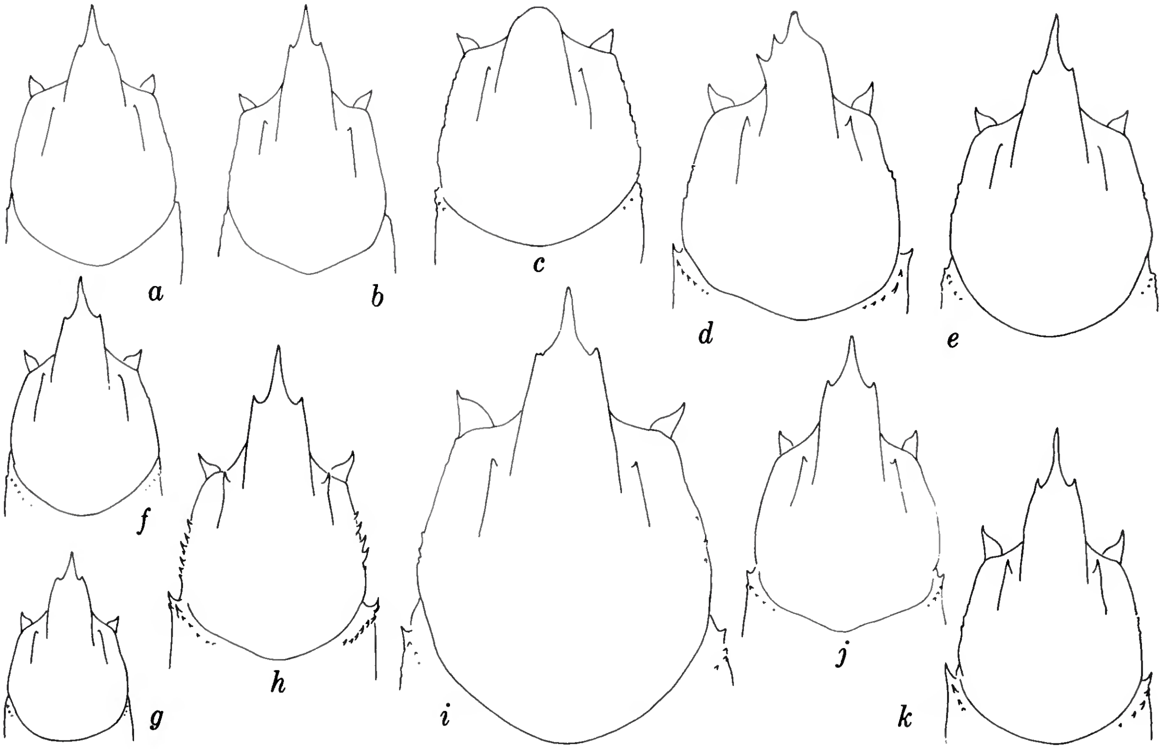
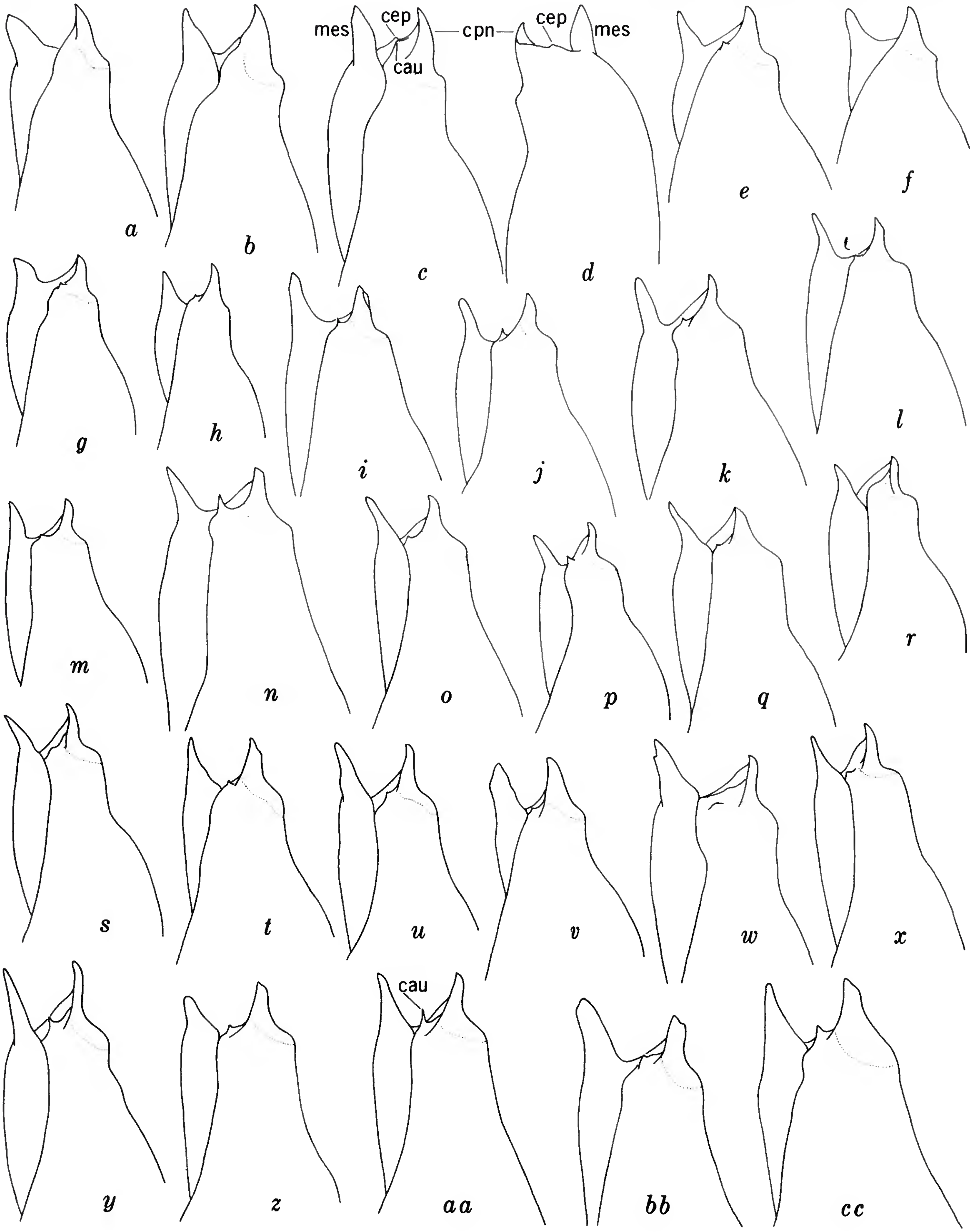


FIGURE 7.—Cephalic portion of carapace of *Orconectes australis australis* illustrating variation in spination (all localities in Alabama): *a,* Paint Rock Cave, Jackson Co. (♀); *b,* Kennamer Cave, Jackson Co. (♀); *c,* Doodlebug Hole, Jackson Co. (♂I); *d,* Big Springs Cave, Madison Co. (♀); *e,* Aladdin Cave, Madison Co. (♀); *f,* Sadler Spring Cave, Madison Co. (♂II); *g,* Fuqua Spring Cave, Madison Co. (♀); *h,* Cold Spring Cave, Madison Co. (♂II); *i,* Burwell Cave, Madison Co. (♂I); *j,* Shelta Cave, Madison Co. (♂II); *k,* Byrd Spring Cave, Madison Co. (♀).

FIGURE 6.—*Orconectes australis australis,* illustrating variation in spination: *a,* Wildcat Cove Cave, White Co., Tenn. (♀); *b,* Ross Cave, White Co., Tenn. (♀); *c,* Indian Cave, White Co., Tenn. (♀); *d,* Ward Cave, White Co., Tenn. (♂I); *e,* Cumberland Caverns, Warren Co., Tenn. (♀); *f,* Turkey Scratch Cave, Warren Co., Tenn. (♀); *g,* Bear Cave, Grundy Co., Tenn. (♂I); *h,* Big Mouth Cave, Grundy Co., Tenn. (♂I); *i,* Wonder Cave, Grundy Co., Tenn. (♂I); *j,* Wet Cave, Franklin Co., Tenn. (♂II); *k,* Walker Spring Cave, Franklin Co., Tenn. (♂II); *l,* Wet Cave, Franklin Co., Tenn. (♂II); *m,* Partin Springs Cave, Franklin Co., Tenn. (♂II); *n,* Caroline Cove Spring, Franklin Co., Tenn. (♂I); *o,* Limrock Blowing Cave, Jackson Co., Ala. (♀); *p,* Fern Cave, Jackson Co., Ala. (♂I); *q,* Doug Green Cave, Jackson Co., Ala. (♀); *r,* Sauta Cave, Jackson Co., Ala. (♂I); *s,* McFarland Cave, Jackson Co., Ala. (♂I); *t,* Salt River Cave, Jackson Co., Ala. (♀); *u,* Guess Creek Cave, Jackson Co., Ala. (♂I); *v,* Jess Elliott Cave, Jackson Co., Ala. (♀); *w,* Saltpeter Cave, Jackson Co., Ala. (♂I).

(T. Barr, manuscript in preparation). To the south (Overton, Fentress, and Pickett counties, Tennessee) are *Pseudanophthalmus beaklei* Valentine, *P. valentinei* Jeannel, and one or more species of the *intermedius* group of *Pseudanophthalmus.* This general zoogeographic phenomenon is thus expressed in two very different groups of troglobitic arthropods. No extrinsic barrier is postulated as the cause, since the various trechine ranges show slight overlap and our interpretation of *australis* s. str. and *packardi* as geographic races of polytypic *australis* implies at least a limited amount of gene flow.

VARIATIONS.—In Wayne County, the single female specimen from Johnson Fork Cave (Figure 5*n*) has two strong cervical spines, and the acumen of the rostrum is distinctly longer than that of those speci-


mes
cep
cau
cpn
cep
mes
a
b
c
d
e
f
g
h
i
j
k
l
m
n
o
p
q
r
s
t
u
v
w
x
y
z
cau
aa
bb
cc

mens from the other two localities. In a number of respects, including the extreme development of spines, the slender cheliped with longer fingers, and the short areola, it resembles specimens from Eureka Cave, McCreary County.

A single small first-form male from Blowing Cave (Figure 5*m*), except for a reduction in the sizes of the cervical and hepatic tubercles, seems fairly typical of the subspecies. The first pleopod has a slight prominence in the area on which the caudal process is so well developed in *O. a. australis*.

The populations in Horse Hollow (Figure 5*k*) and Kogers (Figure 5*l*) caves are quite similar, having most spines on the carapace reduced to tubercles and possessing weak marginal spines on the rostrum. The single first-form male has hooks on both the third and fourth pereiopods, and the first pleopod has a rounded shoulder on the cephalic surface and a very small caudal process (Figure 8*e*).

Among the specimens from McCreary County, all are small, the rostrum is short with convergent margins, and the cervical and hepatic spines are strongly developed in the two from Eureka Cave (Figure 5*i*) but practically obsolete in that from Steele Hollow Cave (Figure 5*j*). The areola is proportionately shorter in these two localities (constituting 37.1 to 38.4 percent of the total length of the carapace) than in any other known for the subspecies except the one specimen from nearby Johnson Fork Cave (Figure 5*n*), Wayne County (37.6 percent). The merus of the cheliped bears unusually long spines in the Eureka Cave specimens, and hooks are present only on the ischia of the third pair of pereiopods. Eureka Cave is seasonally inundated by waters of Lake Cumberland, an impoundment of the Cumberland River, and the long spines may be related to the deep quiet pools in which these individuals live.

In specimens from the type-locality (Figure 5*d, e*), the rostrum is usually short, with an acumen of variable length; a few small hepatic spines are generally apparent. The length of the areola ranges from 38.5 to 43.1 percent of the entire length of the carapace. The spines on the merus of the cheliped are usually well developed, but never so long as in specimens from Eureka Cave, and small or rudimentary hooks are more frequently present on the ischiopodites of the fourth pereiopod than not.

Among other specimens from Pulaski County, those from Old Kentucky Cave possess hooks on both the third and fourth pereiopods but cervical and hepatic spines are reduced to rounded tubercles. Those specimens from other caves in the county exhibit hardly more variations than are noted among individuals from the type-locality, except those from Pourover (Figure 5*g*), Hydens (Figure 5*h*), and Baker caves have fewer spines on the carapace, and have areolae that constitute no less than 40.3 percent of the carapace length. In one male from the latter locality, the major spine on the mesial surface of the carpus of the chela has four corneous tips, and on that of the other male there are three. The latter male possesses an accessory "projection" (Figure 8*c, d*) on the mesiodistal surfaces of both first pleopods that could be interpreted as a vestigial "cephalic process," but comparable prominences are lacking in the pleopods of the other male.

The two first-form males from Rockcastle County have hooks only on the third pereiopod. In most of the specimens, the cervical and hepatic spines are reduced both in number and size; in some, only a single small cervical spine is evident, and the female from Teamers Cave has only a vestige of a cervical spine. The four specimens from Duvalt (Figure 5*a*)

FIGURE 8.—(Abbreviations: cau, caudal process; cep, cephalic process; cpn, central projection; mes, mesial process.) Distal portions of first left pleopods of males, form I, of *Orconectes australis packardi (a–d), Orconectes australis australis (i–cc),* and intergrades *(e–h)* to show variation in the terminal elements. Orientation of all figures except *d,* which is a mesial view, are primarily caudolateral aspects, slightly altered to illustrate best the caudal process (clearly evident in Figure *aa*): *a,* Pine Hill Cave, Rockcastle Co., Ky.; *b,* Cumberland Crystal Cave, Pulaski Co., Ky.; *c,d,* Hydens Cave, Pulaski Co., Ky.; *e,* Kogers Cave, Wayne Co., Ky; *f,* Blowing Cave, Wayne Co., Ky.; *g,* Steele Hollow Cave, McCreary Co., Ky.; *h,* Eureka Cave, McCreary Co., Ky.; *i,* Raven Bluff Cave, Overton Co., Tenn.; *j,* Blind Fish Cave, Putnam Co., Tenn.; *k,* Bridge Creek Cave, Putnam Co., Tenn.; *l,* Johnson Saltpeter Cave, Putnam Co., Tenn.; *m,* Wards Cave, White Co., Tenn.; *n,* Cumberland Caverns, Warren Co., Tenn; *o,* Wonder Cave, Grundy Co., Tenn.; *p,* Bear Cave, Grundy Co., Tenn.; *q,* Big Mouth Cave, Grundy Co., Tenn.; *r,* Caroline Cove Cave, Franklin Co., Tenn.; *s,* McFarland Cave, Jackson Co., Ala.; *t,* Saltpeter Cave, Jackson Co., Ala.; *u,* Limrock Blowing Cave, Jackson Co., Ala.; *v,* Guess Creek Cave, Jackson Co., Ala.; *w,* Doodlebug Hole, Jackson Co., Ala.; *x,* Jess Elliott Cave, Jackson Co., Ala.; *y,* Fern Cave, Jackson Co., Ala.; *z,* Hering Cave, Madison Co., Ala.; *aa,* Shelta Cave, Madison Co., Ala.; *bb,* Matthews Cave, Madison Co., Ala.; *cc,* Burwell Cave, Madison Co., Ala.

and Teamers (Figure 5*b*) caves have proportionately longer areolae (40.5 to 43.7 percent) than do three of the four from Pine Hill (Figure 5*c*) and Fletcher Spring caves.

In the apparent absence of clines, and so few specimens from the assumed area of intergradation, our evidence for the admixture of the gene pools of these two taxa are limited; the continuity of the karst belt occupied by them, however, enhances the supposition that the two represent geographic races of a single species.

SIZE.—The largest specimen available is a female possessing a carapace length of 33.3 mm. This crayfish was collected from Pourover Cave, Pulaski County, Kentucky. The largest first-form male (28.0 mm) was found in Hydens Cave, Pulaski County, and the smallest (13.8 mm), in Baker Cave, Pulaski County.

LIFE HISTORY NOTES.—First-form males have been collected in January, February, March, June, August, September, and October. No ovigerous females have been found, but a single female carrying young was taken in Old Kentucky Cave on 29 January 1967.

SEASONAL COLLECTIONS OF SPECIMENS EXAMINED

Sex	*Jan.*	*Feb.*	*Mar.*	*Apr.*	*May*	*June*	*July*	*Aug.*	*Sept.*	*Oct.*	*Nov.*	*Dec.*	*Not known*	*Total*
♂ I	2	4	2	–	–	2	–	3	6	2	–	–	–	21
♂ II	2	2	1	–	–	4	2	2	4	2	–	–	3	22
♀	9	1	2	4	1	8	9	2	5	–	–	1	–	42
juv. ♂	–	–	1	–	–	–	–	–	1	–	–	–	–	2
juv. ♀	1	–	–	–	–	–	1	–	1	–	–	–	–	3
♀ with young	1	–	–	–	–	–	–	–	–	–	–	–	–	1
Totals	15	7	6	4	1	14	12	7	17	4	–	1	3	91

Orconectes incomptus, new species

FIGURES 2 and 9

Orconectes pellucidus australis.—Hart and Hobbs, 1961:176 [not Rhoades 1941].

Orconectes pellucidus pellucidus.—Hart and Hart, 1966:9 [not Tellkampf 1844a].

DIAGNOSIS.—Albinistic; eyes reduced and without pigment; rostrum devoid of marginal spines or tubercles delimiting base of acumen, margins converging, its upper surface weakly concave and lacking median carina; postorbital ridges terminating cephalically, with or without small tubercles; hepatic area without spiniform tubercles; three or four small cervical tubercles present; areola 4.1 to 5.2 times longer than broad and constituting 39.6 to 43.0 percent of total length of carapace; chelae conspicuously inflated and setose; mesial surface of palm of chela with several irregular rows of tubercles; well-developed hooks on ischiopodites of third pereiopods only. First pleopod of first-form male with length of greatest cephalocaudal diameter of pleopod less than twice that immediately proximal to base of central projection, and terminating in three elements; short, broad, somewhat flattened mesial process directed caudodistad and partially obscuring central projection in caudal aspect; corneous central projection directed laterad; minute caudal process situated between mesial process and central projection; cephalodistal margin with rounded prominence at base of central projection. Annulus ventralis approximately 1.4 times broader than long and as illustrated in Figure 9*k*.

Holotypic Male, Form I: Body (Figures 9*c, l*) subovate, depressed. Abdomen narrower than thorax (8.9 and 9.9 mm in widest parts, respectively). Width of carapace greater than depth in region of caudodorsal margin of cervical groove (9.9 and 7.5 mm). Areola broad (4.6 times longer than wide) with scattered punctations, 4 or 5 across narrowest part. Cephalic section of carapace 1.5 times as long as areola. Length of areola 39.6 percent of length of carapace. Rostrum approximately 1.5 times as long as broad, shallowly excavate, and with acumen, although indistinctly set off at base, 1.5 times longer than width of rostrum at base; cephalic extremity reaching almost to distal end of peduncle of antennule; margins converging, not swollen, only slightly elevated, and devoid of spines or tubercles; upper surface with setiferous punctations; subrostral ridges moderately well defined and evident, in dorsal aspect, from caudal margin of orbit to almost half distance to base of acumen.

Postorbital ridges moderately well developed, grooved dorsolaterally, and terminating cephalically, one bluntly and other in minute corneous tubercle. Suborbital angle lacking. Branchiostegal spine small and acute. Four small cervical tubercles present on each side of carapace immediately caudal to cervical groove. Carapace punctate dorsally and granulate laterally; hepatic area with number of small tubercles but lacking spines. Abdomen shorter than carapace (21.7 and 22.2 mm). Cephalic section of telson with 2 strong spines in each caudolateral corner, mesial ones movable.

Epistome (Figure 9*j*) broadly rounded cephalically, with prominent cephalomedian extension and with cephalosinistral margin slightly undulate. Surface subplane and without setae. Eyes much reduced, not completely hidden beneath rostrum in dorsal aspect and extending cephalically about halfway between caudodorsal margin of orbit and base of acumen. Antennules of the usual form, with prominent spine on ventral surface distal to midlength of basal segment. Antennae extending caudally beyond telson. Antennal scale (Figure 9*i*) broadest distal to midlength and almost half as broad as long; outer thickened portion much narrower than lamellar area and terminating distally in prominent spine. Third maxillipeds extending almost to midlength of distal segment of peduncle of antenna. Chela (only left one present, and it regenerated) with palm inflated and finger long and comparatively heavy; mesial margin of palm approximately 1.2 times longer than width of palm; dorsal surface of palm tuberculate mesially, otherwise punctate; both tubercles and punctations with fine setae; ventral surface with tubercles proximomesially, otherwise punctate; most punctations and tubercles bearing conspicuously long setae; spine lacking from surface opposite base of dactyl; tubercles along mesial portion of palm sublinearly arranged, innermost row consisting of about 8 tubercles; lateral margin of palm subserrate, with 8 emarginations. Fingers not gaping; dorsal and ventral surfaces with poorly defined longitudinal ridges flanked by punctations bearing long setae; opposable margin of immovable finger with row of 9 small tubercles along proximal third and with 2 somewhat larger ones distal to and below row; crowded minute denticles present between tubercles and extending distally to base of corneous tip of finger; lateral margin of finger costate, grooved, and bearing setiferous punctations; opposable margin of dactyl with row of approximately 13 small tubercles along proximal half, with crowded minute denticles between tubercles and extending to corneous extremity of finger; setal tufts on both fingers conspicuously long. Carpus longer than broad, with mesial surface bearing one prominent spine and several tubercles, one of which spiniform; tubercles extending onto dorsomesial and ventromesial surfaces, otherwise punctate; ventrodistal margin with prominent spine mesially and another on boss articulating with ventral socket of propodus. Merus tuberculate dorsally and bearing two rows of spiniform tubercles ventrally, outer row consisting of 9 and inner of 15; additional small tubercles flanking both rows. Ischium with several tubercles along opposable margin but not arranged in discreet row.

Ischia of third pereiopods (Figure 9*h*) with strong, simple hooks; hooks not extending proximal to distal margin of basis. Ischia of fourth pereiopods without hooks. Coxae of fourth pereiopods swollen caudomesially but lacking prominent caudomesially projecting prominences. Coxae of fifth pereiopods with small mesially projecting prominences along cephaloventral base of phallic papilla.

First pleopods (Figures 9*a, e, g*) symmetrical, reaching coxae of third pereiopods when abdomen is flexed, and shallowly situated in sternal groove. Tip ending in three parts as described in diagnosis.

Allotypic Female: Differs from holotype in following respects: margins of rostrum with distinct interruptions at base of acumen; subrostral ridges visible in dorsal aspect for only a short distance cephalic to caudal margin of orbit; postorbital ridges ending cephalically without spines or tubercles; cervical tubercles extremely small and hepatic tubercles almost obsolete; abdomen distinctly longer than carapace (23.4 and 22.2 mm); epistome with cephalolateral angles and ventral surface bearing setae; antennae extending caudad almost to end of telson; chela with mesial row of 10 tubercles along margin of palm; ventral surface of palm with small tubercle at base of articulation with dactyl; opposable margin of immovable finger with row of 7 tubercles (fourth from base largest) along proximal two-thirds and large one below row at base of distal two-fifths, between sixth and seventh tubercles; opposable margin of dactyl with row of 4 tubercles along proximal

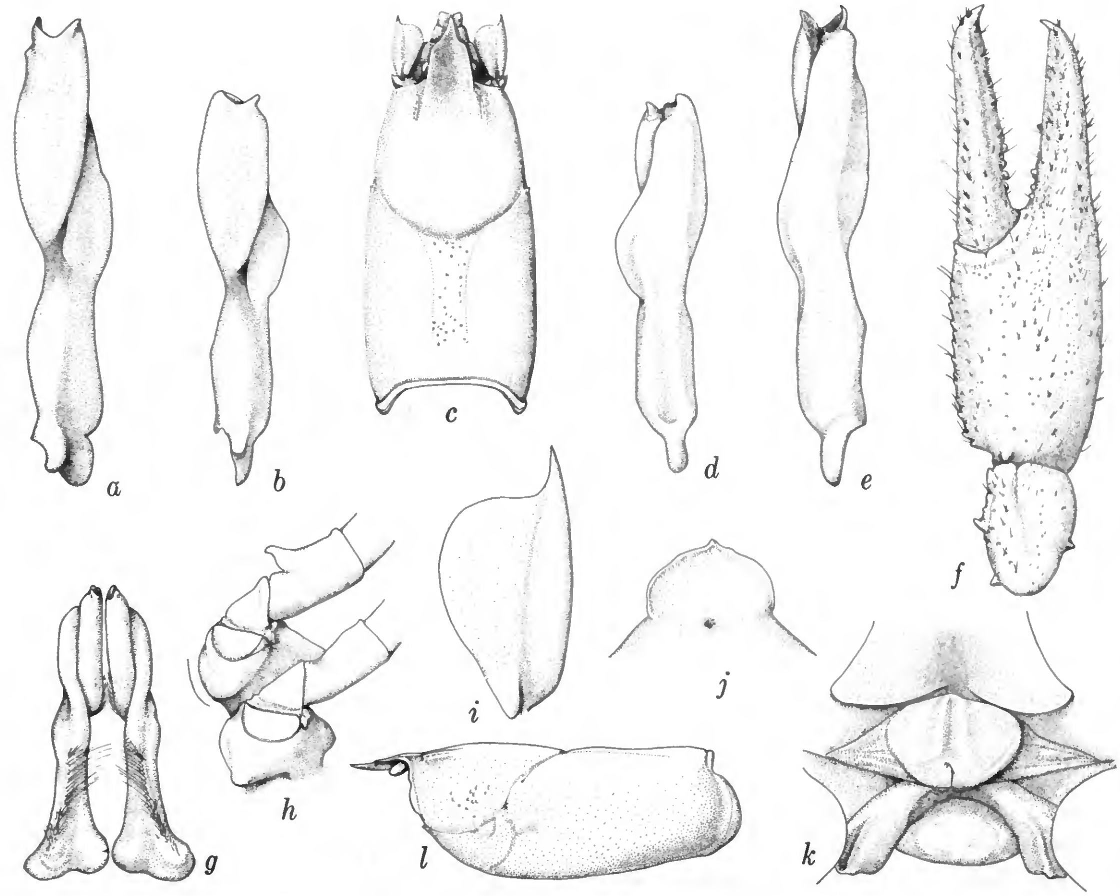


FIGURE 9.—*Orconectes incomptus:* *a,* mesial view of the first pleopod of holotypic male, form I; *b,* mesial view of first pleopod of morphotypic male, form II; *c,* dorsal view of carapace of holotypic male, form I; *d,* lateral view of first pleopod of morphotypic male, form II; *e,* lateral view of first pleopod of holotypic male, form I; *f,* dorsal view of distal podomeres of cheliped of morphotypic male, form II; *g,* caudal view of first pleopods of holotypic male, form I; *h,* basal podomeres of third and fourth pereiopods of holotypic male, form I; *i,* antennal scale of holotypic male, form I; *j,* epistome of holotypic male, form I; *k,* annulus ventralis and portion of sternum of allotypic female; *l,* lateral view of carapace of holotypic male, form I.

two-fifths; ventral surface of merus with two rows of 9 tubercles.

Annulus ventralis (Figure 9*k*) subovate, with median longitudinal elevation somewhat depressed and terrace-like caudal shelf, so obvious in *O. australis australis,* not delimited from general curvature; median longitudinal trough broad and shallow; cephalic end of sinus originating slightly dextral to median line, forming arc to median line and continuing caudally, ending on caudal margin of annulus.

Morphotypic Male, Form II: Differs from holotype in following respects: subrostral ridges scarcely visible in dorsal aspect; postorbital ridges very weak and terminating bluntly; cervical tubercles much reduced and hepatic tubercles almost obsolete; epistome more similar to that of allotype, with cephalolateral angle; antennae barely reaching cephalic margin of telson; right chela (Figure 9*f*) with mesial half of upper surface of palm tuberculate (11 in mesial row), otherwise punctate, lower surface of palm with tubercle at base of dactyl, outer margin of palm not serrate, opposable margin of fixed finger with row of 8 tubercles (fourth from base largest) along proximal two-thirds of finger and with single large tubercle below row near midlength of finger, opposable margin of dactyl with 9 tubercles (fourth from base largest) along proximal four-fifths of finger; ventral surface of merus of cheliped with mesial row of 8 tubercles and lateral one of 12; hooks on ischia of third pereiopods strong but not quite so well developed as in holotype, absent from fourth pereiopods; caudomesial prominences on coxae of fourth pereiopods and prominences on those of fifth obsolete.

First pleopod (Figure 9*b, d*) lacking trace of caudal process but with short tuberculiform mesial process and broad, prominent central projection; neither element corneous.

Type-locality.—Cherry Cave, lat. 36°28′09″N., long. 85°36′28″W, Jackson County, Tennessee. A description of the cave is presented in Barr, 1961: 272–273.

Measurements (in millimeters).—*Orconectes incomptus:*

	Holotype	*Allotype*	*Morphotype*
Carapace:			
Height	7.5	7.4	6.5
Width	9.9	9.5	9.1
Length	22.2	22.4	20.6
Rostrum:			
Width	3.2	3.4	3.2
Length	4.8	3.5	5.1
Areola:			
Width	1.9	2.3	1.9
Length	8.8	9.4	8.3
Chela:			
Length of inner margin of palm	6.2	7.6	7.4
Width of palm	5.2	6.4	6.6
Length of outer margin of chela	16.5	18.2	17.0
Length of dactyl	10.2	9.6	9.1

Disposition of types.—Holotype, allotype, and morphotype, USNM 130299, 130300, and 130301 (♂I, ♀, ♂II). Of the paratypes, 1 male, form II, and 1 ♀ are in the collection of H. H. Hobbs III; 6 males, form II, and 8 females are in the Smithsonian Institution.

Specimens examined.—Specimens from Tennessee were examined as follows:

Jackson County: (1) type-locality, 1♂I, T.C.B., VIII/8/59. (2) Carter Cave, lat. 36°16′53″N, long. 85°44′10″W, 1♂II, T.C.B., VI/9/55; 1♀, T.C.B., IX/1959; 5♂II, 6♀, J.E.C. and M.R.C., IX/21/68; 2♂II, 2♀, H.H.H. III, III/31/70. (3) Haile Cave, lat. 36°20′00″N, long. 85°43′08″W, 1♀, T.C.B., V/6/59.

See Barr, 1961, for detailed locations and descriptions of these caves.

Variations.—The range of variation among the available specimens is negligible, and the differences pointed out in the accounts of the primary types seem adequately to encompass those of any significance.

Relationships.—Although *Orconectes incomptus* has very close affinities with *O. a. australis* and *O. a. packardi,* we have no indication that intergrades exist between it and either of the subspecies of *australis.* Inasmuch as the differences between *incomptus* and *australis* are so similar to those that distinguish *O. i. inermis* from *O. i. testii,* we are tempted to treat *incomptus* as a subspecies of *O. australis.* Despite this similarity, there exists what we consider to be an important difference in that there is abundant evidence of intergradation between the southern *inermis* and the northern *testii.* In view of available data, it seems most improbable that the subterranean passages in Mississippian limestones on the eastern edge of the Cumberland Plateau (the range of *australis*) communicate with those of Ordovician limestones at the base of the Eastern Highland Rim (the range of *incomptus*), and if such connections do not exist, then it is highly unlikely that intergrades between the two might be found. The fact that the epizootic *Dactylocythere ungulata* Hart and Hobbs, the only entocytherid ostracod known to infest *O. incomptus,* occurs on both *australis* and *incomptus* does not necessitate the conclusion that such underground connections are present, for the same ostracod also occurs on *Cambarus tenebrosus* Hay which ranges from the Nashville Basin eastward to the Tennessee Valley, and it could have been responsible for transporting this ostracod via an epigean environment into the two subterranean systems.

Size.—The largest specimen available is a female having a carapace length of 24.5 mm. The only first-form male that we have seen is the holotype, in which the carapace length is 22.2 mm.

Life history notes.—The single first form male was collected on August 9; no ovigerous females or females with young have been observed.

Remarks.—The two bibliographic citations listed are based upon a tentative determination made by the senior author, Hobbs, prior to a thorough study of the crayfishes utilized in the current study. Hart and Hart (1966:9) misinterpreted the identity of the crayfish cited by Hart and Hobbs (1961:176) as occurring in Carter Cave, Jackson County, Tennessee. Thus, *O. incomptus* should be included among the hosts to the entocytherid ostracod, *Sagittocythere barri.*

Orconectes inermis inermis Cope

FIGURES 1, 10, 12*c–z,* 13

Astacus pellucidus.—Cope, 1871a:4.—Cope 1871b:368; 1872c:297.

Orconectes inermis Cope, 1872a:409, 410, 419, 420, fig. 116 [type-locality, Wyandotte Cave, Crawford County, Indiana].—Cope, 1872b:161, 162, 173, 174, fig. 116.—Hagen, 1872:495.—Packard, 1873:94.—Faxon, 1884: 139; 1885a:40, 42–43.—Underwood, 1886:371.—Packard, 1888:39.—Sloan, 1888:[3 letters to Packard; see Packard, 1888:15–16].—Lönnberg, 1894:126.—Lönnberg, 1895:4, 5.—Hay, 1896:484–485.—Blatchley, 1897:171.—Hay, 1897:208.—Faxon, 1914:415.—Hobbs, 1942a:335, 350, 352, 354, 355, fig. 12; 1948a:16, 19, 20, figs. 10, 14.—Eberly, 1955:281, 282.—Holthuis, 1956:113, 116.—Crocker, 957:13.—Eberly, 1958:3.—Rhoades, 1959:399, 400, 401.—Eberly, 1960:30.—Creaser, 1962:2, 3.—Rhoades, 1962:65.—Fitzpatrick, 1963:60.—Barr, 1967a: 186; 1967b: 481.—Fitzpatrick, 1967:141, 142.—Poulson and White, 1969:974, 975.

Cambarus pellucidus.—Packard, 1872a:30; 1873:94 [in part].—Smith, 1873:639 [in part].—Collett, 1874:305.—Smith, 1875:477 [in part].—Faxon, 1884:139 [in part]; 1885a:42, 158, 168 [in part].—Sloan, 1888:15, 39–41, 82 [in part].—Packard, 1888:15, 16, 19, 39, 40, 41, 42, 82, 86, 118, 119, 122, 123 [in part].—Faxon, 1890:621, 626, 628 [in part].—Packard, 1890:393.—Hay, 1891:147, 148.—Ortmann, 1892:11 [in part].—Hay, 1893:283–286, figs. 1, 3, 4, 7, 8, 9, 13, 14.—Lönnberg, 1894:126 [in part].—Hay, 1896:478, 482–485, 489, fig. 3.—Blatchley, 1897: 138, 142, 144, 170, 171, 174 [in part].—Hay, 1897:208, 209, 210.—Faxon, 1898:647 [in part].—Hay, 1899:959, 966 [in part]; 1902a:235 [in part].—Ortmann, 1902:277, 278, 279 [in part].—Steele, 1902:16 [in part].—Eigenmann, 1903:169 [in part].—Harris, 1903b:77, 112, 117–118, 152 [in part].—Ortmann, 1905a:92, 107, 108 [in part].—Graeter, 1909:470.—Osborn, 1912:923.—Faxon, 1914:392.—Spurgeon, 1915:385–394 [in part].—Ortmann, 1918: 838, 848 [in part].—Spandl, 1926:95, 141 [in part].—Pope, 1926:170.—Chappuis, 1927:91, 120 [in part].—Ortmann, 1931:64 [in part].—Bolivar et Jeannel, 1931:302.

Orconectes pellucidus inermis.—Smith, 1873:639.—Faxon, 1885a:83.—Packard, 1888:41.—Rhoades, 1959:401.—Nicholas, 1960:133.—Hart and Hobbs, 1961:176 [in part].—Rhoades, 1962:68, 79, 81, 90.—Jegla et al., 1965: 639.—Jegla, 1965a:647; 1966:345–357.—Hart and Hart, 1966:8.—M. Cooper, 1969:203, 204, 206–207.—Jegla and Poulson, 1970: 347–355.

Cray fish [sic.].—Shaler, 1875:362.

Crayfishes.—Collett, 1874:303.—Collett, 1879:362.

Orconectes.—Hovey, 1882:223 [in part].

Blind crayfish.—Packard, 1888:14.—Pope, 1926:163, 169.—Jackson, 1953:31; 1955:57.

Eyeless crayfishes.—Sloan (in Packard), 1888:16.

Orconectes pellucidus.—Cope, 1879:492, 494, 495, 503, 505, 506 [in part], fig. 116.—Packard, 1888:128, 155 [in part], pl.-figs. 21:5, 22:5, 6, 7.—Pennak, 1953:458 [in part].—Eberly, 1955:281, 282; 1958:1–6 [in part]; 1960:29, 30, 31, 32 [in part].—Huheey, 1961:43–45.—Penn and Fitzpatrick, 1963:793.—Poulson, 1964:759.—Vandel, 1964:509, 570, 575 [in part].—Jegla, 1964:81.—Jegla, 1965b:1421.—Mohr and Poulson, 1966:119, 120, 122, 123.—Poulson and Jegla, 1966:88.—Jegla and Poulson, 1968:273–282.—Jegla, 1969:135–137.

Cambarus (Orconectes) pellucidus.—Hovey, 1882:222 [in part].

Cambarus pellucidus inermis.—Packard, 1888:41.

Cambarus pellucidus variety *inermis.*—Hay, 1893:284.

Cambarus inermis.—Faxon, 1898:647.

Orconectis inermis.—Harris, 1903b:113 [erroneous spelling].

Cambarus (Faxonius) pellucidus.—Ortmann, 1905a:107, 108 [in part]; 1905b:435 [in part]; 1931:64 [in part].—Fage, 1931:373 [in part].

Blind crawfish.—Pope 1926, fig. 157.

Cambarus.—Bolivar et Jeannel, 1931:298, 299 [in part].

Cambarus pellucidus var. *testii.*—Wolf, 1934–38:105 [in part].

Orconectes (Orconectes) inermis.—Hobbs, 1942b:154 [by implication].—Hobbs, 1959:890.

Cambarus (Cambarus) pellucidus testii.—Balss, 1955:1311.

Orconectes pellucidus pellucidus.—Eberly, 1960:30 [in part].—Minckley, 1963:47, 51, 74.—Hart and Hart, 1966:8 [in part].—Hart and Hart, 1969:167.

Orconectes pellacious.—Jegla, 1965b: 1421 [erroneous spelling in abstract].

Orconectes.—Mohr and Poulson, 1966:123.—Barr, 1968: 85, 95 [in part].

Orconectes inermis testii.—Barr, 1966:17.

Orconectes sp.—Hart and Hart, 1966:8.

Cave crayfish.—Mohr and Poulson, 1966:91–92, 120, 121, 123.

Orconectes inermis inermis.—Barr, 1967a:161.—Prins, 1968:672.

Orconectes "probably *O. inermis*".—Barr. 1968:90.

REVIEW OF LITERATURE.—The first record of the existence of this crayfish was that of Cope (1871a:4) who listed *"Astacus pellucidus"* among the species obtained in Wyandotte Cave in the Indianapolis Journal on 5 September 1871. Later the same year he (1871b:368) again referred to it as he did in the newspaper. "We descended a wall to the water, some twenty feet below the surface, and found it to communicate by a side opening, with a long, low channel, through which flowed a lively stream of very cool water. Wading up the current in a stooping posture, we soon reached a shallow expansion or pool. Here a blind crawfish was detected crawling around the margin, and promptly consigned to the alcohol bottle." This description has led us to conclude that this was not Wyandotte Cave; instead, it is the cave nearby known as Sibert's Well Cave. The following year, in identical papers Cope (1872a and 1872b), quoted parts of the original newspaper account but described, figured, and assigned the crayfish to a new genus and species, *Orconectes inermis,* indicating that "The blind crawfish above mentioned is specifically distinct from that of Mammoth Cave, though nearly related to it . . . separating it generically from *Cambarus,* or the true crawfishes, on account of the absence of visual organs." He also assigned the albinistic *pellucidus* from Mammoth Cave to his new genus. Cope (1872c) reiterated the presence of this crayfish in Wyandotte Cave.

Early in 1872, Packard (1872a) referred to Cope's species as *Cambarus pellucidus.*

In the same year, Hagen (1872) ridiculed Cope's assigning the two crayfishes to a new genus on the basis of rudimentary eyes, and indicated that "the description of the single specimen does not give any character by which to separate it from the old species, *C. pellucidus.*"

Packard (1873) also relegated Cope's species to synonymy with *Cambarus pellucidus* but Smith (1873) utilized the combination *O. pellucidus inermis* which in 1875 was apparently rejected in favor of *Cambarus pellucidus.* Collett (1874) reported this crayfish from Donaldson's and Hamer's caves, Lawrence County, Indiana. Shaler (1875) in describing the cave fauna of Indiana mentioned the crayfish in Wyandotte and other caves, and Collett (1879) referred to those in Rhodes Cave, Harrison County, Indiana. Cope (1879) published an account of this species which is almost identical with those which appeared in 1872, but the crayfish is referred to as *Orconectes pellucidus,* and the descriptions are omitted.

Hovey (1882) utilized a new combination, *Cambarus (Orconectes) pellucidus* but contributed no new data. Faxon (1884) included Cope's *O. inermis* as a synonym of *C. pellucidus.*

Faxon (1885a) compared Cope's type, which was a second form male, with specimens from Mammoth Cave and he was of the opinion that this specimen exhibited some of the variations of the typical form of *C. pellucidus.* He commented on relationships and included locality records from Indiana.

Underwood (1886) also treated Cope's species as synonymous with *C. pellucidus.* Sloan (1888), in a letter to Packard, reported eyeless crayfishes in caves at Clifty which Packard indicated as being located in Bartholomew County, Indiana. The location of the caves is in error; actually they are 3.5 miles north of Campbellsville, in Washington County. Packard (1888) cited several new locality records for "*Cambarus pellucidus,*" but in commenting on the food of the crayfish (page 24) refers to it as *O. pellucidus,* and in discussing the eye and vision there assigned the species to both genera! He indicated that "the food of the blind crayfish appears to consist of living *Caecidotea*" [=*Asellus*], an observation made by Mr. Moses N. Elrod, on a crayfish taken from a well in Orleans, Orange County, Indiana (page 24). In his explanation of plate-27, figure 5 (page 156), he indicated that it was "after Cope" but it is obviously the same figure utilized in Packard (1871) "after Hagen" and is an illustration of *O. pellucidus* rather than *O. i. inermis.*

Faxon (1890) summarized the Indiana localities from which *C. pellucidus* had been reported, and discussed the similarities between the species and *C. setosus* and *C. hamulatus.* In the same year, Packard discussed the possible origin of *C. pellucidus* and indicated that the "optic lobes and nerves" persist but that there was a "total atrophy of the rods and cones, retina (pigment) and facets." Packard (1890) referred to the occurrence of *C. pellucidus* in Bradford Cave (also known as Stierstaedter Cave, located 0.5 mile east of Bradford on the east side of Corn Creek), Harrison County, Indiana.

Hay (1891) indicated that *Cambarus pellucidus* "occurs in many of the caves of southern Indiana. They are usually small, the largest I have ever seen, among 40 specimens, being barely 2 inches in length. They are kept from extinction only by the inaccessibility of their home. They are very conspicuous when in the water, and are very easily caught. When startled they are utterly at loss where to go, and often dart out upon the shore. I think it may be safely said that as a rule they grow spinier as one advances southward, although there are exceptions.

A female collected in Wyandotte Cave is almost without spines, but three specimens from a small cave near there are exceedingly spiny."

Ortmann (1892) simply repeated known locality records. Hay (1893) presented perhaps the best observations made on this species in describing his experience in catching members of the intergrade population in Shiloh Cave which he designated *Cambarus pellucidus inermis.* "When first observed, the crayfish were generally, I might almost say always, resting quietly in some shallow part of the stream on one of the banks of clay. They lay with all their legs extended and their long antennae gently waving to and fro. Once or twice I saw them on the shore a foot, at least, from the water, and one of these appeared to have been digging in the soft mud. When in the water I found it almost impossible to catch them with the net, and after a few trials threw it aside as useless. A much surer method was to approach them slowly with the hand and then suddenly seize them. When once touched they started off in great haste for some protecting rock, but often in their alarm would dart out upon the banks where they would lie unable to get back to the water. They did not appear to be at all sensitive to the light. I have often tried the experiment of slowly passing my candle back and forth a few inches above them, or of suddenly removing the light and then bringing it close again, but with no effect whatever.

"Noise has no effect; a loud call or a shrill whistle they do not notice. Nor does disturbing the waters seem to affect them, and it is only when they are touched that they manifest fear.

"It may also be stated that, as a rule, *Cambarus pellucidus* is smoother the further north it occurs. The material which I have collected myself, and all that I have been able to obtain from others, will uphold me in this statement.

"The small cave near Wyandotte produces individuals of exceeding spininess, it being the exception to find there a comparatively smooth one.

"Coming further north, to Paoli, we can find much smoother specimens, and at Shiloh they are smoother still, while at Mayfield's Cave, in Monroe County, occurs a form entirely without spines. So constant is this feature of smoothness in the Mayfield Cave specimens and so different is its appearance from the typical *pellucidus* that I think it is worthy of being characterized as a subspecies."

Hay also cited all the known localities in Indiana in which troglobitic crayfishes had been found.

Lönnberg (1894, 1895) treats *O. inermis* as a synonym of *C. pellucidus* and compares it with his new troglobite from Florida, which is described in the latter paper as *Cambarus acherontis.*

In his "Crawfishes of the State of Indiana," Hay (1896) described and figured *"C. pellucidus"* indicating that "the form *'inermis'* is now hardly recognized even as a variety of pellucidus." Again, he summarized the range of the species in Indiana, citing caves in Lawrence, Bartholomew, Orange, Crawford, Harrison, and Jefferson counties.

Hay (1897) presented a synonomy of the species, reviewed the localities from which the Indiana *pellucidus* had been collected, and Blatchley (1897:209) included the following annotation: "The blind crayfish inhabits shallow pools with muddy bottom rather than rapid flowing water. It moves slowly with its antennae spread out before it, and gently waving to and fro, feeling, as it were, every inch of its way. It is wholly non-sensitive to light and seemingly so to sound, but when disturbed by any movement in the water it is extremely active, much more so than ordinary terrestrial forms, leaping upward and backward with quick, powerful downward blows of its abdomen." Blatchley (1897:171) compared in tabular form Cope's (1872a, 1872b) list of species occurring in Wyandotte Cave with his own.

Faxon (1898) commented that *C. pellucidus* in Shiloh, Down's, and other caves in Lawrence County and in a small cave near Paoli, Orange County, Indiana, "belong rather to the form described by Cope as *C. inermis* (Wyandotte Cave) than to the typical form commonly found in the Mammoth Cave of Kentucky." He also indicated that Hay has shown a "transition" from typical *pellucidus* in southern Indiana to the more northerly occurring form in which there is a reduction of the spines.

In his "Synopsis of North American Invertebrates," Hay (1899) combined *inermis* and *pellucidus* under the latter name in his key and indicated the range to encompass Kentucky and Indiana. In a discussion of the crustacean fauna of the Mammoth Cave region, he referred to the occurrence of *C. pellucidus* in Indiana. Hay (1902a), in discussing the relationships of *O. inermis testii,* indicated that "this subspecies is found in a very small area in Indiana at the very northern limits of the range of *C. pellucidus."*

Neither Ortmann (1902) nor Steele (1902) added any additional information concerning their *C. pellucidus,* and Eigenman (1903) simply indicated that *pellucidus* from caves near Mitchell, Indiana have "an eye structure much more degenerate than specimens of the same species from Mammoth Cave."

Harris (1903b) summarized the habitat and range of the species, combining, as had most of his predecessors, the Indiana and Kentucky *"Cambarus pellucidus."*

Ortmann (1905a, 1905b) discussed the affinities of *C. pellucidus* (including the Indiana representatives) and indicated its closer relationship with crayfishes now assigned to *Orconectes* than to those belonging to the genus *Procambarus.* Osborn (1912) added no original data.

Graeter (1909) briefly summarized the literature on cave-dwelling species from 1900. Faxon (1914) repeated (page 392) the fact that Hay and Banta had found *C. pellucidus* associated with *C. bartonii laevis* in caves in southern Indiana and included in his check-list (page 415) *O. inermis* as a synonym of *C. pellucidus.*

Spurgeon (1915) compared the eyes of *C. setosus* and his *C. pellucidus* [=*O. i. inermis* and *O. i. testii*] and found no important differences. He expressed the opinion that the eyes of these troglobites represent arrested development rather than degeneracy. He also cited a new locality record (which is for the intergrade population *inermis* x *testii*) and indicated that the Clifty Caves are located in Washington County, Indiana.

Ortmann (1918) mentioned the "blind cave-species, *C. pellucidus*" from Kentucky and Indiana.

Pope (1926) included observations on individuals in captivity and a photograph of a topotype.

Spandl (1926) simply referred to certain previous works. Chappuis (1927) added nothing new but again reported *C. pellucidus* from Indiana. Bolívar and Jeannel (1931) and Fage (1931) indicated the presence of this crayfish in "Donnelson's Cave" [=Donaldson Cave, Spring Mill State Park, Lawrence County, Indiana], and the former added Wyandotte Cave. Ortmann (1931) cited this crayfish within the range of *"pellucidus."*

Wolf (1934–1938) cited localities for *Cambarus pellucidus* in Indiana together with several erroneous records for *"C. pellucidus* var. *testii"*; these latter records are for *O. i. inermis* and intergrades between the two subspecies.

Hobbs (1942a), in revising the genus *Cambarus,* reinstated Cope's generic name, *Orconectes,* expressed the opinion that *inermis* was a valid species, and illustrated the first pleopod of the male. Hobbs (1942b) recognized the subgenus *Faxonella,* thereby implying that *Orconectes inermis* belonged to the typical subgenus.

Rhoades (1944) indicated that the range of *O. pellucidus pellucidus* "with its subspecies" ranges "from southern Indiana to northern Alabama," and proposed the recognition of two groups of the Limosus Section of the genus *Orconectes.*

Hobbs (1948a) illustrated the pleopods of topotypes of *O. inermis* along with those of its closest relatives, presented a key to the members of the Limosus Section, and questioned the subdivision of the Section as proposed by Rhoades. In addition, he indicated that the status of *O. inermis* remained unsolved and stated: "Perhaps it will be shown to be a subspecies of *O. pellucidus*; however, until future work will indicate intergradation between the two, it seems advisable to retain its specific status" (page 19).

Pennak (1953) cited Indiana as being within the range of *O. pellucidus.* Jackson (1953) presented observations on this crayfish in Wyandotte Cave.

Jackson (1954, 1955) mentioned that blind crayfish and blind fish are plentiful in the stream in Donaldson's Cave.

Balss (1955) erroneously reported *"Cambarus (Cambarus) pellucidus testii"* from Wyandotte Cave. Eberly (1955) cited a new locality record for *O. inermis,* but relegated most of the Indiana locality records to *Cambarus pellucidus.*

Holthuis (1956), in an application to the International Commission on Zoological nomenclature, requested that the genus *Orconectes* be placed on the "Official List of Generic Names in Zoology," the type-species being given as *O. inermis.*

Crocker (1957) added no additional information relative to the species, simply citing it as the type-species of the genus.

The 1958 paper of Eberly is a mimeographed, almost identical version of Eberly (1960). Although this study is centered around competition between *C. laevis* and *Orconectes inermis* (probably an intergrade population), other pertinent data are presented, including the fact that *C. laevis* consumes 1.2

to 2.8 times the amount of oxygen per gram of body weight as does the troglobite. Among them is an expression of "the opinion that all of these cave crayfish [subspecies of *pellucidus* and *inermis*] in the Indiana-Kentucky-Alabama cave region are descended from a once wide-spread surface population that was relatively undifferentiated at that time. After entering the cave, the cave adaptations mentioned earlier developed while certain features which are now used in taxonomic determinations, e.g., the form of the male genitalia, remained relatively unchanged." This work is cited by Poulson (1964).

Hobbs (1959) designated the two subspecies of Indiana troglobites as members of the subgenus *Orconectes: Orconectes (Orconectes) inermis.*

Rhoades (1959) reviewed the status of *O. inermis* and gave an account of the events transpiring in Cope's describing the species. He analyzed the descriptions of Cope's species and that of Hay's *O. pellucidus testii,* and concluded that Hay's subspecies is synonymous with *Orconectes inermis.* He further pointed out that *"O. inermis* intergrades freely with *O. pellucidus pellucidus* (Tellkampf) (1844) in the southern counties of Indiana." In view of this conclusion, he proposed the name, *"Orconectes pellucidus inermis,* for the smoother, less spinous subspecies of south central Indiana." Of the affinities and distribution Rhoades stated that "There can be little doubt of the affinity of the blind crayfish of Indiana with those of the solution caverns of Kentucky. In fact, the blind crayfishes from the caves of Harrison and Crawford counties on the Ohio River are decidedly similar to the Mammoth Cave species with only an occasional smooth spineless specimen. The underground waters of Orange, Washington and Lawrence counties a few miles to the north have populations of blind crayfish which are truly transitional between the species and subspecies. Smoothness, spine reduction and other *inermis* characteristics reach a climax in the cave populations in Monroe, Brown, and Bartholomew counties on the northern border of the range."

Nicholas (1960) included *O. p. inermis* in his checklist.

Utilizing the observations of Eberly (1958, 1960), Huheey (1961) proposed a model for the cyclical evolutionary process in a subterranean habitat frequented by a troglobitic and a troglophilic crayfish. He proposed that following the extinction of the troglobite (A) [*O. pellucidus*=*O. i. inermis*], the population of the troglophile (B) [*C. bartonii*=*C. laevis*] will be greatly reduced because of a reduction in food supply (A); B, in turn, will become better adapted to cave life, thus coming to resemble more closely the previously existing A; and "At some point it will be possible for another epigean form (C), although poorly cave-adapted, to compete successfully with B and eventually replace it by virtue of its greater robustness."

Hart and Hobbs (1961) cited *O. p. inermis* as one of the hosts of *Entocythere barri (=Sagittocythere barri).*

Creaser (1962) contended that the genus *Orconectes* should be composed of only three known species: *lancifer, inermis,* and *pellucidus* "(with subspecies—if they are subspecies)," and refuted the supposed relationships to other members of the genus as was proposed by Hobbs (1942a).

Rhoades (1962) in his discussion of the evolution of the Limosus Section of the genus *Orconectes* retained the Limosus and Rafinesquei groups he had proposed earlier (1944), assigning the several subspecies of *O. pellucidus* to the latter group, but in characterizing *O. pellucidus pellucidus,* he stated (page 68) "Pleopods of the form I male short with typically divergent tips," that is, possessing the sole character (see page 69) on which he based his "Group *limosus*." Unfortunately, the characters of the two groups are reversed on page 75. Rhoades postulated "that the genus originated on the northwest flank of the Mississippi embayment particularly in the rocky streams of the Ozarkian Highlands." From there the stock moved eastward from "the Springfield Plateau of central Missouri through southern Illinois to western Kentucky" to occupy "the lower reaches of the Pliocene Teays and Ohio rivers," with populations becoming "isolated into two groups on the basis of: 1) occupation of the Pliocene Teays River, the discharge of which poured into the head of the Mississippi embayment, and 2) continued migration along the escarpment streams to the Pliocene Ohio River." Rhoades concluded that "There can be little doubt that the Group *rafinesquei* has occupied the streams of the Cumberland Plateau since very ancient times" and that the Pliocene surface species perhaps "entered rock-fissure springs and lived in subterranean water courses." Although he did not hazard a guess in which part of the Plateau the invasion took place, he stated that "It appears that a specific population of *Orconectes pellucidus* was widely distributed in the labyrinth of Cumberland caves by the beginning of Pleistocene time. Perhaps their wide distribution occurred in the late Pliocene when cave corrosion was at its deepest stage and all channels were free from filling. Isolation, which was a factor in subspeciation of *O. pellucidus,* came about as a function of river entrenchment and subsequent aggradation. . . . With glacial filling of the [Ohio] river channel and sedimentation in the interrupted end of cave tunnels, especially in Illinoian time, a barrier was formed which isolated a population north of the Ohio River" thus isolating the ancestors of *inermis.* "Similar entrenchment and sedimentation in the upper Cumberland River could lead to the separation of a segment of *O. pellucidus* in the caves of southeastern Kentucky" isolating the ancestors of *packardi.* "The blind *Orconectes* in the subterranean channels of the Mussel Shoals region were similarly isolated . . ." Fitzpatrick (1963) only mentioned *pellucidus* in discussing Creaser's concept of generic assignments.

Penn and Fitzpatrick (1963) and Vandel (1964) referred to Eberly's work, and the latter designated "*Orconectes pellucidus* [= *O. i. inermis,* in part] "un cavernicole ancien." Minckley (1963) reported this species as *O. p. pellucidus* from Doe Run, Meade County, Kentucky.

Jegla (1964), in studying an integrade population of *inermis* x *testii* in Shiloh Cave, found a preponderance of first-form males in the fall and the fewest numbers in the summer months; females apparently lay their eggs during the spring and summer months, and young were found as early as the "first part of May." The adult males undergo two major molting periods each year, during the fall and late winter to spring, the former increasing the number of first-form males and the latter, the number of those in the second form. The same author (1965a) reported that although the eyes of this crayfish have lost, through degeneration, some of the optic elements, "the sinus gland is present and neurosecretory cell groups are located on the surface of the medulla terminalis neuropile in approximately the same position as they are in a normal-eyed crayfish." Differences noted in time-lapse of molting following eyestalk ablation were thought perhaps to be due to "a difference in concentration of molt-inhibiting hormone in the blood of crayfish" at the time the eyestalks were removed.

Jegla et al. (1965) in comparing interpopulation variations in cave crayfishes found that in selected caves three subspecies of "*O. pellucidus,*" *(inermis, pellucidus,* and *australis)* differ by 20 mm in maximum length attained, by 20 mm in length at maturity. They concluded that interpopulation size differences are not due to basic differences in physiology but probably to differences in available food and perhaps "interspecific competition resulting in character displacement." Jegla (1965b), in an abstract of his doctoral dissertation, summarized part of the above and the following citations by him. The combination, *Orconectes pellacious,* was also introduced inadvertently.

Jegla (1966) enlarged upon and detailed the evidence supporting his abstract published in 1964.

Barr (1966) referred to Jegla's ecological studies "on the crayfish *O. i. testii.*"

Poulson and Jegla (1966) published an abstract concerning the reproductive cycle and the circadian rhythm of oxygen consumption in this crayfish.

Hart and Hart (1966), primarily interested in the entocytherid ostracods occurring on crayfish hosts, cited several new locality records for *O. i. inermis.*

Mohr and Poulson (1966) presented excellent photographs of this crayfish, comparing it with epigean species, and recounted seeing it in "Bronson-Donaldson Cave." They outlined the reproductive cycle in Shiloh Cave, associating it with "biological clocks."

Barr (1967a) introduced the combination *Orconectes inermis inermis,* anticipating that this manuscript would appear in print prior to his ecological summary, and indicated that this subspecies "replaces *O. pellucidus* immediately north of Mammoth Cave in the Pennyroyal (Hobbs and Barr, in preparation). . . ." In discussing the Pennyroyal, Barr (1967b) pointed out that the extent of this plateau limits the range of many of its endogenous cavernicoles, including *O. inermis.*

Fitzpatrick (1967) discussed the supraspecific structure of the Cambarinae that was proposed by Creaser, and, in so doing, referred to *O. inermis.*

Barr (1968) cited data from Eberly and Jegla, and discussed the possible origin of the troglobitic members of the genus *Orconectes.*

Jegla and Poulson (1968), investigating circadian rhythms in *O. i. inermis* from McCubbin's Cave, Breckenridge County, Kentucky, and *O. inermis* x *testii* from Shiloh Cave, Lawrence County, Indiana, reported that mechanisms for circadian rhythms have apparently persisted in some of these crayfishes despite the period of time they have been restricted to an environment in which daily light cycles do not exist. The minimum and maximum oxygen consumption of the crayfishes were approximately 0.015 and 0.085 ml/g/hour. Their discussion of the observations of Park et al. (1941) and the later analysis by Brown (1961) applies to *O. pellucidus* rather than to *O. inermis.*

Prins (1968) recorded the presence of this crayfish in a surface stream, Doe Run, Meade County, Kentucky, and indicated that individuals are found in the stream frequently, "especially during high discharges" from the headwater spring.

Jegla (1969) continued his study of the intergrade population in Shiloh Cave and found that whereas molting occurs throughout the year, two periods of approximately two-months duration constitute the maximum molting periods, February-March and August-September. The adult male population consists of a preponderance of those in form II in the summer months (60 to 70 percent) and those in form I during the winter months (77 to 97 percent). An annual ovarian cycle was observed in the females, beginning during the early fall, with oviposition occurring during the summer. Although the incubation period is not precisely known, Jegla estimated a duration of approximately two months. Young crayfish are found throughout the year but are most abundant in the summer and autumn, and "most conspicuous" in August.

M. Cooper (1969) compared the length of time required "for detecting, actively seeking, and locating food stimuli" by this crayfish with that of the epigean *O. limosus.* She found that *O. i. inermis* detected a moving worm much more quickly than it did introduced glycine, and whereas the epigean species sensed the presence of the latter more quickly, once the troglobite "started seeking the chemical, it located the source in much less time than did *O. limosus.*" The time required for the capture of the worm by the troglobite was one-half that utilized by the epigean crayfish.

Poulson and White (1969), in their discussion of cave environments, pointed out the lack of morphological differentiation in *O. inermis* on either side of the Ohio River, and indicated that "the troglophilic crayfish *Cambarus bartoni* [= *C. laevis*] is much rarer in the deep cave when the troglobitic *Orconectes* is present."

Hart and Hart (1969) expressed the opinion that either this crayfish or *Cambarus tenebrosus* [actually *C. laevis*] served as a host to *Entocythere donnaldsonensis* [= *Donnaldsoncythere donnaldsonensis*].

Jegla and Poulson (1970) found a circannian rhythm with respect to reproduction in *O. inermis,* with periodicity of 338 to 396 days. They hypothesized that "some event associated with heavy run-off from surface precipitation triggers egg-laying and synchronizes the individuals' circannian rhythms in the cave."

COMMENTS ON PREVIOUSLY RECORDED DATA.—On the basis of information available to Hagen (1872), his criticism of Cope's (1872a) designating *Orconectes inermis* as a species distinct from Tellkampf's *Astacus pellucidus* was entirely justified. Not until Hobbs (1948a) made comparisons of the first pleopods of the males of the two did it become questionable that the two were, in all probability, conspecific. Through Cope's folly of basing his genus *Orconectes* on the eyeless condition of his new species, he established a generic name, which although largely relegated to synonomy for 70 years, had to be resurrected in 1942 when Hobbs revised the genus *Cambarus.* Most of the references within the 70 year span consist of the addition of new locality records and brief statements indicating the belief that Cope's species was a synonym of *pellucidus.* Outstanding, however, were some of Hay's observations on the habits and reactions of the intergrade population *(inermis* x *testii)* in Shiloh Cave, Lawrence County, Indiana. The observations of Eberly (1958, 1960) are noteworthy, particularly the conclusions concerning cave adaptations and competition between this species and the pigmented *Cambarus laevis* Faxon.

Rhoades' (1959) belief that *O. inermis* intergrades freely with *O. p. pellucidus* does not coincide with our interpretations. His discussion of reasons for recognizing *testii* as a synonym of *inermis* was not without merit, in view of the fact that the males of the Kentucky segment of the latter (which Rhoades presumably considered to be *O. pellucidus*) possess pleopods typical of *inermis* rather than being intermediate between *inermis* and *pellucidus.* We believe it appropriate, however, to recognize *inermis* and *pellucidus* as distinct species and to retain the subspecific designation *O. inermis testii* for those aspinous populations occurring in the northernmost part of the range. The only reservation we have in suggesting this treatment is based on the observations of Banta (1907:70) who stated that "some individuals from Mayfield's [Cave, Monroe County, Indiana] show some tendency toward rostral spines, while a single specimen taken in Mayfield's was fully as spiny as the average individual from Mitchell." We have seen no spiny individuals among the material available to us from Monroe County (see under *O. i. testii*), and our specimens from Donaldson's Cave [=Banta's Cave at Mitchell] include moderately spiny to almost aspinous individuals.

The hypotheses of Rhoades (1962) relative to the evolutionary history of these troglobites are not in complete agreement with those outlined above; however, they are most worthy of consideration.

Among recent studies, the contributions to our knowledge of the biology of the species by Jegla (1964–1969) are outstanding. Despite the many more references in the literature to *O. pellucidus* than to *O. inermis,* much more is known of the biology of the latter than that of *O. pellucidus.* Chiefly through the work of Jegla and Hay, more data have been accumulated on the intergrade population in Shiloh Cave than for any other troglobitic crayfish.

Barr (1967a) introduced the combination *Orconectes inermis inermis,* and his hypotheses concerning the origins of the troglobitic members of the genus *Orconectes* (1968) are essentially those which are detailed elsewhere in this study.

DIAGNOSIS.—Albinistic; eyes reduced and without pigment; rostrum with marginal spines, tubercles, or at least angular emargination at base of acumen; margins convergent, upper surface without median carina; postorbital ridges terminating cephalically in spines or tubercles; hepatic area often with two to many spines; at least one, often several, cervical spines present; areola 4.5 to 6.7 times longer than broad and constituting 37.0 to 42.5 percent of entire length of carapace; chelae not conspicuously setose but with ciliated tubercles, mesiodorsal surface of palm with several irregular rows of tubercles; hooks on ischiopodites of third and fourth pereiopods. First pleopod of first-form male with greatest cephalocaudal diameter of pleopod less than twice that immediately proximal to base of central projection, always terminating in only two elements; non-corneous mesial process broad basally, suddenly contracting to form tapering subacute distal portion, latter directed caudodistally and slightly exceeding tip of central projection distally; central projection corneous, flattened in cephalocaudal plane, slightly concavoconvex with convexity extending mesially; shoulder lacking at base of central projection but cephalic surface with convexity along distal third of appendage. Annulus ventralis is illustrated in Figure 10*l*.

Topotypic Male (Form I): Body (Figure 10*c, h*) subovate, depressed. Abdomen narrower than thorax (8.5 and 10.3 mm in widest parts, respectively). Width of carapace greater than depth in region of caudodorsal margin of cervical groove (10.3 and 7.2 mm). Areola moderately broad (5.1 times longer than wide) with 5 or 6 minute punctations across narrowest part. Cephalic section of carapace 1.5 times longer than areola; length of areola 40 percent of entire length of carapace. Rostrum slightly longer than twice width at base, excavate, and with acumen about 1.2 times longer than maximum width; cephalic extremity reaching beyond antennular peduncle and almost as far as distal end of peduncle of antenna; margins not swollen, little elevated, and with pair of well-developed, corneous-tipped marginal spines at base of acumen; upper surface with regularly spaced, minute, setiferous punctations; subrostral ridges moderately well developed and evident in dorsal aspect along basal third of rostrum.

Postorbital ridges comparatively low, short, with dorsolateral grooves, and terminating cephalically in strong, corneous-tipped, acute spines. Suborbital angle lacking. Branchiostegal spines acute and well developed. Cervical spines represented by row of 3 or 4 tubercles on each side of carapace immediately caudal to cervical groove; tubercles progressively larger ventrally, and ventral two spiniform. Carapace punctate dorsally and granulate laterally; hepatic area with three or four small spiniform tubercles on each side. Abdomen longer than carapace (25.5 and 23.0 mm). Cephalic section of telson with 2 strong spines in sinistral caudolateral corner (mesial one movable) and 1 in dextral.

Protruding portion of epistome (Figure 10*g*) almost twice as broad as long and resembling silhouette of shortened minaret; surface flattened, with fine setae, and with fovea present caudally. Eyes much reduced, without pigment, completely hidden beneath rostrum in dorsal aspect, and extending cephalically

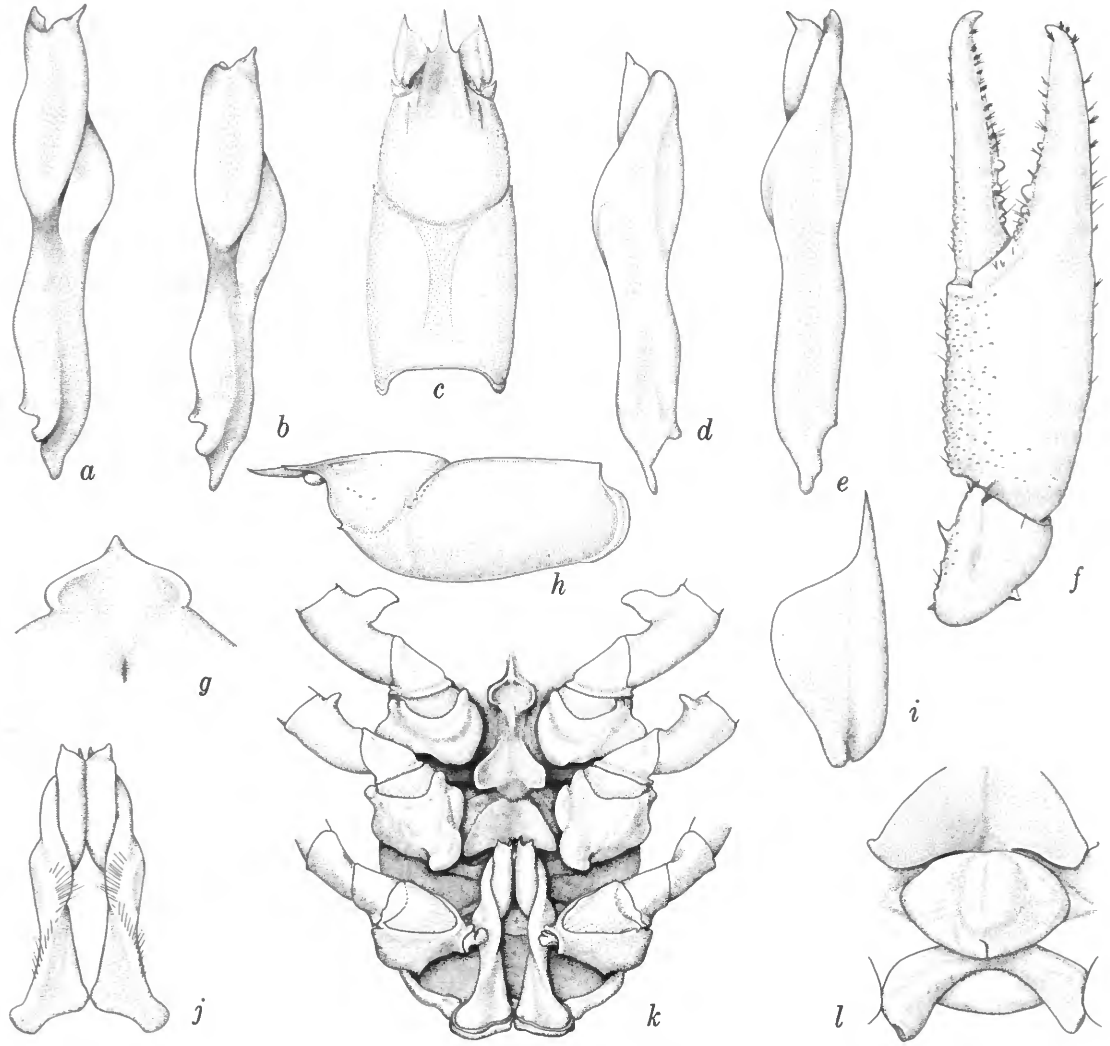


FIGURE 10.—*Orconectes inermis inermis: a,* mesial view of first pleopod of topotypic male, form I; *b,* mesial view of first pleopod of topotypic male, form II; *c,* dorsal view of carapace of topotypic male, form I; *d,* lateral view of first pleopod of topotypic male, form II; *e,* lateral view of first pleopod of topotypic male, form I; *f,* dorsal view of distal podomeres of cheliped of topotypic male, form I; *g,* epistome of topotypic male, form I; *h,* lateral view of carapace of topotypic male, form I; *i,* antennal scale of topotypic male, form I; *j,* caudal view of first pleopods of topotypic male, form I; *k,* ventral view of caudal thoracic region of topotypic male, form I; *l,* annulus ventralis and portion of sternum of topotypic female.

about half way between margin of orbit and marginal spines of rostrum. Antennules of usual form with strong spine on ventral surface of proximal podomere at base of distal fifth. Antennae extending caudally slightly beyond caudal margin of telson. Antennal scale (Figure 10*i*) broadest slightly distal to midlength, distinctly less than half as broad as long; outer thickened portion much narrower than lamellar area and terminating distally in very prominent corneous-tipped spine. Third maxillipeds extending slightly beyond midlength of distal podomere of peduncle of antenna.

Chela (Figure 10*f*) slender and little inflated; mesial margin of palm 1.1 times longer than width of palm; dorsal surface of palmar area tuberculate mesially and punctate laterally, punctations and distal bases of tubercles setose; ventral surface of palm tuberculate and with corneous-tipped spine opposite base of dactyl; more mesial tubercles larger and arranged sublinearly, with 13 or 14 comprising most mesial row of palm; lateral surface tuberculate. Fingers not gaping; dorsal and ventral surfaces with broad, rounded, submedian, longitudinal ridges flanked by setiferous punctations; opposable margin of immovable finger with row of 7 tubercles, fifth from base largest, along proximal two-fifths, single tubercle below level of row slightly proximal to midlength of finger, and single row of minute denticles between proximal five tubercles; distally, crowded denticles forming slightly broader series to base of corneous tip of finger; lateral surface of immovable finger subcostate. Opposable margin of dactyl with row of 5 tubercles along proximal two-fifths, distalmost largest, with denticles arranged as on immovable finger; mesial surface of dactyl with small tubercles, decreasing in size distally, along proximal half and punctations along distal half. Carpus longer than broad, with mesial, dorsomesial, and ventromesial surfaces tuberculate, otherwise punctate; mesial surface with 3 tubercles somewhat larger than others, largest spiniform; distoventral margin with 2 spines, 1 adjacent to base of ventrolateral articulation with propodus and 1 near median line. Merus tuberculogranulate dorsally, with group of 3 corneous-tipped spines slightly proximal to distal end; except for tubercles, weakly scabrous; ventrolateral margin with row of 9 spikelike tubercles and ventromesial margin with 11; few scattered tubercles flanking two rows; distolateral extremity with corneous-tipped spine. Ischium with ventromesial row of 5 small tubercles and additional smaller ones laterally; dorsal margin with subserrate row of 7 or 8 small tubercles.

Ischia of third and fourth pereiopods (Figure 10*k*) with hooks; those on third stout and recurved to level of cephalic articulation with basis; those on fourth much smaller and, while slightly recurved, leaving broad gape between tip and corresponding basis. Coxae of fourth pereiopods with caudomesially projecting prominences; coxae of fifth pereiopods without prominences except for small mesioventral projection partially ringing base of phallic papilla.

First pleopods (Figure 10*a, e, j, k*), symmetrical, reaching bases of third pereiopods when abdomen is flexed, and comparatively shallowly situated in sternal groove; tip ending in two parts as described in Diagnosis.

Topotypic Female: Differs from the male in the following respects: subrostral ridges evident almost to base of marginal spines; 4 cervical spines on right side and 2 on left; hepatic areas with 4 spines on right and 5 on left; antennal scale broadest slightly proximal to midlength; third maxillipeds extending to distal end of antennal peduncle; ventral surfaces of both chelae with crowded small tubercles, right with prominent median tubercle near midlength; immovable finger of chela with row of 14 tubercles along mesial four-fifths of finger (sixth from base largest) and prominent tubercle below tenth tubercle from base; opposable margin of dactyl of chela with row of 19 tubercles along proximal four-fifths (sixth from base largest); carpus of chelipeds tuberculate with single prominent spine on mesial surface of right and row of 3 on left, latter tubercles increasing in size distally, ventral surface with 3 prominent spines, 1 adjacent to base of ventrolateral articulation with propodus and 2 mesial to it; merus of cheliped with mesial row of 14 tubercles and lateral row of 7 on right and 9 on left; ischia of chelipeds with row of 7 small tubercles on right and 5 on left. (See Measurements.)

Annulus ventralis (Figure 10*l*) shallowly situated in sternum and not firmly fused to sternal plate immediately cephalic to it; outline subovate, 1.5 times broader than long with median portion elevated ventrally and forming asymmetrical arc with highest segment caudal to midlength; arched portion bearing shallow longitudinal groove ending caudally on steep slope of arc; sinus originating on slope dextral to median line, making gentle arc to median line and extending caudally to midcaudal margin of annulus.

Topotypic Male, Form II: Differing only slightly from first-form male: 3 cervical spines on each side of carapace; telson with 2 spines in each caudolateral corner of cephalic section; right antennal scale with strong accessory spine on middle third of lateral margin; both chelae regenerated, left larger than right, but neither well developed; hooks on ischia of third and fourth pereiopods comparatively more reduced, but boss on coxa of fourth only slightly smaller. (See measurements.)

First pleopod (Figure 10*b, d*) reaching base of third pereiopod when abdomen is flexed and markedly resembling pleopod of first-form male, except central projection much shorter, more swollen, and noncorneous.

Measurements (in millimeters).—*Orconectes inermis inermis,* topotypes:

	Male Form I	*Female*	*Male Form II*
Carapace:			
Height	7.2	11.0	8.0
Width	10.3	14.4	10.6
Length	23.0	34.3	25.5
Rostrum:			
Width	3.5	4.8	3.5
Length	6.0	9.1	7.0
Areola:			
Width	1.8	2.5	2.1
Length	9.2	14.0	10.4
Chela:			(no chela)
Length of inner margin of palm	7.5	11.0	
Width of palm	6.6	7.5	
Length of outer margin of chela	19.3	29.1	
Length of dactyl	10.6	16.6	

Types.—Not extant.

Type-locality.—Wyandotte Cave, Indiana. Actually Sibert's Well Cave, just below Wyandotte Cave, Crawford County, Indiana (Hobbs, 1942a:335).

Specimens examined.—Specimens from Kentucky and Indiana were examined as follows (those localities considered to be frequented by weakly spined *testii*-like populations are preceded by an asterisk):

Kentucky—*Breckenridge County:* (1) Cave and stream, 5 miles W of Big Spring, 6♂II, 5♀, W. L. Minckley, VI/5/58. (2) Bandy Cave, 3.0 miles S of Irvington, 1♂I, 8♂II, 6♀, T.C.B., IX/20/64. (3) Thornhill Cave, 3 miles W of Big Spring, 7♂I, 1♂II, 5♀, T.C.B., R. McAdams, X/18/64. (4) Lockard Cave, 3 miles SE of Bewleyville, 3♂I, 3♂II, 7♀, T.C.B., IX/20/64. (5) Bat Cave [location not determined], 1♀, 1j♀, J. Rhines, 1961. *Greene County:* (1) Brush Creek Cave, 0.8 mile E of Lobb, 4♂II, T.C.B., IX/28/63. (2) Scott Cave, 1.9 miles ESE of Eve, 1j♂, T.C.B., IV/2/66; 1♂II, 1♀, T.C.B. and T. C. Barr III, XI/1/70. *Hardin County:* (1) Bland Cave, 7 miles W of Sonora, 1♂I, 8♂II, 13♀, 1j♂, T.C.B., R.A.K., and R. Taylor, XII/8/62; 2♂I, 1♀, Hugh Thomas, XII/27/62. (2) Nelson Cave, 1.5 miles W of Star Mills, 1♂I, 1♂II, 4♀, 1j♀, T.C.B. and R.A.K., XI/2/63. *Hart County:* (1) Turner Cave, 3.7 miles SE of Magnolia, 1♂II, T.C.B., VIII/25/63. (2) Cooch Webb Cave, 0.4 miles N of Bear Wallow, 2♂I, 1♂II, 9♀, 1j♂, 2j♀, T.C.B. and R.A.K., XI/2/63. (3) Riders Mill Cave, 2.5 miles N of Priceville, 6♂I, 1♂II, 2♀, T.C.B. and R.M.N., X/5/63. (4) Cub Run Cave, near town of Cub Run, 2♀, T.C.B. and W.M.A., XI/28/64; 1♀, L.H., II/29/56. *Meade County:* (1) *Joe Jones Cave, near lower reaches of Doe Run, 1♂I, 3♀, W.L.M., VII/16/60; 1j♂, 1j♀, J.R., VII/25/61; 2j♀, R. Prins, III/2/63; 1♀, Rudolph Prins, III/16/63. (2) *Rockhaven Cave in Otter Creek State Park, 2♂II, 3♀, T.C.B. and R.A.K., XII/2/61. (3) *Shackletts Cave, SW of Garrett, 2♀, T.C.B. and R.A.K., XII/2/61. (4) *Lime Kiln Cave, 1.35 mi. NW of Battletown, T.C.B. and W.M.A., 3♂II, 2♀, VI/29/65.

Indiana: *Crawford County:* (1) Archibald Cave, SE ¼, NE ¼, SE ¼, sec. T.3S, R.1E, 1♂II, R.M.N., III/8/64. (2) Crawfish Spring, Wyandotte Cave, NW ¼, SW ¼, NW ¼, sec. 27, T.3S, R.2E, 1♀, W. P. Hay, date ?. (3) Stream in Sibert's Well Cave, NE ¼, SE ¼, sec. 28, T.3S, R.2E, 1♂I, 1♂II, 1♀, L.H., IX/1/39. (4) Wyandotte Cave, "From Mr. Palmer's room," 1♂II, coll. and date?. (5) Small cave near Wyandotte [=Sibert's Well Cave ?], 1j♀, W.P.H., date ?. (6) *Marengo Cave, SW ¼, NE ¼, NW ¼, sec. 31, T.3S, R.1E, 1j♀, R.R., date ?. *Harrison County:* (1) *Bradford Cave, SE ¼, SE ¼, SE ¼, sec. 3, T.2S, R.4E, 1♂I, T.C.B., VIII/17/57. (2) *Small cave, 4 miles NE of Mauckport, 1♂I, 1♀, Sherman Minton, date?. (3) King's Cave, NE ¼, SE ¼, SW ¼, sec. 34, T.3S, R.4E, 1♂II, 1♀, T.C.B., VIII/17/57; 1♂I, L.H., VIII/17/57. *Lawrence County:* (1) *Blue Spring Cave, SW ¼, SE ¼, SW ¼, sec. 6, T.4N, R.1W, 2♂I, 1♂II, H.H.H. III, X/25/69; 1♂I, H.H.H. III, VII/7/70. (2) *Shiloh Cave, NW ¼, SE ¼, NW ¼, sec. 18, T.5N, R.1W, 1♂II, 3♀, W.P.H., date?; 1♂II, 2♀, W.P.H., date?; 8♂II, 9♀, W.P.H., date ?; 1♂I, 1♀, T.C.B., I/7/56; 1♀, Thomas C. Jegla, I/27/59; 1♀, T.C.J., I/29/59; 1♂I, 1♀, T.C.J., IX/26/59; 1♂II, 1♀, T.C.J., VI/4/60; 1♀, T.C.J., XII/10/60; 1♂I, 1♂II, T.C.J., IX/23/61; 2♀, T.C.J., XI/19/61; 1♂II, T.C.J., III/12/62; 1♀, T.C.J., VI/30/62; 1♂I, T.C.J., XI/17/62; 1♂I, 2♂II, T.C.J., II/24/63; 2♂II, T.C.J., III/31/63; 1♂II, T.C.J., IV/20/63; 1♂I, 1j♂, T.C.J., V/?/63; 1♂I, T.C.J., VI/20/63; 1♂I, 1♂II, T.C.J., VI/30/63. (3) *Sullivan Cave, NW ¼, SW ¼, SE ¼, sec. 20, T.6N, R.2W, 1♂I, T.C.J., XII/13/59; 1♂II, H.H.H. III, I/23/70. (4) *Donaldson's Cave, NW ¼, NE ¼, NE ¼, sec. 4, T.3N, R.1E, 1♂I, 1♀ with eggs, F. N. Blanchard, date?. (5) *Stream flowing from Donaldson's Cave, 1♂II, C. W. Hart and Dabney G. Hart, VI/26/64. (6) *Wagoner Cave, SW ¼, NE ¼, NE ¼, sec. 19, T.5N, R.2W, 1♀, H.H.H. III, II/21/70. (7) *Harrison Cave, NW ¼, NE ¼, SW ¼, sec. 15, T.3N, R.1W, 1♀, H.H.H. III, V/2/70. (8) *Pless Cave, SE ¼, NE ¼, SE ¼, sec. 5, T.4N, R.1W, 1♂I, H.H.H. III, X/4/70. *Orange County:* (1) *Murray Spring Cave, SE ¼, NW ¼, NW ¼, sec. 6, T.1N, R.1E, 1♂II, H.H.H. III, II/28/70. *Washington County:* Series from each of the two Clifty Caves—(1) *River Cave, NE ¼, SE ¼, SE ¼, sec. 14, T.3N, R.2E, 1 ♀, J.R.R., VI/3/65. (2) *Endless Cavern, NE ¼, SE ¼, SE ¼, sec. 14, T.3N, R.2E, 1 ♂ I, 1 ♂ II, 1 ♀, H.H.H. III, II/28/70; 1 ♂ I, H.H.H. III, VI/28/70. (3) *Fredericksburg Cave, SE ¼, NW ¼, SE ¼, sec. 4, T.1S, R.3E, 2 ♂ I, 1 ♀, H.H.H. III, IX/27/70.

RANGE.—*Orconectes inermis inermis* ranges from Green County, Kentucky, northward into Crawford County, Indiana, intergrading with *O. i. inermis* northward to Monroe County, Indiana.

VARIATIONS.—*Orconectes inermis* is, with little doubt, the most highly variable of the four troglobitic members of the genus. Not only are there variations associated with restricted portions of its range but also the variations that occur within a single locality far exceed those that might be anticipated. The most conspicuous of the variations noted are those of the armature of the carapace and chelipeds, and there is no evidence of sexual dimorphism in the relative numbers or degrees of development of the spines and tubercles. In most other respects, the variations within a single population are neither greater nor less than those which occur in most epigean and other troglobitic crayfishes. Generally, there is a marked direct correlation between the relative development of spines and tubercles on the carapac and chelipeds, and although there are exceptions to the generalization that the southern members of the species have more and larger spines than do the northern members, it is apparently true that none of the Indiana forms approach in their armature that of the most spiny individuals from Kentucky. By selecting individuals, one could demonstrate an almost uninterrupted cline between the very spiny individuals from Hart and Hardin counties, Kentucky, and the almost spineless members from Monroe County, Indiana. Although inadequate series of specimens from most portions of the range of the species prevent our being able to make meaningful ratios of the numbers of spiny to aspinous members occurring in the various populations, it seems clear that, whereas in the extreme north there are no spiny individuals, in many if not in most of the southern localities the spiny individuals far outnumber the aspinous ones. In the area from Lawrence County, Indiana, southward to Meade and Breckenridge counties, Kentucky, there is more nearly a balance between the two, with the most conspicuous breaks occurring between the populations of Monroe and Lawrence counties and between those of Meade and Breckenridge counties.

To illustrate the limits of variation in the armature of the carapace among the specimens available to us, a series of camera lucida sketches of individuals from throughout the range of the species are presented in Figures 12 and 13.

Four localities are represented in our collections from Hart County, Kentucky. In both Riders Mill Cave (Figure 13*c, d*) and Cooch Webb Cave (Figure 13*e, f, g*) there are considerable variations in the development of the marginal spines of the rostrum, the postorbital, cervical, and hepatic spines. Most individuals have moderately prominent spines and approach the maximum development shown in Figure 13*c*, but fewer numbers more nearly resemble the individual depicted in Figure 13*d*. The two specimens from Cub Run Cave (Figure 13*a, b*) are vastly less ornamented, and that from Turner Cave has, at least, as poorly developed spines as the smoother specimen from Cub Run Cave. Among the specimens from Hart County, the areola ranges from 37.4 to 41.5 (average 39.2) percent of the entire length of the carapace and is from 4.4 to 6.7 times longer than wide.

Strongly developed spines are characteristic of the populations in the two caves in Hardin County (Figures 12*y, z* and 13*i*), and among them are the most prominently armored members of the species. Even the least spiny individual has well-developed cervical, postorbital, and rostral spines together with two hepatic spines on each side of the carapace. The development of the long acumen seems to be responsible for the apparently short areola which constitutes 38.4 to 40.7 (average 39.3) percent of the length of the carapace and is 4.7 to 6.7 times longer than wide.

In Breckenridge County, the population in Lockard Cave (Figure 12*v, w*) has the most spines. In Thornhill Cave (Figure 12*t, u*) and the cave near Big Spring (Figure 12*q*), the range of variation is greatest. Although the crayfish in Bandy Cave (Figure 12*r, x*) are variable, most have weakly developed spines, and in some even the marginal spines on the rostrum are more tuberculiform than spiniform. In Bat Cave the animals have an almost smooth carapace with spines no more strongly developed than the least spiny of those from Bandy Cave. In Breckenridge County, the areolae constitute from 37.0 to 42.4 (average 40.0) percent of the carapace length and range from 4.7 to 6.3 times longer than broad.

The populations from Meade County (Figure 12*n, o, p*) may be categorized as almost aspinous; not even the single small cervical spines and marginal spines on the rostrum are consistently acute, and none exhibits a single moderately well-developed hepatic spine. Nevertheless, there is always at least a tubercle at the base of the acumen. The areolae range from 39.0 to 42.4 (average 40.8) percent of the carapace length and is 4.7 to 6.4 times longer than broad.

Across the Ohio River in Crawford County, Indiana, variation is much more pronounced than in Meade County, Kentucky. Those specimens from Sibert's Well Cave (Figure 10*c, h*), Archibald Cave (Figure 12*g*), and the small cave near Wyandotte all have moderately well-developed rostral and as many as three cervical spines, and the Sibert's Well specimens all have hepatic spines as well. In sharp contrast, the specimens from Marengo Cave (Figure 12*h*) and one of those from Blue Spring Cave not only lack rostral spines or tubercles but also possess an areola constituting more than 44 percent of the length of the carapace, thus possessing the characteristics of *O. i. testii.* The other specimen from Blue Spring Cave, that from Crawfish Spring, and one from Wyandotte Cave are somewhat intermediate between these two types and their areolae constitute 41.9 to 42.3 percent of the carapace length. The areolae of the Crawford County specimens range from 38.0 to 44.5 (average 41.3) percent of the length of the carapace and is 5.1 to 6.6 times longer than wide.

Our single specimen from Orange County agrees rather well with those from Sibert's Well Cave; its areola constitutes 41.5 percent of the carapace length and is 6.8 times longer than broad.

Among our four specimens from Harrison County, the two from Kings Cave (Figure 12*l*) have small rostral spines and cervical spines, but those from the other two localities (Figure 12*m*) are devoid of rostral spines, and that from the small cave northeast of Mauckport lacks even a cervical spine. None of the Harrison County specimens have hepatic spines. The areola of these specimens ranges from 42.2 to 43.6 (average 43.0) percent of the carapace length and from 6.3 to 7.1 times longer than broad.

The four specimens from Washington County (Figure 12*k*) exhibit almost as much variation as those from Shiloh Cave in Lawrence County (see below). All have small cervical spines; the rostrum of one specimen lacks marginal spines, that of two has weak tubercles, one has small spines, and their areolae constitute 41.2 to 41.8 percent of the carapace length and are 5.3 to 7.1 times longer than broad.

The much larger series from Lawrence County, mostly from Shiloh Cave, is quite variable, but not nearly to the extent of those from Crawford County. The extremes of variation are depicted in Figure 12*c-e* in which it may be seen that all specimens bear small cervical tubercles or spines, and the rostral margins frequently bear short spines or tubercles, and most are angular at the base of the acumen. Some, however, have rostra with uninterrupted margins, in this respect resembling typical *O. i. testii.* Only one specimen (Figure 12*f*) from Sullivan Cave has moderately strong cervical and hepatic spines. Nevertheless, only one of the specimens measured has an areola constituting less than 40 percent of the carapace length, the range of which is 39.2 to 44.0 (average 42.3) percent and its length 4.3 to 6.5 times its width.

All the specimens from Monroe County (Figure 12*a, b*) consistently lack rostral and hepatic spines, and the cervical spines are reduced to spiniform or blunt tubercles of which generally there is but one. The areola constitutes from 42.3 to 45.9 (average 44.6) percent of the length of the carapace and ranges from 4.9 to 6.4 times as long as broad.

Were not the Monroe specimens so uniformly less spinous than those forms in the more southern localities, and did they not possess areolae which are generally distinctly proportionately longer than those of almost all of their close relatives that range to the south, we would be inclined to agree with Rhoades (1962) and treat Hay's *Cambarus pellucidus testii* as a synonym of *Orconectes inermis.* There is the further disqueting fact that the type-locality of *O. inermis* is situated near the middle of the range of the species. In spite of this fact, it seems more desirable to emphasize the uniform divergence of the Monroe County populations from the more southern ones; therefore, we recognize them as constituting the subspecies *O. inermis testii.* In summary, we view the specimens from Sibert's Well Cave and the populations from Breckenridge, Hardin, and Hart counties, Kentucky, as typical *O. i. inermis,* those from Monroe County, as typical *O. i. testii,* and those from the intervening area as intergrade populations.

That an occasional specimen of what might appear to be typical of one of the two subspecies should be found within the range of intergradation may, perhaps, cause some concern, but if there is a gene flow between the two extremities of the range of the species, then the presence of such individuals in the area might well be anticipated. With respect to the development of the spines on the carapace and chelipeds, if it is under the control of some genetic mechanism rather than an ecophenotypic effect, then the flow from north to south seems to have been greater than that in the reverse direction.

Such an hypothesis would help to explain the apparent semi-isolation of the more spiny individuals in Sibert's Well and Archibald caves (perhaps also the population in Murray Spring from which we have only one specimen). If it could be demonstrated that they represent small isolated populations off the mainstream of gene flow, then one might postulate that, in a sense, in them are preserved the primitive spiny characteristic which is gradually being replaced by the more advanced aspinous one in the populations along the path of the mainstream of gene flow. As has been pointed out above, it is our belief that *O. i. inermis* is distinctly more primitive than *O. i. testii* and that the invasion of the Indiana caves was from an *inermis* stock moving northward in subterranean channels from Kentucky. Somewhere in its trek across southern Indiana, a segment of the stock lost its spines and came to dominate the northernmost portion of the range. That the innovation was a successful one can hardly be questioned, and our materials indicate that the gene, or combinations of genes, responsible for the reduced spination is now moving in a southerly direction, invading the ancestral range of the species.

SIZE.—The largest specimen among those that we have examined is a female having a carapace length of 36.9 mm, and was collected in Bat Cave, Breckenridge County, Kentucky. The largest first-form male, 32.9 mm, was found in Lockard Cave, also in Breckenridge County, and the smallest first-form male, 18.2 mm, in Blue Spring Cave, Lawrence County, Indiana.

LIFE HISTORY NOTES.—Among the specimens examined in this study, first-form males were present in collections made throughout the year except in March and April, months represented by a total of only seven specimens. A single ovigerous female was collected in Donaldson's Cave in June, 1924; this specimen has a carapace length of 23.9 mm, and 27 eggs are either attached to her pleopods or are in the bottom of the container. Jegla (1969) observed four females carrying eggs during his study in Shiloh Cave: one on June 30, two on August 16, and one on August 20. These crayfish carried an average of 45 eggs each.

SEASONAL COLLECTIONS OF SPECIMENS EXAMINED

Sex	*Jan.*	*Feb.*	*Mar.*	*Apr.*	*May*	*June*	*July*	*Aug.*	*Sept.*	*Oct.*	*Nov.*	*Dec.*	*Not known*	*Total*
♂I	2	1	–	–	1	2	1	1	7	13	4	4	11	38
♂II	3	4	3	1	–	12	3	2	14	2	5	11	12	72
♀	3	1	1	–	–	10	–	1	13	7	16	19	14	84
juv. ♂	–	–	–	–	1	–	1	–	–	–	1	1	–	4
juv. ♀	–	–	2	–	–	–	1	–	–	–	2	–	–	3
Totals	8	6	6	1	2	24	6	4	34	22	28	35	37	206

Orconectes inermis testii (Hay)

FIGURES 1, 11, 12*a–b*

Cambarus pellucidus.—Packard, 1888:16 [in part].—Faxon, 1890:621 [in part].—Blatchley, 1897:127.—Ortmann, 1902:277, 278, 279 [in part]; 1905a:92 [in part].—Harris, 1903b:167.—Graeter, 1909:470.—Spurgeon, 1915:387–394.—Ortmann, 1918:838, 848 [in part].—Hobbs, 1942a:352 [in part].

Orconectes pellucidus inermis.—Packard, 1888:41.—Rhoades, 1959:401–402 [in part].—Nicholas, 1960:133 [in part].—Hart and Hobbs, 1961:176 [in part].—Rhoades, 1962:68 [in part].

Cambarus pellucidus var. *testii* Hay, 1891:148.—Spandl, 1926:95.—Wolf, 1934–1938:105 [in part].

Cambarus pellucidus testii Hay, 1893:283, 285, 286, pls. 44, 45, figs. 2, 5, 6, 10, 11, 12; 1896:478, 484, 485, fig. 4; 1897:209.—Faxon 1898:647.—Hay, 1899:959, 966.—Harris, 1903a:606; 1903b:58, 112, 118, 151, 152, 162.—Banta, 1907:69–71, 87, 90.—Faxon, 1914:415.—Spurgeon, 1915:385–394 [in part].—Creaser, 1932:336.—Rhoades, 1941:144; 1959:400, 401.

Cambarus pellucidus testi.—Hay, 1902a:233, 235.

Blind cray-fish.—Banta, 1905:853.

Cambarus (Faxonius) pellucidus.—Ortmann, 1905a:97, 107, 108 [in part]; 1905b:435 [in part].

Cambarus (Faxonius) pellucidus testi.—Ortmann, 1931:64 [by implication].

Orconectes pellucidus.—Spandl, 1926:95.—Pennak, 1953: 458 [in part], 459, fig. 286.—Eberly, 1958:1–6 [in part].

Orconectes pellucidus testii.—Hobbs, 1942a:352 [by implication].—Rhoades, 1944:117.—Hobbs, 1948a:19, 20.—Eberly, 1954:59; 1955:281, 282; 1958:3; 1960:30.—Holthuis, 1964:43.—Hart and Hart, 1966:8.—Hobbs, 1967b:12.

Orconectes (Orconectes) pellucidus testii.—Hobbs, 1942a: 352 [by implication].

Cambarus (Cambarus) pellucidus testii.—Balss, 1955:1311.

Orconectes (Orconectes) pellucidus.—Hobbs, 1959:890 [in part].

Blind crayfish.—Powell, 1961:82, 89.

Photograph.—Stenuit and Jasinski, 1964:75; 1966:75.

Orconectes.—Barr, 1968:85 [in part].

REVIEW OF LITERATURE.—The earliest reference to this crayfish is that of Packard (1888) who indicated that Mr. C. H. Bollman had visited Mayfield's Cave and found *Cambarus pellucidus* there. Faxon (1890) repeated the localities given by Packard and Hay (1891) proposed the varietal name *testii* for the crayfishes in Mayfield's and Truett's caves.

Hay (1893) elevated his varietal name, employing the combination *Cambarus pellucidus testii*, pointed out its diagnostic features and presented illustrations. In 1896, he included this crayfish in his key to the crayfishes of Indiana, outlined its outstanding features, presented three figures, and made the statement that the "first abdominal appendages of the male do not differ in any respect from those of typical *C. pellucidus*."

Blatchley (1897) gave a brief description of Mayfield's Cave, and indicated that *C. pellucidus* was one of its inhabitants. Hay (1897) mentioned the species but added no new information.

Faxon (1898) added no additional information but made the following statement: "So this form comes to bear a close likeness to *C. bartonii* and suggests the possible derivation of *C. pellucidus* from *C. bartonii*."

Hay (1899) included this crayfish in his list and key to the Astacidae of North America. In a later observation he (1902a) added no additional data but, in commenting on its relationships, stated that "Regarding the relationship of *C. pellucidus testi* Hay, I will say that so far as is known this subspecies is found in a very small area in Indiana at the very northern limits of the range of *C. pellucidus*. *C. bartoni* [=*C. laevis*] occurs in the same cave, but it does not resemble the blind species in any way, and has not even characters by which we can mark it as a permanent resident. Were the conditions reversed and *C. bartoni tenebrosus* [=*C. tenebrosus*] found anywhere in company with *C. pellucidus testi* there might be some grounds for regarding them both as possible intermediates between *C. pellucidus* and *C. bartoni*, but under conditions as they exist such a view is untenable."

Ortmann (1902, 1905a, 1905b), in discussing the affinities of *C. pellucidus*, did not mention Hay's subspecies, but his remarks about the species were presumably intended to apply to it. The species was assigned to his subgenus *Faxonius* (1905a).

Harris (1903b) catalogued the information published by the above authors, but most of the natural history data (pages 113–118) included under *Cambarus pellucidus testii* are based on observations on *O. pellucidus* or those of Hay on the intergrades *inermis* x *testii* in Shiloh Cave. Banta (1905) added no new data.

Banta (1907) adopted Hay's subspecific designation for the troglobite in Mayfield's and Truett's caves but indicated that the "subspecies is not clearly defined." Inasmuch as his observations represent the only significant account of observations on this crayfish in its native habitat, most are quoted here.

"This crayfish is usually seen quietly resting on the bottom of a pool. Rarely one is observed walking slowly. When roughly disturbed it acts and swims much as other crayfish do when excited; that is, it swims without regard to the edge of the pool or even the direction of the bank. However, if there is a disturbance of the water and the crayfish becomes aware of the pursuer while at a distance or before being touched, it in nearly every case, swims or crawls toward protecting rocks shelving over the edge of the pool, or to some other such means of concealment. If there is no such protection it moves toward the opposite side of the pool. It occasionally retreats to a hole under a rock. *C. bartoni* [=*C. laevis*] is quite often found in such holes. Possibly *C. bartoni* alone forms these holes and *C. pellucidus* makes use of them when deserted by *C. bartoni*. Often when slightly disturbed by an object close at hand *C. pellucidus* backs off, then turns around, and crawls forward. However, when disturbed it usually starts to swim immediately. If crowded when crawling forward toward a place of concealment, it begins to swim caudal end foremost without first turning about and really swims toward its pursuer. But the moment it begins to swim it either turns squarely over ventral side up or turns to one side so as to move in the direction in which it was crawling. After changing the direction of its course it rights itself and soon disappears if there is ready means of concealment. In its swimming and crawling motions this crayfish is not less active than other crayfish.

"This species is sensitive to a jar in the water at a distance of several feet if the disturbance is quite pronounced, like that produced by dropping a pebble into the pool. But considerable rippling or slow swishing about in the water often fails to produce any effect upon individuals at a little distance. It seems insensible to sound, although a heavy jar on the bank of the pool may cause it to move. Light often fails to have any apparent effect, but on two occasions when a bright light was suddenly flashed upon perfectly quiet individuals they moved immediately, swimming rapidly from the lighted area. In these two cases there could have been no jar or other disturbance, for I had quietly crept to near the individuals from a distance and then suddenly thrown the light full upon them. Sometimes when the light was held upon individuals for several minutes they failed to respond at all; usually, however, they moved after two or three minutes."

On the basis of laboratory observations, Banta stated the belief that "they moult two to four or five times a year depending upon the size, the smaller or younger ones molting oftener." "Very young individuals were seen during February and March, the earliest date being February 17."

Graeter (1909) summarized the observations of Hay and Banta, referring to this crayfish as "Varietät." Faxon (1914) only included this subspecies in his checklist.

Spurgeon (1915), in studying the eyes of two troglobitic species, utilized specimens of both *O. i. inermis* and *O. i. testii.* (See Review of Literature for *O. i. inermis,* page 39.) Ortmann (1918) mentioned that *C. pellucidus* occurs in caves in Indiana.

Spandl (1926) added no new data but mentioned Hay's variety *testii* "in den Mayfield- und Tuett [sic]-Höhlen." Similarly, Ortmann (1931) and Creaser (1932) only recorded the crayfish from Indiana; the former, however, discussed the ranges of *C. pellucidus testii* and its relatives.

Wolf (1934–1938) misinterpreted distribution records for this crayfish in previous literature, thus adding several erroneous records.

Rhoades (1941) stated that "no doubt *C. pellucidus australis* of the South bears the same affinity to *C. pellucidus pellucidus* as does *Cambarus pellucidus testii* Hay (1893) of the North."

In his generic revision, Hobbs (1942a) assigned *Cambarus pellucidus,* including its subspecies, to the genus *Orconectes,* and in recognizing the subgenus *Faxonella* (1942b) implied that these crayfishes were members of the typical subgenus.

Rhoades (1944) assigned *O. p. testii* to his "Group rafinesquei" because "the gonopods are short and the tips are separated for only a short distance" and "the tips are both recurved in the same direction." Hobbs (1948a) discussed the affinities of the crayfishes of the Limosus Section, questioning the validity of Rhoades' Limosus and Rafinesquei groups but did not contribute any new data for this subspecies.

Pennak (1953) recorded *O. pellucidus* from Indiana, and his figure 286 is redrawn from Hay's (1893) illustration of *O. p. testii.*

Eberly (1954) discussed the association of this crayfish with *Cambarus laevis,* and (1955) added two new locality records in Monroe County, Indiana. Later (1958 and 1960) he cited the occurrence of the subspecies in the same county. Balss (1955) presented no original information and erroneously cited this crayfish from Wyandotte Cave. Hobbs (1959) did not refer to the subspecies by name, but in his key indicated that four subspecies of *O. (O.) pellucidus* ranged from Indiana to Alabama.

Rhoades (1959) compared the descriptions of Cope's *O. inermis* and Hay's *O. pellucidus testii* and concluded that the latter is synonymous with *O. inermis* and adopted the combination *O. pellucidus inermis* for both. Although he mentioned populations occurring in Brown and Bartholomew counties, Indiana, he cited no specific localities.

In his checklist of troglobites in North America, Nicholas (1960) followed Rhoades (1959) in recognizing *O. p. inermis* as the only troglobitic crayfish other than *O. p. pellucidus* occurring in Indiana.

Powell (1961) reported "blind crayfish" from two caves in Monroe County, Indiana.

Hart and Hobbs (1961) cited *O. pellucidus inermis* in May's and Eller's caves as a host of *Entocythere barri (=Sagittocythere barri).*

Rhoades (1962) again treated *O. p. testii* as a synonym of *O. p. inermis* in his discussion of the evolution of the crayfishes of the Limosus Section of the genus.

Stenuit and Jasinski (1964 and 1966) published a photograph of this crayfish.

Holthuis (1964) mentioned the subspecies in comparing the descriptions of *O. pellucidus* with Joseph's *Cambarus stygius.* Hart and Hart (1966) cited this crayfish as a host of the commensal entocytherid, *Sagittocythere barri,* in May's Cave, Monroe County, Indiana. Hobbs (1967b), in discussing parallel evolution in relatives of *Procambarus pecki* and *O. limosus,* referred to this subspecies.

The most recent reference to this crayfish was that of Barr (1968) who alluded to it in briefly discussing the origin of the troglobitic *Orconectes* fauna.

COMMENTS ON PREVIOUSLY RECORDED DATA.—Along with Packard's (1888) citation of the occurrence of this crayfish in Mayfield's Cave, he also quoted from a letter from Dr. John Sloan who reported that "three eyeless crayfishes" had been collected in "Caves at Clifty," a locality which Packard reported as being located in Bartholomew County. Actually the caves referred to are in Washington County. Spurgeon (1915) mentioned collecting crayfishes in Clifty Cave in the latter County. We have specimens from River and Endless caves (the Clifty caves) and they belong to what we consider to be the intergrade population, *inermis* x *testii.*

Hay's (1893) statement that the first pleopods "do not differ in any respect from those of" *O. pellucidus* obviously is incorrect (cf. Figures 11*a, e, g* and 14*a, e, j*) .It seems highly probable to us that Hay's comparison was made with specimens which were from the more southern Indiana counties and which he considered to be conspecific with *O. pellucidus* but were either *O. i. inermis* or intergrades between *O. i. testii* and the latter.

Faxon's (1898) statement that *O. i. testii* might represent an intermediate form between *O. pellucidus* and *C. bartonii,* suggesting a possible derivation of *O. pellucidus* from the latter, was refuted by Hay (1899) and has received no further consideration.

Our reasons for not adopting the treatment of this subspecies proposed by Rhoades (1959) have been discussed under *O. i. inermis.* His statement (1962: 68), however, that *Orconectes pellucidus inermis* "is the blind crayfish of cave waters of Monroe, Brown, and Bartholomew counties in south central Indiana" leaves some doubt as to his concept of Cope's *inermis,* for the type-locality of the latter is in Crawford County. Rhoades' reference to specimens from Brown County is the only one that we have encountered, and, unfortunately, he cited no specific locality. If his reference, without specific locality, to specimens in Bartholomew County is based on the "Clifty Caves" record of Packard, then there are no records of this or any other troglobitic crayfish for that county. None of the Indiana speleologists, including Mr. Richard L. Powell of the Indiana Geological Survey, consulted by us is aware of the existence of caves in either Bartholomew or Brown counties.

See also the comments on previously recorded data under *Orconectes i. inermis* (page 42).

DIAGNOSIS.—Albinistic; eyes reduced and without pigment; rostrum without marginal spines or tubercles, acumen not delimited at base from remainder of rostrum, margins convergent, upper surface without median carina; postorbital ridges terminating cephalically without tubercles or spines; hepatic area devoid of spines; at most, cervical spines represented by very small tubercles; areola 4.6 to 6.4 times longer than broad and constituting 42.3 to 45.8 percent of entire length of carapace; chelae not conspicuously setose but with ciliated tubercles and punctations and a few long stiff setae; mesiodorsal surface of palm with several irregular rows of tubercles; hooks on ischiopodites of third and fourth pereiopods. First pleopod of first-form male with greatest cephalocaudal diameter of pleopod less than twice that immediately proximal to base of central projection, always terminating in only two elements; non-corneous mesial process broad basally, suddenly contracting to form tapering subacute distal portion, latter directed caudodistally and extending distally to about level of, or slightly exceeding tip of, central projection; central projection corneous, flattened in cephalocaudal plane, slightly concavoconvex with convexity extending mesially; shoulder lacking at base of central projection but cephalic surface with convexity on distal half of appendage. Annulus ventralis as illustrated in Figure 11*k*.

Topotypic Male (Form I): Body (Figure 11*c, l*) subovate, depressed. Abdomen narrower than thorax (8.8 and 9.6 mm in widest parts, respectively). Width

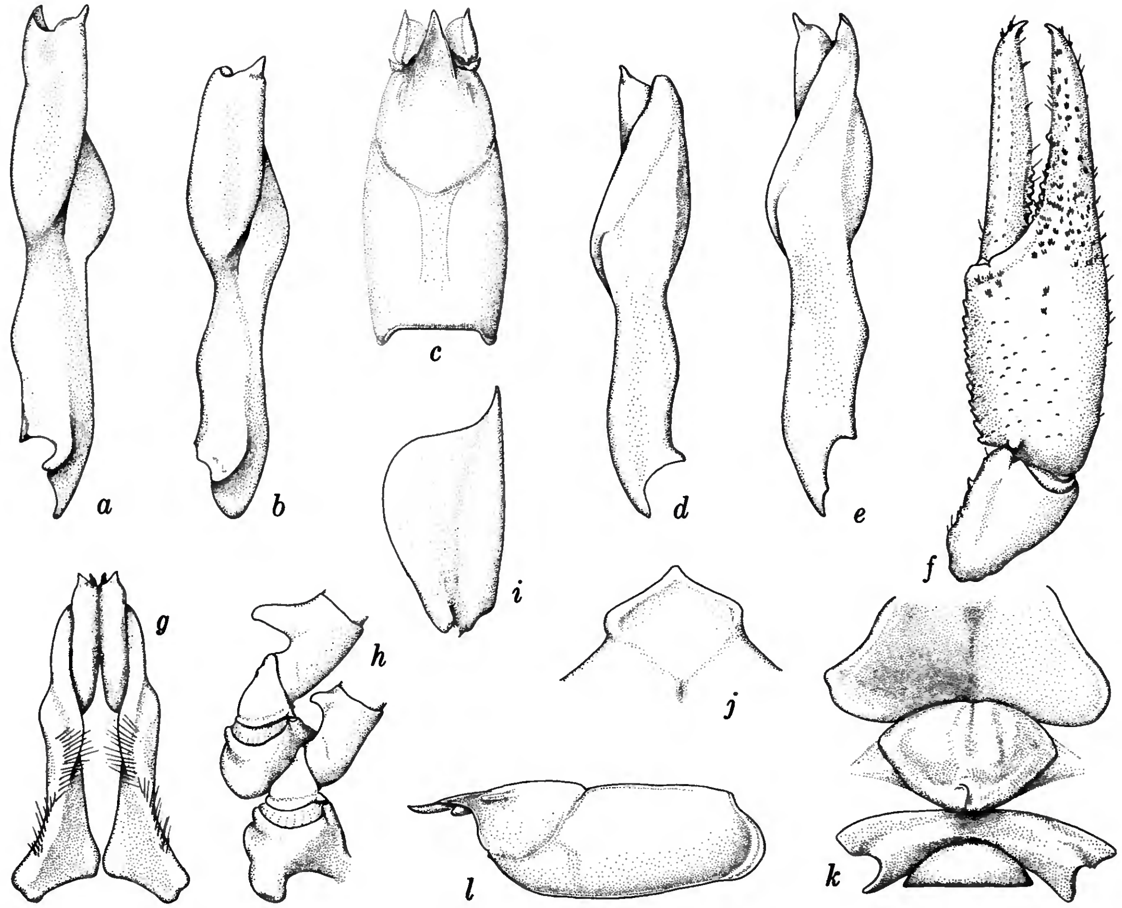


FIGURE 11.—*Orconectes inermis testii:* *a*, mesial view of first pleopod of topotypic male, form I; *b*, mesial view of first pleopod of topotypic male, form II; *c*, dorsal view of carapace of topotypic male, form I; *d*, mesial view of first pleopod of topotypic male, form II; *e*, lateral view of first pleopod of topotypic male, form I; *f*, dorsal view of distal podomeres of cheliped of topotypic male, form I; *g*, caudal view of first pleopods of topotypic male, form I; *h*, basal podomeres of third and fourth pereiopods of topotypic male, form I; *i*, antennal scale of topotypic male, form I; *j*, epistome of topotypic male, form I; *k*, annulus ventralis and portion of sternum of topotypic female; *l*, lateral view of carapace of topotypic male, form I.

of carapace greater than depth in region of caudodorsal margin of cervical groove (9.6 and 7.5 mm). Areola moderately broad (5.5 times longer than wide) with 5 or 6 minute punctations across narrowest part. Cephalic section of carapace 1.3 times longer than areola; length of areola 43.1 percent of entire length of carapace. Rostrum with length about 1.5 times width at base, excavate, and with acumen approximately 0.65 times as long as maximum width; cephalic extremity reaching only to end of antennular peduncle; margins not swollen, little elevated, and uninterrupted by marginal spines or tubercles; upper surface with regularly spaced, minute, setiferous punctations; subrostral ridges moderately well developed and evident in dorsal aspect along basal third of rostrum.

Postorbital ridges weakly developed, short, with shallow dorsolateral grooves, and terminating cephalically without spines or tubercles. Suborbital angle lacking. Branchiostegal spines acute but small. Cervical spines represented by row of 2 or 3 very small tubercles on each side of carapace immediately caudal to cervical groove, tubercles progressively larger ventrally. Carapace punctate dorsally and very weakly granulate laterally; hepatic area with inconspicuous granuliform tubercles but lacking spines. Abdomen longer than carapace (25.0 and 21.7 mm). Cephalic section of telson with 2 well-developed spines in each caudolateral corner (mesial ones movable).

Protruding portion of epistome (Figure 11*j*) approximately twice as long as broad and resembling silhouette of shortened minaret; surface flattened and with fine setae; fovea present posteriorly. Eyes much reduced, without pigment, almost completely hidden beneath rostrum in dorsal aspect and extending cephalically slightly more than half distance between margin of orbit and base of acumen. Antennules of usual form with moderately well-developed spine on ventral surface of proximal podomere at base of distal fifth. Antennae extending caudally beyond end of telson for distance equivalent to length of telson. Antennal scale (Figure 11*i*) broadest distal to midlength, about half as broad as long; outer thickened portion much narrower than lamellar area and terminating distally in prominent corneous-tipped spine. Third maxillipeds extending to about midlength of distal podomere of peduncle of antenna.

Chela (Figure 11*f*) comparatively slender and not much inflated; mesial margin of palm approximately 1.4 times longer than width of palm; dorsal surface of palmar area tuberculate mesially and punctate laterally, punctations and distal bases of tubercles setose; ventral surface of palm with weak tubercles and with small corneous-tipped spiniform tubercle opposite base of dactyl; more mesial tubercles on palm larger and sublinearly arranged, with 9 or 10 comprising most mesial row; lateral surface tuberculate. Fingers not gaping; dorsal and ventral surfaces with broad, rounded, submedian, longitudinal ridges flanked by setiferous punctations; opposable margin of immovable finger with row of 7 tubercles, fifth from base largest, along proximal two-fifths, single tubercle below level of row slightly proximal to midlength of finger, and single row of minute denticles between proximal five tubercles, distally forming two rows extending almost to base of corneous tip of finger; lateral surface of immovable finger subcostate. Opposable margin of dactyl with row of 5 tubercles along proximal two-fifths, distalmost largest, with denticles arranged as on immovable finger; mesial surface of dactyl almost smooth. Carpus longer than broad, with mesial, dorsomesial, and ventromesial surfaces tuberculate, otherwise mostly punctate; mesial surface with 2 tubercles somewhat larger than others, largest distinctly acute; distoventral margin with 2 acute tubercles, 1 adjacent to base of ventrolateral articulation with propodus and 1 near median line. Merus tuberculate dorsally, with 2 corneous-tipped tubercles slightly proximal to distal end; mostly punctate mesially and laterally; ventrolateral margin with row of 9 prominent tubercles, and ventromesial margin with 12; few scattered tubercles flanking both rows; distolateral extremity with small corneous-tipped spine. Ischium with ventromesial row of 6 small tubercles; dorsal margin scabrous but with only 2 well-defined tubercles.

Ischia of third and fourth pereipods (Figure 11*h*) with hooks; those on third stout and recurved to or beyond level of cephalic articulation with basis; those on fourth much smaller and, although recurved, leaving broad gap between tip and corresponding basis. Coxae of fourth pereiopods with caudomesially projecting prominences; coxae of fifth pereiopods without prominences except for small mesioventral projection partially surrounding base of phallic papilla.

First pleopods (Figure 11*a, e, g*) symmetrical, reaching bases of third pereiopods when abdomen is flexed, and comparatively shallowly situated in sternal groove; tip ending in two parts as described in Diagnosis.

Topotypic Female: Differs from male in following respects: apex of rostrum reaching only midlength of ultimate podomere of peduncle of antennule; cervical spines represented by 4 minute tubercles, ventralmost largest but scarcely larger than other tubercles on hepatic and branchiostegal regions; cephalic section of telson with only 1 spine in caudodextral corner; opposable margin of immovable finger of chela with row of 11 tubercles along basal three-fifths, fourth from base largest; opposable margin of dactyl of chela with row of 15 small tubercles and with 2 larger tubercles below level of row and between fourth and fifth tubercles.

Annulus ventralis (Figure 11*k*) shallowly situated in sternum and not firmly fused to sternum immediately cephalic to it; outline subovate, 1.6 times broader than long, with median portion elevated ventrally forming asymmetrical arc with highest segment approximately at midlength; arched portion bearing shallow longitudinal groove ending caudally on steep slope of arc; sinus originating on slope dextral to median line, making gentle arc to median line and extending caudally to midcaudal margin of annulus.

Syntypic Male, Form II: Differing from first-form male in following respects: rostrum reaching almost to distal end of peduncle of antennule; cervical tubercles exceedingly minute, only one at all larger than granulations cephalic and caudal to it; branchiostegal spines almost obsolete; lower surface of palm of chela with few tubercles on lower proximomesial surface; opposable margin of immovable finger of chela with row of 20 small tubercles along proximal five-sixths of finger and with 2 larger ones situated below level of row between fourteenth and sixteenth tubercles; opposable margin of dactyl of chela with row of 26 along proximal six-sevenths of finger and with 2 larger ones situated below level of row between seventh and ninth tubercles. Hooks on ischia of third and fourth pereiopods comparatively more reduced, but boss on coxa of fourth only slightly smaller. (See measurements.)

First pleopod (Figure 11*b, d*) reaching base of third pereiopod when abdomen is flexed and with most features of first-form male; however, central projection non-corneous, shorter, and more inflated.

MEASUREMENTS (in millimeters).—*Orconectes inermis testii:*

	Topotypic Male Form I	*Topotypic Female*	*Syntypic Male Form II*
Carapace:			
Height	7.5	9.8	9.2
Width	9.6	13.0	12.3
Length	21.7	27.8	26.7
Rostrum:			
Width	3.2	3.8	4.1
Length	4.9	6.0	5.5
Areola:			
Width	1.7	2.3	2.3
Length	9.4	12.8	11.9
Chela:			
Length of inner margin of palm	6.8	7.6	9.2
Width of palm	5.0	6.2	6.7
Length of outer margin of chela	16.6	19.5	25.6
Length of dactyl	9.2	10.6	14.6

TYPES.—Syntypes, USNM 17702 (2♂II, 1♀), Museum of Comparative Zoology 7431 (1♂II, 1♀).

TYPE-LOCALITY.—Mayfield's Cave, SW ¼, NE ¼, SW ¼, sec. 26, T.9N, R.2W, Monroe County, Indiana.

SPECIMENS EXAMINED.—Specimens from Indiana were examined as follows:

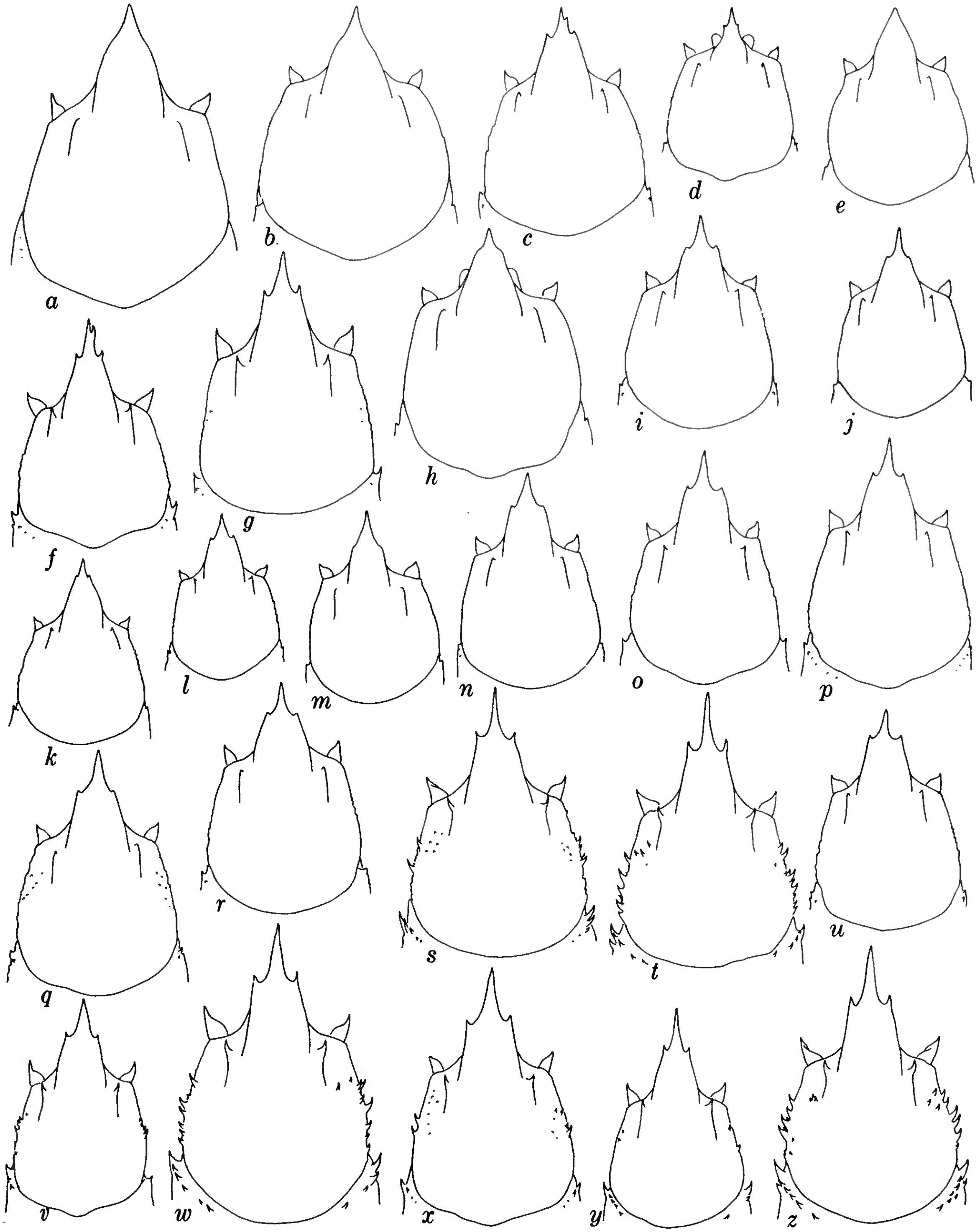
Monroe County: (1) Carmichael Cave, NW ¼, NW ¼, SW ¼, sec. 19, T.7N, R.1W, 1♂I, H.H.H. III, X/4/69. (2) Eller's Cave, NW ¼, NW ¼, SW ¼, sec. 15, T.8N, R.2W, 3♂I, 1♂II, 1♀, W. R. Eberly, I/10/53; 1♂II, 1♀, H.H.H. III, X/21/69; "probably from Eller's Cave," 2♂I, 2♂II, 1♀, date and collector unknown. (3) Mayfield's Cave, SW ¼, NE ¼, SW ¼, sec. 26, T.9N, R.2W, 2♂II, 1j♀ [syntypes], W.P.H., date unknown; 2♂II, 3♀, 1j♂, W.P.H., date unknown; 1♂I, 1♀, T.C.J., X/17/59; 1♂I, T.C.J., II/19/60; 1♂II, H.H.H. III, IX/20/69. (4) May's Cave, SW ¼, SE ¼, NE ¼, sec. 24, T.8N, R.2W, 1♂II, 1♀, 1951, collector unknown; 1♀, C.E.B., I/18/51; 1♂II, 1♀, T.C.B., VIII/19/57; 1♀, H.H.H. III, IX/26/69; 1♂II, collector and date unknown. (5) Reeve's Cave, SW ¼, SW ¼, NE ¼, sec. 34, T.8N, R.2W, 1♀, H.H.H. III, X/3/69. (6) Salamander Cave, SW ¼, SW ¼, NW ¼, sec. 9, T.8N, R.2W, 1♀, H.H.H. III, X/8/69. (7) Shaft Cave, NE ¼, NE ¼, SE ¼, sec. 8, T.8N, R.2W, 1♂I, 1♀, H.H.H. III and K. Burdsall, XII/5/69.

This crayfish was reported by Hay (1891) and others to occur in Truett's [sic] Cave in Monroe County, and it is probable that the "blind crayfish" observed in Goode's Cave and Ranard School Cave by Powell (1961:82, 89) were member of this subspecies. No specific localities are known for Bartholomew and Brown counties.

RANGE.—*Orconectes inermis testii* is thus restricted to the subterranean waters of Monroe County, Indiana, but intergrades with the typical subspecies in the more southern counties of the State.

The restricted gene flow between *inermis testii* and *inermis inermis* is geographically paralleled in the troglobitic beetle *Pseudanophthalmus shilohensis* Krekeler (Carabidae). Nominate *shilohensis* occurs in most Lawrence County caves north of the East Fork of the White River, but the Monroe County caves are occupied by *P. s. mayfieldensis* Krekeler (T. Barr, manuscript in preparation). The biogeographic similarities in the distribution of these two polytypic species of arthopods suggest a limited and only partially effective extrinsic barrier between the Bedford area caves and those of the Bloomington area.

VARIATIONS.—Although minor variations are abundant in our comparatively few specimens of this crayfish, all of them seem to be individual ones, rather insignificant, and, except for those mentioned below,


a
b
c
d
e
f
g
h
i
j
k
l
m
n
o
p
q
r
s
t
u
v
w
x
y
z

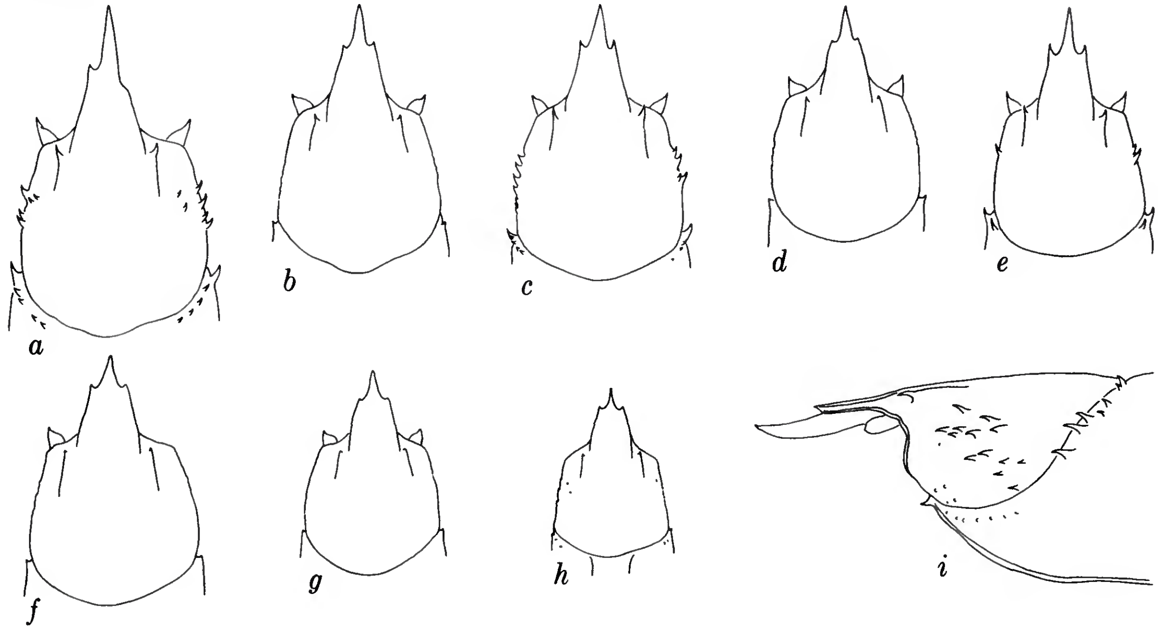


FIGURE 13.—Cephalic portion of carapace of *Orconectes inermis inermis* illustrating variation in spination (all localities in Kentucky): *a, b,* Cub Run Cave, Hart Co. (♀, ♀); *c, d,* Riders Mill Cave, Hart Co. (♂ I, ♂ I); *e–g,* Cooch Webb Cave, Hart Co. (♂ I, ♀, ♀); *h,* Brush Creek Cave, Green Co. (♂ II); *i,* Bland Cave, Hardin Co. (♀).

scarcely exceed those variations noted in the above descriptions.

In the single first-form male from Salamander Cave, the carapace of which is damaged, the rostrum bears a pair of minute corneous tubercles. The rostral margins are strongly convergent and *testii*-like, and the tubercles are so small as to be evident only on close examination. This is the only specimen of this subspecies that we have seen that has marginal ornamentation of any kind on the rostrum.

FIGURE 12.—Cephalic portion of carapace of *Orconectes inermis testii (a, b), O. i. inermis (c, z,),* and intergrades between them, illustrating variation in spination: *a, b,* Eller's Cave, Monroe Co., Ind. (♀, ♂ I); *c–e,* Shiloh Cave, Lawrence Co., Ind. (♂ II, ♀, ♂ II); *f,* Sullivan Cave, Crawford Co., Ind. (♂ I); *g,* Archibald Cave, Crawford Co., Ind. (♂ II); *h,* Marengo Cave, Crawford Co., Ind. (♀); *i,* Wyandotte Cave, Crawford Co., Ind. (♂ II); *j,* Donaldson's Cave, Lawrence Co., Ind. (♂ I); *k,* River Cave, Washington Co., Ind. (♀); *l,* King's Cave, Harrison Co., Ind. (♂ II); *m,* Bedford Cave, Harrison Co., Ind. (♂ I); *n,* Lime Kiln Cave, Meade Co., Ky. (♀); *o,* Doe Run, Meade Co., Ky. (♀); *p,* Rockhaven Cave, Meade Co., Ky. (♀); *q,* Cave, 5 mi. E of Big Spring, Breckenridge Co., Ky. (♂ II); *r,* Bandy Cave, Breckenridge Co., Ky. (♀); *s,* Same as *q* (♂ II); *t, u,* Thornhill Cave, Breckenridge Co., Ky. (♂ I, ♂ I); *v, w,* Lockard Cave, Breckenridge Co., Ky. (♀, ♂ I); *x,* Same as *r* (♀); *y, z,* Nelson Cave, Hardin Co., Ky. (♀, ♀).

Only three of our specimens, two from Mayfield's Cave and one from Eller's Cave, have areolae that constitute less than 44 percent of the carapace length: those from Mayfield's Cave comprise 43.3 (♂ I) and 43.6 (♂ II) percent, and that from Eller's Cave, 42.3 (♀) percent. Their carapace lengths are 21.7, 23.6, and 19.4 mm, respectively. All three are spineless and have strongly convergent rostral margins; thus, except for the proportionately shorter areolae, they are typical of the subspecies.

Perhaps the most conspicuous variations are in the chelipeds, some being more robust than others, some with the tubercles along, immediately above, or below the mesial margin of the palm arranged in almost perfect rows, and others with scarcely any sort of alignment evident. The number and arrangement of tubercles on the opposable surfaces of the fingers of the chelae are likewise exceedingly variable (see the descriptions of the fingers of the chelae of the two males described herein). We strongly suspect that much of this variation will eventually be correlated with the loss of the original appendage and subsequent regeneration.

Hay (1893:285) discussed the hooks on the ischia of the third and fourth pereiopods in his *C. pellucidus* from Indiana. In all of the first-form males of both subspecies of *O. inermis* that we have examined, hooks are present on both pairs of legs. In young second-form and juvenile males, they are exceedingly small, reduced to tubercles, or apparently lacking.

SIZE.—The largest specimen that we have is a female from Eller's Cave which has a carapace length of 33.9 mm. The largest first-form male, carapace length 30.9 mm, was collected in Mayfield's Cave, and the smallest, which was taken from the same cave, has a carapace length of 22.9 mm.

LIFE HISTORY NOTES.—Collections available to us were made during the months of January, February, and August through November, and first-form males are among those made in January, February, October, and November. No ovigerous females or those carrying young have been reported. Banta (1907) indicated that "very young individuals" had been observed in February and March and "at no other time of the year."

SEASONAL COLLECTIONS OF SPECIMENS EXAMINED

Sex	*Jan.*	*Feb.*	*Mar.*	*Apr.*	*May*	*June*	*July*	*Aug.*	*Sept.*	*Oct.*	*Nov.*	*Dec.*	*Not known*	*Total*
♂I	3	1	–	–	–	–	–	–	–	2	–	–	4	10
♂II	1	–	1	–	–	–	–	1	1	–	–	–	5	9
♀	2	–	1	–	–	–	–	1	1	3	–	1	5	14
juv. ♂	–	–	–	–	–	–	–	–	–	–	–	–	1	1
juv. ♀	–	–	–	–	–	–	–	–	–	–	–	–	1	1
Totals	6	1	2	–	–	–	–	2	2	5	–	1	16	35

Orconectes pellucidus (Tellkampf)

FIGURES 1, 14–16

Krebse.—Anonymous, 1843a:49.

Astacus Bartoni?.—Anonymous [not Fabricius], 1843b: 175.—Putnam [not Fabricius], 1872:10.

Astacus pellucidus Tellkampf, 1844a:684; 1844b:383.—Thompson, 1844:111.—Tellkampf, 1845:85, 93.—Erichson, 1846:87, 89, 95.—Gibbes, 1850:195.—Dana, 1852: 522.—Newport, 1855:164.—Lucas, 1864:iv.—Hagen, 1870:6, 7, 11, 55.—Smith, 1873:639.—Faxon, 1885a:10. —Rhoades, 1944:112; 1959:399.

Astacus (Cambarus) pellucidus.—Erichson, 1846:95, 96.—Rabé, 1890:9.

Craw-fish.—Silliman, 1851:336.

Cambarus pellucidus.—Girard, 1852:87, 88.—Hagen, 1870: 8, 27, 30, 31, 32, 33, 34, 55, 56, 97, 101, pl. 1, figs. 68–71, pl. 3, fig. 148, pl. 6.—Packard, 1871:750, 751, fig. 131.—Cope, 1872a: 410, 419.—Packard, 1872b:17, 18, fig. 131.—Hagen, 1872:494, 495.—Packard, 1873:94.—Smith, 1873:639 [in part].—Packard, 1874:209.—Putnam, 1875a:222; 1875b:191, 198.—Smith, 1875:477 [in part].—Putnam, 1877:16–19.—Packard, 1879:315, 316, 317, figs. 268, 269.—Hubbard, 1880:38.—Leydig, 1883: 38, 39, 40.—Faxon, 1884:139, 140 [in part]; 1885a:4, 5, 7, 8, 9, 11, 16, 18, 19, 40, 41, 42, 43, 44, 45, 46, 59, 82, 83, 84, 111, 158, 169, 174, 178, 179 [in part]; 1885b:358.—Underwood, 1886:371 [in part].—Packard, 1888:8, 10, 12, 19, 24, 25, 38, 39, 40, 41, 42, 82, 86, 110, 111, 112, 119, 122, 123, 125, 127 [in part].—Garman, 1889:235, 236.—Faxon, 1890:626, 628.—Packard, 1890:393 [in part].—Parker, 1890:153, 154, 155, 157–161, pl. 1, figs. 2, 3, 4, 5, 6.—Hovey, 1891:72.—Ortmann, 1892:11 [in part].—Cunningham, 1893:537.—Stebbing, 1893:208.—Lönnberg, 1894:126; 1895:4–6, 9.—Hay, 1896:485 [in part].—Call, 1897:103, 104.—Hay, 1897: 208 [in part].—Faxon, 1898:647 [in part].—Eigenmann, 1899:60.—Hay, 1899:959, 966 [in part].—Call, 1901: 103, 104.—Ortmann, 1902:227, 278, 279 [in part].—Hay, 1902a:226, 228, 230, 232, 234, 235 [in part]; 1902b:436.—Steele, 1902:7, 16, 18 [in part].—Eigenman, 1903:169 [in part].—Harris, 1903a:602, 606; 1903b:58, 67, 70, 80, 112–118, 151, 153, 157, 162, 167 [in part].—Ortmann, 1905a:92, 95, 96, 97 [in part].—Bell, 1906:300, 304, 305.—Banta, 1907: 6, 59, 70, 71, 72, 73, 102, 103 [in part].—Graeter, 1909:470 [in part]. —Pearse, 1910:10.—Hovey, 1912:80, 81, 108, 109, 115, 119, 124, 2 figs.—Osborn, 1912:923 [in part].—Faxon, 1914:415, pl. 7, fig. 2a–c [in part].—Spurgeon, 1915: 385, 386 [in part].—Pratt, 1916:391, 392, fig. 625 [in part].—Ortmann, 1918:838, 848 [in part].—Garman, 1924:88, 89.—Spandl, 1926:95, 141–142, 148 [in part]. —Stiles and Hassell, 1927:219 [in part].—Chappuis, 1927:91, 120 [in part].—Creaser, 1931:10; 1932:336.—Giovannoli, 1933a:618–619, fig. 90; 1933b:236–237, fig. 90.—Wolf, 1934–38:104 [in part].—Turner, 1935:876.—Park, 1938:209.—Fleming, 1939: 304, 305.—Bouvier, 1940:68 [in part].—Park et al., 1941:154–171, 5 figs.—Rhoades, 1941:141, 142, 144.—Hobbs, 1942a: 335, 338, 342, 351, 352 [in part].—Jeannel and Henrot, 1949:21.—Bott, 1950:25.—Dearolf, 1953:229.—Hobbs and Barr, 1960:19.—Vandel, 1964:448, 453, 461, 501, 502, fig. 76.—Hobbs, 1967a:125.

Crabs.—Darwin, 1859:137.

Eyeless Crabs.—Binkerd, 1869:86.

Cambarus pelulcidus.—Hagen, 1870:106 [Erroneous spelling].

Orconectes pellucidus.—Cope, 1872a:409, 410, 419; 1872b: 161, 162, 173, 174; 1879:492, 494, 495, 505, 506 [in part].—Cope and Packard, 1881:879, 881, 882.—Joseph, 1882:12.—Wright, 1884:272, 273.—Faxon, 1884:139.—Underwood, 1886:371.—Packard, 1888:24, 126, 140, 155, pl. 21, fig. 2, pl. 22, fig. 7.—Packard, 1894:735, 742.—Hobbs, 1948a:19.—Pennak, 1953:458 [in part].—Eberly, 1954:59; 1958:1, 2, 3 [in part].—Wells, 1959:5–7.—Eberly, 1960:29, 30, 31 [in part].—Brown, 1961: 929, 930.—Creaser, 1962:3 [in part].—Rhoades, 1962: 68, 79, 94.—Fitzpatrick, 1963:60.—Holthuis, 1964:42, 43, 45, 47.—Vandel, 1964:509, 570, 575 [in part].—Mohr, 1964:828.—Poulson, 1964:752, 756, 757, 759, 762, 764.—Frey, 1965:623, 624.—Fitzpatrick, 1967:141, 142.—Mohr and Poulson, 1966:166, 204.—Barr, 1967a: 160, 161, 186, 187, 192, pl. 46, fig. 10; 1967b:480.—Hobbs, 1967a:130; 1967b:12 [in part].—Thompson, 1967:46, 47.—Barr, 1968:65, 91, fig. 18; 1971:71, 72.

Astacidae.—Shaler, 1875:361; 1876:10.

Cray fish.—Shaler, 1875:362, 363; 1876:11, 12.

Cambarus typhlobius Joseph, 1880:202.—Faxon, 1884:139; 1885a:7, 45.—Underwood, 1886:373.—Hay, 1896:477.—Harris, 1903b:131, 151.—Faxon, 1914:427.—Bouvier, 1940:68.—Van Straelen, 1942:2.—Bott, 1950:25.—Villalobos, 1953:348.—Villalobos, 1955:11.—Holthuis, 1964: 42, 43, 44, 45, 46, 47.

Cambarus stygius Joseph, 1881:241, 249 [nomen nudum]; 1882:12 [homonym].—Underwood, 1886:373.—Packard, 1888:86, 123.—Faxon, 1914:427.—Spandl, 1926:95.—Stammer, 1932:608.—Wolf, 1934–1938:105.—Holthuis, 1964:42, 43, 44, 45, 47. [Not *Cambarus stygius* Bundy, 1876.]

Cambarus coecus Joseph 1881:237 [nomen nudum].—Faxon, 1884:139; 1885a:7, 45; 1914:427.—Holthuis, 1964:42, 45.

Blind crayfish.—Semper, 1881:77.—Call, 1901:101.

Cambarus (Orconectes) pellucidus.—Hovey, 1882:222 [in part].

Orconectes.—Hovey, 1882:223 [in part].—Barr, 1968:85; 1971:72, 85, 86.

Cambarus Stygius.—Faxon, 1884:139; 1885a:7, 45, 46.—Bott, 1950:25.

Camtarus (Orconectes) pellucidus, form *inermis.*—Packard, 1888:156, pl. 27, fig. 5. [Erroneous spelling of *Cambarus.*]

Astacus Cambarus Stigius.—Rabé, 1890:9.

Cambarus.—Apfelbeck, 1895:24.—Bolivar et Jeannel, 1931: 306, 307, 309.—Vandel, 1964:494, 495, 512.

Cambrus pellucidus.—Price, 1900:155 [erroneous spelling].

Crayfish.—Call, 1901:100.

Cambarus (Faxonius) pellucidus.—Ortmann, 1905a:107, 108, 111, 114, [in part]; 1905b:435 [by implication]; 1931:64, 65 [in part].—Fage, 1931:373 [in part].—Turner, 1935:876.

Cambarus caecus.—Bouvier, 1940:68 [erroneous spelling of *coecus*].

Cambarus pellucidus pellucidus.—Rhoades, 1941:144.

Cambarus pelludicus.—Dearolf, 1942:50 [Erroneous spelling].

Crawfish.—Dearolf, 1942:52.

Cambarus Pellucidus.—Jackson, 1942:4.

Cambarus (Cambarus) pellucidus.—Balss, 1944:402; 1955: 1311, 1312.

Orconectes pellucidus pellucidus.—Rhoades, 1944:112, 113, 115, 117, 120, 121.—Hobbs, 1948a:16, 19, 20.—Rhoades, 1959:401.—Cole, 1959:81.—Eberly, 1960:30.—Hobbs and Barr, 1960:19.—Nicholas, 1960:133.—Barr, 1961:32.—Rhoades, 1962:68, 90, 91.—Wolfe and Cornwell, 1964: 1467, 1468.—Jegla et al., 1965: 639.—Hart and Hart, 1966:8, 9.—Jegla, 1966:346, 347, 353.—Hobbs, 1967a: 131; 1967b:7.—Barr, 1968:60.

Orconectes pellucidus pelluicdus.—Hobbs, 1948a:16 [erroneous spelling].

Cambarus Coecus.—Bott, 1950:25.

Gambarus typhlobius.—Croizat, 1958:908 [Erroneous spelling].

Orconectes (Orconectes) pellucidus.—Hobbs, 1959:890 [in part].

Crayfishes.—Barr, 1964:79; 1966:15.

REVIEW OF LITERATURE.—The first reference to this crayfish that has come to our attention is an anonymous account of the occurrence of a white crayfish in Mammoth Cave published in "Das Ausland" on 13 January 1843. In the same year, an anonymous record of a gift of "a white eyeless crayfish (*Astacus Bartoni* ?)" from Mammoth Cave, Kentucky, by W. T. Craige to the Academy of Natural Sciences appeared. In 1844, Thompson reported a blind "crayfish" from Mammoth Cave and considered it to be conspecific with *A. bartonii.* Tellkampf (1844a), however, disagreed with Thompson as to the identity of the crayfish occurring in Mammoth Cave and referred to it in a footnote in "Das Ausland," on 19 June as follows: "*Astacus pellucidus,* unserem *A. fluviatilis* verwandt, dessen Grosse er jedoch nicht erreicht. Die Scheren des ersten Fusspaares, sind schlank und zart, des vorderste Glied wenig gebogen, schwach gezähnt. Die Augen liegen unter dem Kopfschilde versteckt." In the text referring to this footnote he stated that "Nur wenige Schritte waren wir gegangen, als ich einen kleinen, ungefähr 1¾ Zoll longen Krebs*) in dem seichten Wasser erblickte, den ich ohne Mühe fing. Er war weiss und seine Schale so durchsichtig, das man die Bewegung der Kiemen und die innern Thiele durchscheinen sah." Whereas in the same year (Tellkampf 1844b), a more complete description appeared that has consistently been cited as the original description, it bears no specific date of publication. Therefore, it seems to us that the description quoted above must take precedence. The more complete description is as follows:

"Der *Astacus pellucidus* Nob. ist unserem *A. fluviatilis* verwandt, erricht aber nicht dieselbe Grösse. Die Scheeren des ersten Fusspaares sind schlank und zart, des vorderste Glied wenig gebogen, schwach gezähnt. Die Augen stehen nicht vor, sondern sind unter dem Kopfschilde verstechkt. Die Fühler lang und sehr grazil. Die ersten Glieder der zwei vorleitzien Fusspaare haben auf ihrem vorderen Rande ein nach vorn und inner gerichtetes, etwas gebogenes Horn, das Horn des letzten Fusspaares ist nur angedeutet. Thomson sagt, dass der Krebs mit *Astacus Bartoni* ubereinstimme, allein er ist davon bestimmt verschieden." The following year, an English translation of Tellkampf's paper appeared.

Erichson (1846) redescribed the species, adding several additional characters, and assigned it to his new subgenus *Cambarus.* Gibbes (1850) and Silliman (1851) referred to specimens from and in Mammoth Cave.

Girard (1852) elevated the subgenus *Cambarus* to generic rank and was the first person to mention the "anterior pair of abdominal legs" of male crayfishes, indicating that the tips are "twisted in *C. pellucidus.*" In the same year, Dana discussed the relationships of the American crayfishes to those occurring elsewhere and to the lobsters and other Reptantia.

In 1855, Newport recorded the first detailed observations on the eyes of this crayfish, and Lucas (1864) indicated that organs of vision were lacking. Darwin (1859) referred to the eyes of blind crabs in Carniole and Kentucky but added no original data. Binkerd (1869) referred to *pellucidus* as an eyeless crab which was rather scarce and seems to be "destitute of the power of hearing, but any motion imparted to the water seemed to create alarm. They probably have a high nervous sensibility, which is not inconsistent with their fair, soft, gelatinous appearance, in which they do not differ from the fish." He further supposed that they were viviparous.

Hagen (1870), in his monograph of the American Astacidae, presented a description of the species in Latin together with illustrations. He discussed its affinities with his Group I [=*Procambarus*] and Group II [=*Orconectes*], and pointed out that it is the most aberrant species of the genus.

Cope (1872a and 1872b, essentially identical articles) compared the fauna of Wyandotte and Mammoth caves and erected the genus *Orconectes* to receive the albinistic crayfishes occurring in them, defending the rationale of proposing a new genus to receive the two troglobites. Packard (1871 and 1872b) are essentially identical. In discussing the inhabitants of Mammoth Cave and their evolution, he emphasized Hagen's observations on the atrophied eyes and presented a dorsal view of the animal which was redrawn from Hagen's figure.

Hagen (1872) not only pointed out the folly of Cope's erecting the genus *Orconectes* but also added that Cope had not given "any character by which to separate it [*O. inermis*] from the old species, *C. pellucidus.*"

Putnam (1872) simply quoted a sentence from the anonymous article (1843). Packard (1873) and Smith (1873 and 1875) agreed with Hagen that Cope's *O. inermis* was not specifically different from *C. pellucidus* and that the species should be retained in the genus *Cambarus.*

Packard (1874), at an entomological meeting of the Boston Society of Natural History, exhibited drawings of the supraoesophageal ganglia of this crayfish and of an epigean species; the differences noted were mainly in the enlargement of the "sides of the ganglion in the blind species." He showed further that the pigment cells are white and stated that the whole eye was "in a state of arrested development."

Putnam (1875a) demonstrated several living *pellucidus* from Mammoth Cave at the 2 December 1874 meeting of the Boston Society of Natural History, and (1875b) the same specimens had been exhibited at the Essex Institute on 25 November, 1874. He added another locality for the species—a cave several miles down the Green River from Mammoth Cave and on the opposite bank (perhaps Ganter's Cave).

Shaler (1875) referred to the Astacidae in Mammoth Cave and speculated on its origin with reference to Pleistocene glaciation. He expressed the view that the cave fauna had been derived from, and was being reinforced by interbreeding with, the epigean fauna.

Putnam (1877) recounted observations of feeding behavior, molting, and regeneration of appendages among specimens retained in the laboratory from 13 November 1874 until 7 August 1875. One female molted twice, 28-29 January and again on 20 April with almost complete regeneration of legs and antennae following the second molt. During this time the animals withstood temperatures varying from a heated room to those which froze "the water in their jars."

Cope's (1879) reference to the crayfish is only a slightly modified version of his 1872 contribution. Packard (1879) discussed and figured the eyes and brain of this crayfish, comparing them with those of an epigean crayfish from Iowa. The figure of the entire crayfish is the same as that published in 1871.

Hubbard (1880) simply recorded having collected "good specimens" of *pellucidus* in Mammoth Cave. Joseph (1880), in a brief note, proposed the name *C. typhlobius* for a cave crayfish ostensibly inhabiting a cave in Yugoslavia. The following year (1881) he referred to the species as both *C. coecus* and *C. stygius,* and in a third paper (1882) compared the specimen, to which he referred as *C. stygius,* with Packard's description of *Cambarus pellucidus.* Hovey (1882) utilized a new combination, *Cambarus (Orconectes) pellucidus,* but contributed no original information.

Cope and Packard (1881), in discussing Cope's *O. hamulatus,* indicated that it and *O. pellucidus* probably arose from different species of *Cambarus* and Cope contrasted the two species. Semper (1881) added no additional information, simply stating that the blind crayfish of Mammoth Cave was well known!

Leydig (1883) presented a histological study of the eyes and antennae of specimens of *pellucidus* from Mammoth Cave, extending the earlier observations of Newport and Packard.

Faxon (1884) considered Cope's *O. inermis* to be conspecific with *Cambarus pellucidus.* He cited Joseph's work and indicated that "until a more satisfactory account of this discovery is published, one may well hesitate to admit the Carniola *Cambarus* [*typhlobius*] into the list."

Wright (1884) reviewed Leydig's findings and compared the "olfactory cones" of *O. pellucidus* with those of *C. propinquus* [=*O. propinquus*], reporting many more in the former.

Faxon (1885a) presented an excellent summary of, and commented on, the contributions of previous authors concerning this species. He discussed its affinities, and, in so doing, assigned it to his Group I (=*Procambarus,* in part). He considered Cope's *O. inermis* a synonym of *Cambarus pellucidus* from the Mammoth Cave region and, erroneously, from Wyandotte Cave and a cave in Bradford, Harrison County, Indiana. He also recorded Joseph's work and quoted his description of *C. stygius* in full, lamenting the fact that a fuller description had not followed. In a later paper (1885b), Faxon cited a new locality for *O. pellucidus,* White Cave, Kentucky.

Underwood (1886), in his list of North American freshwater crustaceans, presented a partial synonomy of *C. pellucidus* and recorded it from Kentucky and Indiana, following Faxon in considering Joseph's *C. typhlobius* and *C. stygius* doubtful species.

Packard (1888) constitutes the broadest treatment in existence of the then known troglobitic crayfishes. He quoted extensively from and summarized the contributions of previous investigators, treating taxonomy, distribution, food and feeding habits, auditory, optic, and olfactory senses, ecology, and evolution. While he considered *O. inermis* to be a synonym of *C. pellucidus,* he relegated Cope's genus to subgeneric rank and indicated that the two cave species, *pellucidus* and *hamulatus,* constituted its members (page 42). In considering the origin of *C. pellucidus,* he stated (page 39) that "it either is derived, with *C. affinis* [=*O. limosus* Rafinesque], from a common ancestor; or . . . what seems more probable, it is a modification of *C. affinis* or an allied species, e.g., *rusticus.* The characteristics which separate *C. pellucidus* from *C. affinis* or *C. bartonii* or any out-of-door species are those which have been induced by its life in total darkness and the diminution of its food-supply." Perhaps through a printer's error, he utilized the combination, "*Camtarus (Orconectes) pellucidus,* form *inermis*" to designate plate-figure 27:5, which is identical to the figure to which he referred earlier (1871) as *Cambarus pellucidus,* one that had been redrawn from Hagen, 1870.

Garman (1889) was impressed by the fact that *C. pellucidus* is more closely allied to the Missouri *C. virilis* than is *C. setosus* which, in turn, is more similar to the Kentucky *C. bartonii* than is *C. pellucidus,* and he suggested the derivation of *C. setosus* from *C. bartonii,* concluding (page 236) that, "Such close affinities as exist between *C. bartonii* and *C. setosus* do not permit their separation into different genera, and the retention of the latter in the genus *Cambarus* cannot but be followed by the disestablishment of the genus *Orconectes* and the return to the older genus of the two species heretofore included in the latter."

Faxon (1890) compared the arrangement of the olfactory setae of this species with that of *C. setosus;* he further postulated that "The closer *superficial* likeness between *C. pellucidus* and *C. hamulatus,* belonging to different sections of the genus, than between *C. hamulatus* and *C. setosus* belonging to the same section, may be explained by the longer period of time during which the subterranean influences have probably been exerted upon the first two species." In the same year, Rabé indicated that *Astacus Cambarus pellucidus* occured in Mammoth Cave and *Astacus Cambarus Stigius* [sic] had been found in the caves of Carniole.

Packard (1890) in his discussion of the effect of cave life on animals and its bearing on the evolutionary theory referred to the eyes of *pellucidus.* Parker (1890) compared the eyes of *pellucidus* with those of *C. setosus* and found those of the former to be without pigment, shaped like a blunt cone, lacking facets but possessing an optic ganglion and nerve, of which the terminus of the latter was "not discoverable." At the apex of the cone he found a "lenticular thickening of the hypodermis, in which there exist multinuclear granulated bodies."

Hovey (1891) stated that *pellucidus* feeds on "*Crangonyx* and other minute crustacea." Nothing of significance was added by Ortman (1892), Cunningham (1893), or Stebbing (1893). Packard (1894) noted that the "eyes of the young are perceptibly larger in proportion to the rest of the body than in the adult," and quoted Tellkampf (1844), "the eyes are rudimentary in the adults, but are larger in the young." Packard also stated that "the blind crayfish of Mammoth Cave . . . have, as we have ascertained by anatomical investigation, degenerate ears, so that the sense of hearing is with little doubt, nearly, if not quite obsolete."

Lönnberg (1894 and 1895) contrasted *Procambarus acherontis* with *pellucidus* and suggested that the latter is probably an older species. In the same year Packard referred to *pellucidus* but contributed no additional information relative to it.

Apfelbeck (1895) stated that specimens of an eyeless *Cambarus* from the subterranean waters of Herzegovina were in the Musée de Vienne.

Hay (1896) contrasted his *C. pellucidus testii* with the nominate subspecies and reiterated the fact that *C. typhlobius* was the only member of the genus which occurs beyond the limits of the North American continent.

Call (1897) cited specific areas in Mammoth Cave where *pellucidus* occurs. Hay, in the same year, presented a synonomy for *C. pellucidus,* including *inermis* as a synonym.

Faxon (1898) referred to Hay's (1893) Indiana records for *pellucidus* [=*inermis*] and indicated that the specimens from them, while transitional between *pellucidus* and *testii,* are more like *O. inermis* (Wyandotte Cave) than like the typical form around Mammoth Cave, pointing out the reduction of spines in northern specimens.

Eigenmann (1899) on 23 November 1898 collected in Mammoth Cave a single female carrying young, the only record, to our knowledge, of a female with young. In the same year, Hay included *pellucidus* in his key to the crayfishes, and, in citing its range, obviously considered *inermis* a junior synonym.

Price (1900) is simply a title without text (see bibliography). Call (1901) contributed no new data relating to this crayfish. Ortmann (1902) believed *pellucidus* to be related to species presently assigned to the genus *Procambarus* and treated *inermis* as a synonym of *pellucidus.*

Hay (1902a), in relating observations on *pellucidus* in Mammoth Cave stated that "when first observed they were usually on the bottom, resting quietly with their legs and antennae fully extended. Unless they were disturbed they would remain in this position for several minutes, and then with no apparent reason start off at a rapid gait, move to another spot and take up the same position," gently moving the antennae to and fro. When disturbed, they move "slightly about in various directions" before swimming away, but "there seemed to be no ability on the part of the animal to select a safe haven of refuge from a distance." When cornered, they would rise high on their forelegs, waving their chelae in the direction of danger. In drying pools, they burrowed or crawled under a stone where, he concluded, they were vulnerable to the cave rat. Disturbances at the surface of the water seemed not to frighten the animals, and he believed that "senses of sight and hearing have entirely disappeared." On the basis of his observations he concluded that copulation occurs in the early fall and stated that the females "are said" to lay their eggs during the winter. In a later paper (1902b), Hay contrasted *pellucidus* and *C. hamulatus* and stated that ". . . *C. pellucidus* and *C. acherontis* [probably *Procambarus l. lucifugus* (Hobbs)], which are very dissimilar in general appearance, are closely related."

Steele (1902), Eigenmann (1903), and Harris (1903a) contributed no additional information about this crayfish, but Harris (1903b) summarized the conclusions and observations of others.

Ortmann (1905a, 1905b) expressed the opinion that *pellucidus* was more closely related to the members of the "fourth group" than to those of the "first," and assigned it to his subgenus *Faxonius* [=*Orconectes*], defending this opinion on morphological and zoogeographic grounds, and placed it in the most primitive section of the subgenus, the Limosus Section. Bell (1906) simply reviewed the observations made by others on the sense organs.

The references to *pellucidus* by Banta (1907), Graeter (1909), and Pearse (1910) include summaries or observations made by others cited above. Osborn (1912) added no original data. Hovey's (1912) contribution consists of photographs of a male and female *pellucidus* together with the statement that the species "feeds on aquatic crustacea which it deftly extracts with its pincerlike claws from under flat stones."

Faxon's (1914) checklist included *O. inermis* as a synonym of *C. pellucidus,* and in it *C. stygius, C. coecus,* and *C. typhlobius* are cited as "doubtful species."

The account of the eye by Spurgeon (1915) is based on observations of *O. i. inermis,* and he made no additional contribution to our knowledge of *O. pellucidus.* Pratt (1916) and Ortmann (1918) included *pellucidus* in their keys but contributed no new data. Ortmann (1931) stated that *C. sloani* and *C. indianensis* [both now assigned to the genus *Orconectes*] are the species most closely allied to *pellucidus* and "probably are the last remnants of the surface-stock from which *C. pellucidus* descended."

The following based their statements about *pellucidus* on data cited above or on other that are essentially identical: Garman (1924), Spandl (1926), Stiles and Hassall (1927), Chappuis (1927), Creaser (1931, 1932), Bolívar and Jeannel (1931), and Fage (1931).

Stammer (1932) expressed the opinion that Joseph's *C. stygius* was identical with *Astacus fluviatilis* [=*Astacus astacus* Linnaeus].

The observations of Giovannoli (1933a, 1933b) on *pellucidus* in Mammoth Cave are essentially identical to those of Hay and others. "Usually it is observed at rest but occasionally it is seen walking along as if it knew where it was going. They seem to lack entirely the inclination so characteristic of above-ground species to retreat under rocks and planks. They pay no attention to such shelters either when undisturbed or when frightened. When merely suspicious of danger they walk slowly towards deeper water, but if startled they swim blindly backward just as any crayfish does." Wolf (1934-1938) contains no new information about *pellucidus.*

Turner (1935), in recording aberrant secondary sexual characteristics in crayfishes, reached the same conclusion as did Ortmann that the presence of hooks on the ischia of the fourth pair of pereiopods in the male represents a derived, rather than primitive, condition. Park (1938), concerned with periodicity of activity in various animals, found *pellucidus* to be arhythmic. Fleming (1939) and Bouvier (1940) made no original contributions, and Rhoades (1941) simply compared *pellucidus pellucidus* with his *C. p. australis.*

Park et al. (1941) reported *pellucidus* to be photonegative and presented data to indicate an arhythmic activity pattern. Neither Dearolf (1942) nor Van Straelen (1942) added to our knowledge of the species. Jackson (1942) gave a brief account of the habits of this crayfish and reported having kept an adult alive in an aquarium for a month.

Hobbs (1942a) assigned *pellucidus* to the resurrected genus *Orconectes,* pointing out that *Faxonius* of previous authors is a synonym of *Orconectes.* Balss (1944 and 1955) contributed no additional information to our knowledge of *pellucidus* and was unique in utilizing the combination *Cambarus (Cambarus) pellucidus.*

Rhoades (1944) presented a description of his new subspecies, *O. pellucidus packardi,* comparing it with the nominate subspecies and *O. p. australis.* He summarized their ranges and assigned the three subspecies of *pellucidus* and three additional epigean species to his "Group rafinesquei." Hobbs (1948a) figured the first pleopods of the males of *O. pellucidus* and related species, questioned Rhoades' division of the Limosus Section, and expressed the opinion that *inermis* represented a species distinct from *pellucidus*. Jeannel and Henrot (1949) reported a new locality for the species, Cave City Cave, Barren County, Kentucky.

Bott (1950), concerned with Joseph's species reported from Carniole, did not reach a conclusion as to its identity. Pennak (1953) added no original information about *pellucidus,* and his figure 286 is an illustration of *O. inermis testii.* Villalobos (1953, 1955) considered the existence of Joseph's *C. typhlobius* as perhaps a relict of the crayfishes "que en otra épocas poblaron el suelo europeo."

Dearolf (1953) cited dates of observations of this crayfish in three Kentucky caves.

Eberly (1954) stated that the cave crayfishes (including *O. pellucidus*) "occupy the highest niche in the biosystem of the cave." In 1958 and 1960, he summarized what he considered to be the adaptations of the crayfishes to a cave environment, agreed with his predecessors on their antiquity, and gave a broad generalization regarding their origin. Croizat (1958) added nothing directly to our knowledge of *O. pellucidus;* however, he consistently used *Gambarus* instead of *Cambarus* for the American genus.

Rhoades' (1959) contribution included a history of the nomenclatural changes among the troglobitic *Orconectes* and an interpretation of the relationships of *pellucidus, inermis,* and *testii,* concluding that the latter is a synonym of *inermis* and that *inermis* freely intergrades with *pellucidus* in southern Indiana, thus recognizing *O. pellucidus pellucidus* and *O. p. inermis.*

Cole (1959) and Wells (1959) presented no original information about *pellucidus* nor did Hobbs and Barr (1960), Nicholas (1960), or Barr (1961). Hobbs (1959) included *O. (O.) pellucidus* in his key to the crayfishes of the United States, indicating that four subspecies occurred from Alabama to Indiana.

Brown (1961) reported that a re-examination of the data of Park et al. (1941) had "indicated a statistically significant . . . 24-hr. rhythm of activity to be present . . . with minimum activity about 9 a.m. and maximum about 7:00 p.m." He further stated that members of *pellucidus* "have no eyes." Creaser (1962) discussed the affinities of *O. pellucidus,* maintaining that only *pellucidus* and *lancifer* should be assigned to the genus *Orconectes.* Rhoades (1962) presented a diagnosis of *O. p. pellucidus* and stated that it is "widely distributed in the solution caverns between the Cumberland River and the counties of southern Indiana" where they "are generally seen in the edges of a clear stygian pools or hiding under rocks." He further postulated the origin of the species from a stock which had "its origin in the Ozarkian Highlands in the late Miocene."

Fitzpatrick (1963), in presenting a background for elevating the subgenus *Faxonella* to generic rank, reviewed Creaser's (1962) remarks about *O. pellucidus.* Barr (1964) contributed no new data or hypotheses concerning the species. Holthuis (1964) reviewed the history of Joseph's three crayfish names and presented a convincing conclusion that *C. typhlobius* is a synonym of *A. pellucidus* Tellkampf, and that Joseph's specimens were simply mislabeled members of Tellkampf's species. *C. coecus* Joseph was declared a nomen nudum, and *C. stygius* Joseph a synonym of *C. typhlobius,* becoming thereby a synonym of *A. pellucidus.* Vandel (1964) presented an excellent account of the various contributions of others to our knowledge of the biology of the species. In the same year, Wolfe and Cornwell reported that although small amounts of B-carotene and lutein were present in *O. p. pellucidus,* "astaxanthin, the principal carotenoid of most Crustacea" is absent, supporting their conclusion that "pigmentation is dependent on the amount of carotenoid in the diet rather than on the presence of light." It is also suggested that this crayfish lacks, and perhaps never had, "the ability to oxidize dietary carotenoids."

Mohr (1964) presented a photograph of *O. pellucidus* and made the statement that it "may live to twice the age of surface kin." Poulson (1964) recounted the observations of Barr (personal communication) that breeding (ovulation?) in *O. pellucidus* "precedes low water by one to two months, and high water, with maximum organic inwash, by four to six months. Further, he stated that "the restriction of . . . young crayfish to springs and backwaters must be related to current, small food-particle size, clay, or other factors because these habitats and adult habitats shows no differences in CO_2 or carbonate alkalinity." Discussing light, Poulson stated: "Light stimulation of the brain area, reduced eye stalk, or 6th abdominal ganglion results in negative reaction to light," and he reported that a "kinetic component is found . . . [in] *O. pellucidus* . . . since they turn away when illuminated on one side."

Frey's (1965) remarks relative to *O. pellucidus* were largely condensed from Rhoades' (1944, 1959) conclusions and postulates. Jegla et al. (1965) compared the maximum lengths of individuals in populations of troglobitic *Orconectes (O. i. inermis, O. pellucidus,* and *O. australis)* and found a difference between them of 20 mm, the same difference in length at which they reached sexual maturity, as well as one "in inflection point for cheliped allometric growth. These variations may be a result of different levels of food supply and interspecific competition. They do not appear to be influenced by two-fold variation in population size, eight-fold variation in population density, or ten-fold variation in available habitat." Predation by fishes was postulated to reduce population density but seemed to have no effect on maximum length attained at sexual maturity. Length was believed to be associated with available food and perhaps influenced by inter-specific competition.

Hart and Hart (1966) reported that *O. pellucidus* is infested with the following entocytherid ostracods: *Dactylocythere ungulata* (Hart and Hobbs, 1961), *Sagittocythere barri* (Hart and Hobbs), and *S. stygia* Hart and Hart. Jegla (1966) reviewed previous references to molting and reproduction in this species.

Barr (1966) referred to Tellkampf's description of this species.

Mohr and Poulson (1966) presented a drawing of *O. pellucidus,* and stated that "Scientists now believe . . . that the ancestors of our commonest cave crayfish, *Orconectes pellucidus,* were isolated in caves at the beginning of the Pleistocene epoch."

Barr (1967a, 1967b) noted the northern boundary of the range of *O. pellucidus,* indicating its occurrence in "the south Pennyroyal fauna," and included a photograph of a living first-form male. Neither Fitzpatrick (1967) nor Hobbs (1967a) added to our knowledge of the species, and Hobbs (1967b) only proposed that "at least some of the similarities" between *Procambarus pecki* and *O. pellucidus* "are due to convergence."

Thompson (1967) observed that *O. pellucidus,* in contrast to epigean crayfish maintained in an aquarium, "rather than folding its antennae back in a streamlined position as the epigeal form did while walking through vegetation, the cave form held them forward for tactile cues, and consequently often became tangled in the litter. It also lacked cryptic responses when startled and spent little time hidden under rocks, compared to the epigeal form." Thompson did not cite the source of his *O. pellucidus,* and it is possible that his animal was a member of one of the subspecies of *O. inermis.*

Jegla and Poulson (1968), reviewing the work of Park et al. (1941) and that of Brown (1961), concluded that the data of Park et al. cannot "be used to distinguish between endogenously and exogenously controlled rhythms." They found "evidence of a circadian clock mechanism" with "average periods of 26, 27, and 34 hours" in *O. pellucidus* [=*O. inermis inermis* and *O. inermis* x *testii*].

Barr (1968) expressed the opinion that the steepening of stream gradients in the Pennyroyal and Cumberland plateaus from Alabama to Indiana at the close of the Pliocene or early Pleistocene was primarily responsible for the extinction of the ancestors of the troglobitic *Orconectes,* and that the quieter streams of caves served as refuges for the evolving troglobites. He also presented a graph redrawn from the 24-hour activity data of Park et al. (1941), and criticized Brown (1961) for not utilizing all of Park's published data.

Barr and Kuehne (1971) discussed the role of this crayfish in the Mammoth Cave ecosystem.

DIAGNOSIS.—Albinistic; eyes reduced and without pigment; rostrum with marginal spines or tubercles delimiting base of acumen, margins subparallel, convex or converging, upper surface concave and without median carina; postorbital ridges usually terminating cephalically in spines or tubercles; hepatic area with or without two to many spines; at least one, often several cervical spines or acute tubercles present; areola 3.7 to 6.0 times longer than broad and constituting 34.1 to 42.2 percent of entire length of carapace; chelae not conspicuously setose but with ciliated tubercles, mesiodorsal surface of palm with several irregular rows of tubercles; hooks on ischiopodites of third and fourth pereiopods. First pleopod of first-form male with greatest cephalocaudal diameter of pleopod more than twice that immediately proximal to base of central projection, always terminating in only two elements; non-corneous mesial process broad basally, triangular, directed distally and slightly caudally and extending considerably beyond distal extremity of central projection, frequently almost obscuring latter in caudal aspect (Figure 14*j*);

central projection small, corneous, flattened in cephalocaudal plane, and directed distad; slight swelling at cephalic base of central projection. Annulus ventralis only slightly broader than long, highest along median portion, and without shelf-like rim along caudal margin (Figure 14*l*).

Topotypic Male, Form I: Body (Figure 14*c, h*) subovate, depressed. Abdomen narrower than thorax (11.0 and 12.6 mm in widest parts, respectively). Width of carapace greater than depth in region of caudodorsal margin of cervical groove (12.5 and 10.2 mm). Areola moderately broad (4.5 times longer than wide), with about 6 widely spaced, minute punctations across narrowest part. Cephalic section of carapace 1.6 times as long as areola; length of areola 38.6 percent of entire length of carapace. Rostrum approximately twice as broad as long, excavate, and with length of acumen subequal to width of rostrum at base; cephalic extremity reaching far beyond antennular peduncle and slightly beyond antennal peduncle; margins not swollen, only slightly elevated, and with prominent corneous-tipped marginal spines at base of acumen; upper surface with evenly spaced minute setiferous punctations; subrostral ridges very weak and evident in dorsal aspect along basal fourth of rostrum.

Postorbital ridges relatively weak, short, with shallow dorsolateral grooves, and terminating cephalically in prominent corneous-tipped spines. Suborbital angle lacking. Branchiostegal spines acute. Six and eight cervical spines present on right and left sides of carapace, respectively. Carapace punctate dorsally and granulate laterally; hepatic area with about 12 spines of various sizes together with several tubercles. Abdomen slightly longer than carapace (32.0 and 30.0 mm). Cephalic section of telson with 2 strong spines in each caudolateral corner, mesial ones movable.

Epistome (Figure 14*g*) subtriangular, with almost straight cephalolateral margins and rounded basal lateral extremities; ventral surface subplane with crowded minute setiferous punctations. Eyes much reduced, completely hidden under rostrum in dorsal aspect and extending only halfway between margin of orbit and marginal spines of rostrum. Antennules of usual form with prominent spine near distoventral extremity of basal segment. Antennae extending caudally at least to caudal margin of telson. Antennal scale (Figure 14*i*) broadest distal to midlength, about 2.2 times longer than broad; outer thickened portion much narrower than lamellar area and terminating in prominent corneous-tipped spine. Third maxilliped extending almost to end of basal third of ultimate podomere of peduncle of antenna.

Chela (Figure 14*f*) slender and little inflated; mesial margin of palm 1.3 times longer than width of palm; palmar area tuberculate, with fine plumose setae at distal bases of tubercles; ventral surface with prominent corneous-tipped tubercle opposite base of articulation of dactyl; tubercles along mesial surface arranged in sublinear series with 12 tubercles in mesialmost row; distal two-thirds of lateral margin of palm and proximal fourth of fixed finger weakly costate. Fingers not gaping; dorsal and ventral surfaces of both with median longitudinal ridges flanked by setiferous punctations; opposable margin of immovable finger with row of 14 rounded corneous tubercles, fourth from base largest; same margin with large tubercles below row and between eighth and ninth tubercle; row of minute denticles broken by 8 basal tubercles and continuous distally to base of corneous tip of finger; opposable margin of dactyl with row of 18 tubercles, fourth and fifth from base subequal in size and larger than others in row, row of minute denticles extending almost entire length of finger and interrupted by tubercles; mesial surface of dactyl with tubercles along proximal half and punctations along distal. Carpus longer than broad and tuberculate; mesial surface of right with 1 (left with 2) large spine and more proximal moderately large acute tubercle; distoventral margin with 2 prominent spines, 1 adjacent to ventrolateral articulation with propodus, 1 situated more mesially. Merus tuberculate except proximolaterally, upper surface with 4 or 5 corneous-tipped spines near distal end, and ventral surface with lateral row of 14 spikelike tubercles and mesial one of 13, few additional tubercles flanking latter two rows. Ischium with row of 6 small tubercles on opposable margin, other smaller ones lateral to row and on outer surface.

Ischia of third and fourth pereiopods (Figure 14*k*) with simple hooks, those on third conspicuously larger than those on fourth but neither extending proximad of distal extremity of corresponding basis. Coxae of fourth pereiopods with heavy, caudomesially projecting prominences; coxae of fifth without prominences except for small mesioventral projection on ventral border of rim surrounding basal portion of phallic papillae.

First pleopods (Figure 14*a, e, j, k*) symmetrical,

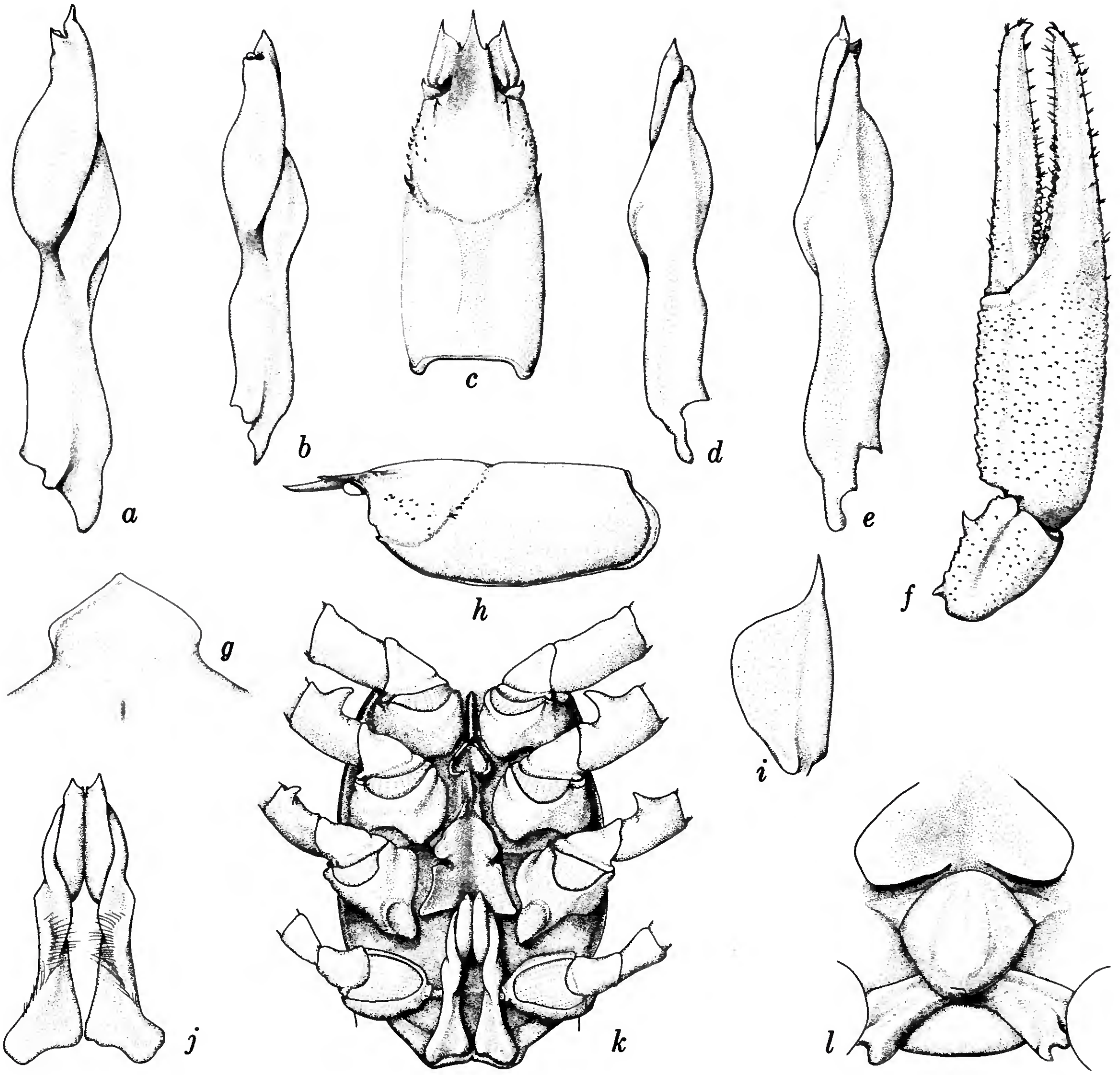


FIGURE 14.—*Orconectes pellucidus: a,* mesial view of first pleopod of topotypic male, form I; *b,* mesial view of first pleopod of topotypic male, form II; *c,* dorsal view of carapace of topotypic male, form I; *d,* lateral view of first pleopod of topotypic male, form II; *e,* lateral view of first pleopod of topotypic male, form I; *f,* dorsal view of distal podomeres of cheliped of topotypic male, form I; *g,* epistome of topotypic male, form I; *h,* lateral view of carapace of topotypic male, form I; *i,* antennal scale of topotypic male, form I; *j,* caudal view of first pleopods of topotypic male, form I; *k,* ventral view of caudal thoracic region of topotypic male, form I; *l,* annulus ventralis and portion of sternum of topotypic female.

reaching coxae of third pereiopods when abdomen is flexed and situated in shallow, broad sternal arch; tip ending in two parts as described in Diagnosis.

Basal podomere of uropods with 2 prominent spines, each overhanging lateral portions of corresponding ramus and small but conspicuous "telsonic condyle" projecting dorsomesially from its mesiodistal angle. Inner ramus of telson without well-defined longitudinal median carina and spine but with spine on distolateral angle; outer ramus with row of spines on distal margin of proximal section, lateral 1 or 2 longer than others.

Topotypic Female: Differing from holotype in following respects: Acumen not quite reaching distal end of antennal peduncle; 5 and 6 cervical spines on left and right sides of carapace, respectively; hepatic area with only 7 well-defined spines; projecting portion of epistome shorter with cephalolateral margins slightly convex; third maxillipeds not quite reaching distal podomere of antennal peduncle; opposable margin of immovable finger of cheliped with row of 15 tubercles, fifth from base largest, that of dactyl with 18, sixth from base largest; upper surface of merus with 5 and 2 spines on left and right chelipeds, respectively, and ventrolateral margin with 11 and ventromesial margin with 17 and 12 on right and left; ischium with 7 irregularly arranged acute tubercles. First pleopods uniramous and reaching midlength of annulus when abdomen is flexed.

Annulus ventralis (Figure 14*l*) shallowly situated in sternum and not firmly fused to sternal plate immediately cephalic to it; outline subovate, only slightly broader than long, with median portion elevated ventrally and forming broad arc having its highest segment distinctly caudal to midlength; arched portion bearing only faint longitudinal groove, ending caudally on vertical wall, plateau-like rim totally lacking; sinus very short, originating dextral to caudal end of longitudinal groove, following gentle arc across median line, passing dorsally and ending on caudal wall sinistral to median line.

Topotypic Male, Form II: Differing from holotype in following respects: areola with only 4 punctations across narrowest part; only 4 cervical spines and only 5 hepatic spines on each side of carapace; opposable margin of immovable finger of cheliped with row of 10 tubercles, corresponding margin of dactyl with 12; merus of cheliped with 3 spines on upper distal surface, 8 in ventrolateral row and 13 in ventromesial row; ischium with row of 5 tubercles. Hooks on ischia of both third and fourth pereiopods much reduced, those on fourth to low tubercles; protuberances on coxae of fourth pereiopods only slightly reduced in size.

First pleopods (Figure 14*b, d*) markedly similar to those of holotype; however, central projection rounded, poorly defined, and non-corneous.

SIZE.—The largest specimen available to us is a first-form male from Crystal Lake in Mammoth Cave, Edmonson County, Kentucky, which has a carapace length of 39.4 mm. The smallest first-form male, carapace length 22.0 mm, was collected in Cooks Cave, Logan County, Kentucky.

MEASUREMENTS (in millimeters).—*Orconectes pellucidus*:

	Topotypic male Form I	*Topotypic female*	*Topotypic male Form II*
Carapace:			
Height	10.2	12.8	9.8
Width	12.6	16.2	11.0
Length	30.0	36.8	27.2
Rostrum:			
Width	4.2	5.2	3.9
Length	8.5	10.0	8.2
Areola:			
Width	2.6	3.0	1.9
Length	11.6	14.7	10.2
Chela:			
Length of inner margin of palm	8.4	10.2	7.3
Width of palm	6.3	7.8	4.8
Length of outer margin of chela	16.6	19.5	25.6
Length of dactyl	9.2	10.6	14.6

TYPES.—Holotype, Zoologisches Museum der Humboldt-Universität, Berlin (♂I).

TYPE-LOCALITY. — Mammoth Cave, Edmonson County, Kentucky.

SPECIMENS EXAMINED.—Specimens from Kentucky and Tennessee were examined as follows:

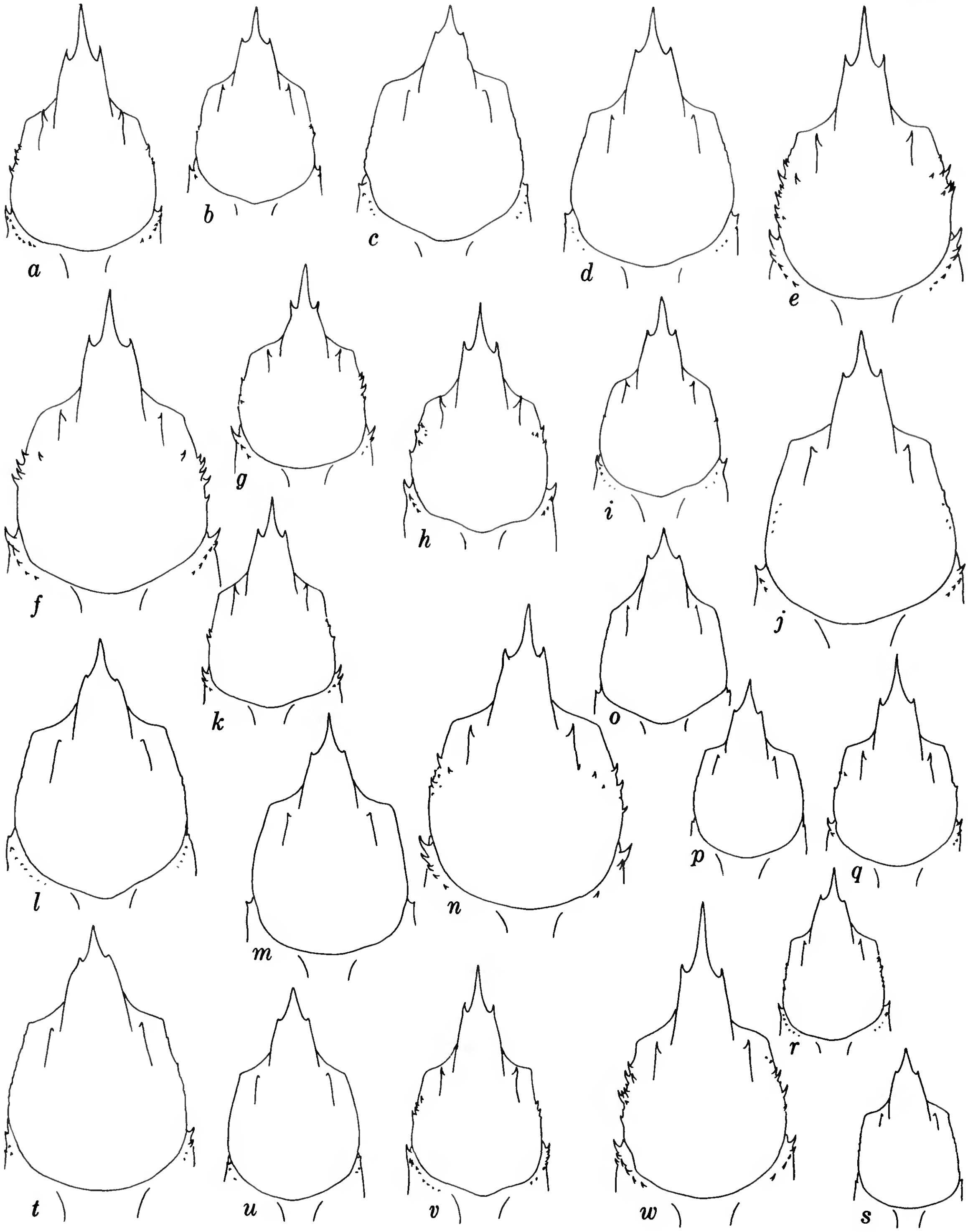
KENTUCKY: *Barren County:* (1) Cave City (=Railroad) Cave, in town of Cave City, 1♂I, T.C.B. and T.G.M., VIII/23/65. (2) Diamond Cave, 2 miles N of Park City on State Rte. 225, 1♂I, T.C.B., S.B.P., J.R.H., and J. F. Fitzpatrick, Jr., VII/25/64. (3) Twyman Cave, 2 miles N of Hiseville, 2♂II, 2♀, R.M.N., IX/11/65. *Christian County:* (1) Glover's Cave, 4 miles SW of Trenton, 2♂II, 2♀, T.C.B., VI/9/57. *Edmonson County:* (1) Mammoth Cave, Echo River, 1♂I, 1♂II, 3♀, 7j♂, 5j♀, W.P.H., date?; 1♂II, 3♀, L.H., VIII/30/39; 4♀, Raymond Nelson, VII/28/58. (2) Mammoth Cave, Roaring River, 5♂I, 1♂II, 5♀, 2j♂, 4j♀, W.P.H., XIII/28/01; 1♂II, C.W.H., XI/29/63. (3) Mammoth Cave, Styx River, 1♂I, T.C.B., IV/28/62; 5♂I, 1♂II, 4♀, T.C.B., V/13/62. (4) Mammoth Cave, Lake Lethe, 3♂I, 1♂II, T.C.B., X/25/61; 1♂I, T.C.B. and R.A.K., X/11/63; 5♀, T.C.B. and R.A.K., XI/25/61. (5) Mammoth Cave, Crystal Lake, 1♂I, T.C.B., II/22/64; 1♂II, T.C.B., IV/?/64. (6) Mammoth Cave, 1♂I, Peter Parker, ?/?/1858; 2j♂, Leonard Giovannoli, VII/19/29; 1♂II, 3♀, 1j♀, L.G. VIII/6/29; 1♂II, 4♀, V. E. Shelford, VII/4/42; 2j♀, ?, VIII/28/41; 1♂I, Kjell Sandved, VI/?/67; 1♂I, 1♂II; 2♀, 1j♂, 1j♀, W.P.H., date?; 1♀, M. E. Mann, date?; 1j♂, Ellsworth Call, date?; 1♂II, 3♀, coll. and date (?). (7) Blowing Spring Cave in Mammoth Cave National Park, 1♀, L.H., XII/1/56; 1♀, O.D. Lee, date?. (8) Cedar Sink Cave, in Mammoth Cave National Park, 1♂II, T.C.B., X/29/66. (9) Stream in Long Cave, Mammoth Cave National Park, 1♂II, 1♀, L.H., I/5/56. (10) Stillhouse Hollow Cave, Mammoth Cave National Park, 1♀, L.H., XI/17/56. (11) White Cave, 3♀, John E. Younglove, date?. (12) Floyd Collins Crystal Cave, in Mammoth Cave National Park, 1♀, Carl Melton, V/28/60. *Hart County:* (1) Bald Knob Cave, 2 miles W of Hardyville, 1♂II, 1♀ with eggs, R. M. Norton, IX/11/65. (2) Buckner Hollow Cave, 1.2 miles SE of Hinesdale, 2♂I, 3♀, J.R.H. and T.C.B., VIII/30/63. (3) Horse (=Hidden River) Cave, in town of Horse Cave, 2♀, 1j♂, 1j♀, E. P. Creaser and M. Becker, VIII/28/29; 1♀, E.P.C. and B., V/13/30; 1♂I, 1♂II, 1♀, 1j♂, L.H., VIII/30/39; 1♂II, 1♀, Nat. Spel. Soc., VIII/29/41. (4) Stream in cave, 2 miles SW of Northtown, 1♂I, 1♀, L.H., III/23/57. (5) Mammoth Onyx Cave on St. Rte. 335, 1♀, R.R., VII/16/39. *Logan County:* (1) Cooks Cave, 1 mile E of Adairville, 2♂I, 1♀, T.C.B., VI/25/57. (2) Mud River Cave, 4 miles E of Russellville, 3♂I, 3♂II, 3♀, J.R.H. and T.C.B., VIII/13/65. *Trigg County:* (1) Cool Spring Cave, on Sinking Fork Creek, 2♂I, S.B.P. and R.M.N., IV/19/64; 4♂I, 1♂II, 5♀, S.B.P., VI/28/65. *Warren County:* (1) By-Pass Cave, Bowling Green, 1♀, K. Haas, VI/?/55. (2) Lost River Cave, 3 miles S of Bowling Green, 15j♀, D. H. Puckett and Herbert Shadowen, VIII/7/64. (3) Pruitt Saltpeter Cave, 0.8 mile SE of Anna, 2♂I, 1♂II, 3♀, T.C.B., C.W.H., and D.G.H., XI/30/64.

TENNESSEE: *Montgomery County:* (1) Sink Hole Cave on Austin Peay College Farm at Clarksville, 4♂II, 3♀, D. A. Etnier, XI/22/68. (2) Bellamy Cave, 3.0 miles S of Oakwood, 1♂II, 1♀, Merlin Tuttle, VIII/29/69.

RANGE.—(Figure 1) The range of *Orconectes pellucidus* extends southwestward from Hart County to Trigg County, Kentucky, and Montgomery County, Tennessee.

VARIATIONS.—Most stable among the features examined in *Orconectes pellucidus* are perhaps the secondary sexual characteristics of the adults. The first pleopods of the male uniformly exhibit a markedly slender (in lateral aspect) distal portion and a mesial process which extends distally much beyond the tip of the central projection. The hooks on the ischia of the third and fourth pereiopods vary in size, particularly that of the fourth, but are always clearly evident in the first-form male. Those on the fourth may be much smaller than those on the third, and neither greatly swollen; occasionally only the hook on the third is markedly robust; but in some males, the hooks on the two pereiopods are subequal in size, and both swollen. The annulus ventralis, while showing minor variations in outline and contour of the ventral surface, always has a rather steep, evenly curved caudal surface and lacks the caudal plateau-like rim characteristic of the other troglobites of the genus.

Whereas, there is comparatively little variation in the secondary sexual characteristics of *O. pellucidus,* the carapace and chela show a wide range of differences. Most of those noted in the carapace, including meristic ones, are associated with the degree of development of the spiny elements. In general, among those individuals that have a number of strongly developed cervical and hepatic spines, the marginal spines of the rostrum, the acumen, the postorbital spines, and that on the antennal scale are longer than those in specimens having reduced, and usually fewer cervical and hepatic spines (see Figure 15*u, v*). Inasmuch as, through convention, the length of the carapace is given as the distance between the tip of the rostrum and the midcaudodorsal margin of the carapace, it is obvious that a spiny (hence, having a longer rostrum) individual of approximately the same size as one that is relatively aspinous has a proportionately greater carapace length. The longer rostrum is also reflected in differences noted in the relative length of the areola, which is expressed in the percentage of the total length of the carapace; that is, an animal having a longer rostrum has a proportionately shorter areola. Comparing the same two illustrations mentioned above, the areolae constitute 41.4 and 38.9 percent of the carapace length, respectively, although there is only 0.1 mm difference in the actual length of the areolae of the two. Thus, the relative lengths of the areola are not so much determined by variation in its length as by the variation in the length of the rostrum, and the latter seems, for the most part, to be correlated with the greater development of the acumen (essentially a spine). Furthermore, it seems at least possible, on


a
b
c
d
e
f
g
h
i
j
k
l
m
n
o
p
q
r
s
t
u
v
w

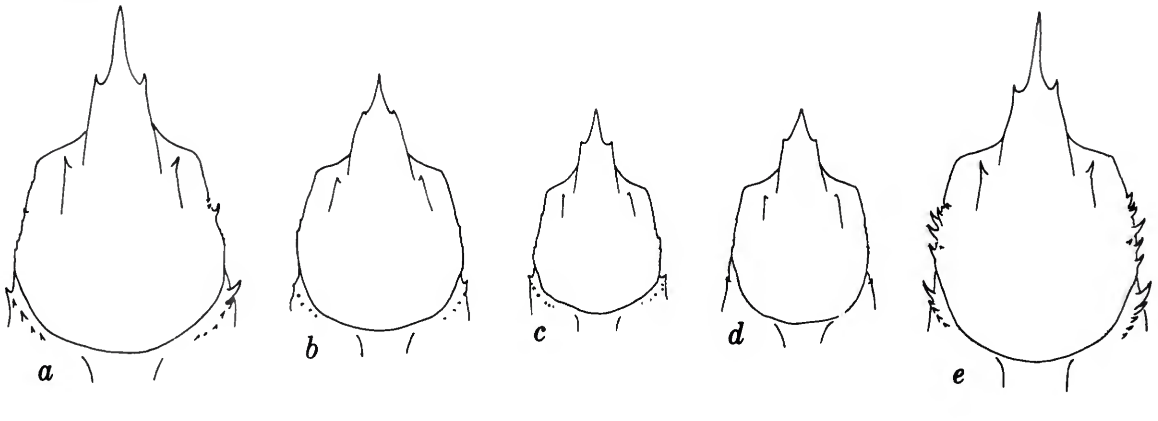


Figure 16.—Cephalic portion of carapace of *Orconectes pellucidus* illustrating variation in spination (all localities in Kentucky): *a*, Mud River Cave, Logan Co. (♂I); *b*, *c*, Cooks Cave, Logan Co. (♂I, ♀); *d*, Glovers Cave, Christain Co. (♀); *e*, Cool Spring Cave, Trigg Co. (♂I).

the basis of our limited data, that the aspinous condition may be correlated with more strongly lotic habitats.

The loss and regeneration of appendages among troglobitic crayfishes is commonplace, and the regeneration is often so complete that frequently it is difficult to determine whether or not a given cheliped is the original one or a replacement. The occasional occurrence of a comparatively robust chela on a large male elicits the conclusion that few individuals reach adulthood without having regenerated at least one member of this pair of appendages. Even with the tremendous range of variation that has been observed in them, an elongate, comparatively narrow, tuberculate palm is characteristic of all of the troglobitic species of the genus. We have been unable to discover any consistent feature of the cheliped which is unique to one of the species.

Figure 15.—Cephalic portion of carapace of *Orconectes pellucidus* illustrating variation in spination (all localities in Kentucky): *a*, Horse Cave, Hart Co. (♂II); *b*, Buckner Hollow Cave, Hart Co. (♀); *c*, Cave 2 mi. W. of Northtown, Hart Co. (♂I); *d*, Horse Cave, Hart Co. (♂I); *e–k*, Mammoth Cave, Edmonson Co. (♀, ♀, ♂II, ♂II, ♂I, ♀); *l*, Long Cave, Edmonson Co. (♀); *m*, Cedar Sink, Edmonson Co. (♀); *n*, White Cave, Edmonson Co. (♀); *o*, Stillhouse Hollow Cave, Edmonson Co. (♀); *p*, By-Pass Cave, Warren Co. (♀); *q*, Pruitt Saltpeter Cave, Warren Co. (♂I); *r*, *s*, Lost River Cave, Warren Co. (♀, ♀); *t*, Diamond Cave, Barren Co. (♂I); *u*, Cave City Cave, Barren Co. (♂I); *v*, Twyman Cave, Barren Co. (♂I); *w*, Mud River Cave, Logan Co. (♀).

Despite the variations in spination, no particular pattern or degree of development of the spines seems to be correlated with a major portion of the range of the species. In some localities, all the specimens collected have been very spiny, and in others, the only traces of spines on the carapace are limited to a single, small cervical spine and one or two adjacent small tubercles, weak marginal spines on the rostrum, and a broad, short acumen. Yet in other localities, while one of the two types seem to predominate, both are represented in the population. Further, to make more difficult correlation with a portion of the range of the species or with ecological factors, there is considerable variation in the degree of development of the individual spines, so that two specimens from the same or different localities may have virtually an identical number of spines, but in one they are very prominent and in the other comparatively weak.

From the eastern portion of the range in Barren, Edmonson, and Hart counties, we have 131 specimens from 15 localities. In Hart County, only in Horse Cave are there specimens which might be classified as spiny (Figure 15*a*), but even there, only 3 of the 15 specimens could be so designated. The others have very weak spines, or the hepatic spines are reduced or lacking (Figure 15*d*). Among them the areola constitutes from 38.5 to 40.6 percent of the length of the carapace. A single specimen from

Floyd Collins Crystal Cave has a large number of small spines, and its areola constitutes 38.6 percent of the carapace length. From Buckner Hollow Cave (Figure 15*b*) are 5 specimens, of which 3 are almost smooth, and only 1 moderately spiny; their areolae range from 39.1 to 41.1 percent. The remaining 5 specimens from Bald Knob Cave, Mammoth Onyx Cave, and the unnamed cave two miles southwest of Northtown (Figure 15*c*) have few poorly developed spines, and the areola ranges from 39.6 to 41.7 percent of the carapace length.

In Edmonson County, the range of variation in the 95 specimens from Mammoth Cave is almost as great as that from all the other caves in the county combined (Figure 15*e-k*), and the areola ranges from 38.0 to 41.6 percent of the total length of the carapace. Our 3 specimens from White Cave are comparatively spiny (Figure 15*n*) and their areolae constitute 38.9 to 40.4 percent of the carapace length. In the remaining localities, the 5 available specimens are relatively aspinous (Figure 15*l, m, o*), and their areolae vary from 39.7 to 42.4 percent of the carapace length.

The collection from Twyman Cave, Barren County, consists of 3 very spiny individuals (Figure 15*v*), and 1 which is almost spineless, resembling the 3 specimens from Diamond Cave and Cave City Cave (Figure 15*t, u*). In the specimens from the former cave the areola ranges from 38.5 to 40.5 percent of the carapace length, and in the latter two, 41.8 and 41.4 percent, respectively.

In the central portion of the range, in Warren and Logan counties, a similar range of variation exists. Among 6 specimens from Pruitt Saltpeter Cave and 15 specimens from Lost River Cave, both moderately spiny and aspinous (Figure 15*q-s*) individuals are present in which the areola comprises 38.9 to 41.3 percent of the length of the carapace. Our single specimen from By-Pass Cave is aspinous (Figure 15*p*), with the areola constituting 40.5 percent.

In Logan County, the 3 specimens from Cooks Cave are very weakly spined (Figure 16*b, c*), with areolae constituting 38.1 to 39.9 percent of the carapace length. In contrast, the 9 specimens from Mud River Cave are more spiny (Figure 16*a*) and, except for the largest first-form male, which has an areola comprising 40.6 percent of the carapace length, they exhibit a range of 37.6 to 39.8 percent.

In the three caves in the southwestern part of the range there is essentially a repetition of what exists elsewhere. Our 4 specimens from Glover Cave, Christian County, are relatively smooth (Figure 16*d*) and have areola constituting 39.6 to 41.6 percent of the carapace length. The 12 specimens from Cool Spring Cave, Trigg County, are among the most spiny specimens (Figure 16*e*) we have observed, and their long acumen is reflected in the relative areola length which ranges from 37.6 to 38.7 percent of the carapace length. None of the 9 specimens from Montgomery County, Tennessee is so spiny as those from Cool Spring Cave, and considerable variation exists among them, as might be assumed by the range of their relative areola length, 39.3 to 44.2 percent of the carapace length.

LIFE HISTORY NOTES.—First-form males have been collected each month of the year except January, September, and December. Collections made during these months consist of two, six, and one specimens, respectively; thus there is little reason to doubt that breeding males occur throughout the year. The only female carrying eggs that we have examined was collected on 11 September 1965 in Bald Knob Cave, Hart County, Kentucky. No female carrying young has been reported since Eigenman (1899) collected a specimen on 23 November 1898.

SEASONAL COLLECTIONS OF SPECIMENS EXAMINED

Sex	*Jan.*	*Feb.*	*Mar.*	*Apr.*	*May*	*June*	*July*	*Aug.*	*Sept.*	*Oct.*	*Nov.*	*Dec.*	*Not known*	*Total*
♂I	–	1	1	3	5	7	1	9	–	4	2	–	6	39
♂II	1	–	–	1	1	3	–	10	3	2	6	–	7	34
♀	1	–	1	–	6	9	1	15	2	–	12	1	20	68
juv. ♂	–	–	–	–	–	–	2	4	–	–	–	–	9	15
juv. ♀	–	–	–	–	–	–	–	23	–	–	–	–	6	29
ovig. ♀	–	–	–	–	–	–	–	–	1	–	–	–	–	1
Totals	2	1	2	4	12	19	4	61	6	6	20	1	48	186

Literature Cited

Anonymous

1843a. Die Mammuthhöhle. *Das Ausland,* number 13, pages 19–20.

1843b. [Notice of Eyeless Crayfish and Eyeless Fish from Mammoth Cave, Kentucky.] *Proceedings of the Academy of Natural Sciences of Philadelphia,* 1:175.

Apfelbeck, M. Victor

1895. Sur la faune des cavernes de Bosnie et d'Herzégovine. *Spelunca, Bulletin de la Société de Spéléologie,* number 1, pages 23–24.

Balss, Heinrich

1944. Decapoda, III Morphologischer Teil. Pages 321–480, Textabb. 361–516, in *H. G. Bronn's Klassen und Ordnungen des Tierreichs,* Band V. Abteilung I, Buch 7, Lieferung 3.

1955. Decapoda, VI Ökologie. Pages 1283–1367, Textabb. 1043–1069, in *H. G. Bronn's Klassen und Ordnungen des Tierreichs,* Band V, Abteilung I, Buch 7, Lieferung 10.

Banta, Arthur M.

1905. The Fauna of Mayfield's Cave. *Science,* new series, 21(544):853–854.

1907. The Fauna of Mayfield's Cave. *Carnegie Institution of Washington,* Publication 67, 114 pages.

Barr, Thomas C., Jr.

1961. Caves of Tennessee. *Bulletin of the Tennessee Department of Conservation and Commerce,* number 64, 567 pages, 150 figures.

1964. The Fauna of Mammoth Cave: A Study in Community Composition and Evolution. *Bulletin of the National Speleological Society,* 26(2):78–79.

1966. Evolution of Cave Biology in the United States, 1822–1965. *Bulletin of the National Speleological Society,* 28(1):15–21.

1967a. Ecological Studies in the Mammoth Cave System of Kentucky I: The Biota. *International Journal of Speleology,* 3:147–204, plates 37–64.

1967b. Observations on the Ecology of Caves. *The American Naturalist,* 101(922):475–491, 4 figures.

1968. Cave Ecology and the Evolution of Troglobites. Pages 35–102, 24 figures, in volume 2 of *Evolutionary Biology,* by Theodosius Dobzhansky, M. K. Hecht, and W. C. Steere. New York, Appleton-Century-Crofts.

Barr, Thomas C., Jr., and Robert A. Kuehne

1971. Ecological Studies in the Mammoth Cave System of Kentucky. II. The Ecosystem. *Annales de Spéléologie, Revue Trimestrielle,* 26(1):47–96, 12 figures.

Bell, J. Carlton

1906. The Reactions of Crayfish to Chemical Stimuli. *Journal of Comparative Neurology and Psychology,* 16(4):299–326.

Binkerd, A. D.

1869. *The Mammoth Cave and Its Denizens: A Complete Descriptive Guide.* vi + 95 pages. Cincinnati, Robert Clarke & Co.

Blatchley, W. S.

1897. Indiana Caves and Their Fauna. *Twenty-first Annual Report of the Indiana Department of Geology and Natural Resources,* pages 121–212, plates 4–13.

Bolivar, C., and R. Jeannel

1931. Biospeologica LVI. Campagne spéologique dans l'Amérique du nord en 1928. *Archives de Zoologie Expérimentale et Générale,* 71:293–499, 212 figures.

Bott, Richard

1950. Die Flusskrebse Europas (Decapoda, Astacidae). *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft,* number 483, 36 pages, 25 figures, 6 plates.

Bouvier, E. L.

1940. *Fauna de France, 37, Decapodes Marcheurs.* 339 pages, 222 figures, 14 plates. Paris, Paul LeChevalier et Fils, 12 Rue de Tournon.

Brown, Frank A.

1961. Diurnal Rhythm in Cave Crayfish. *Nature,* 191 (4791):929–930.

Bundy, W. F.

1876. Appendix, pages 24–25, in List of Illinois Crustacea with Descriptions of New Species, by S. A. Forbes. *Bulletin of the Illinois Museum of Natural History,* number 1, 25 pages.

Burroughs, W. G.

1923. A Pottsville-filled Channel in the Mississippian. *Kentucky Geological Survey,* series 6, 10:115–126.

Call, Richard Ellsworth

1897. The Natural History of the Cave. 116 pages, 24 figures, in *Mammoth Cave of Kentucky,* by H. C. Hovey and R. E. Call. Louisville, Kentucky, John P. Morton and Co.

1901. [The natural history of the cavern; a reprint of the above.] In *Mammoth Cave of Kentucky, an Illustrated Manual,* by H. C. Hovey and R. E. Call. v+112 pages. Louisville, Kentucky, John P. Morton and Company.

Chappuis, P. A.

1927. Die Tierwelt der Unterirdischen Gewässer. Volume 3, 175 pages, 62 figures, 4 plates, in *Die Binnengewässer,* by August Thienemann. Stuttgart, E. Schweizerbart'sche Verlagsbuchhandlung.

Cole, Gerald A.

1959. A Summary of Our Knowledge of Kentucky Crustaceans. *Transactions of the Kentucky Academy of Science,* 20(3–4):66–81.

Collett, John

1874. Geology of Lawrence County, Indiana. *Fifth Annal Report of the Geological Survey of Indiana,* pages 260–312.

1879. Geological Report on Harrison and Crawford Counties, Indiana. *Eighth, Ninth, and Tenth Annual Reports of the Geological Survey of Indiana,* pages 291–522.

Cooper, John E.

1966. Preliminary Observations on the Biology of Shelta Cave, Alabama. *Bulletin of the National Speleological Society,* 28(2):96–97.

1967. Animals in Alabama Caves. Pages 14–16 in *The Caves of Alabama,* A Guide for the 1967 Convention of the National Speleological Society at Birmingham and Huntsville, Alabama, June 1967, by John Veitch and John E. Cooper.

1968. Shelta Cave, a Biological Marvel. *NSS News,* 26(2):33–35.

Cooper, J. E., and Martha Riser Cooper

1969a. Comments on Alabama Cave Biology. Pages 25–30 in Section 2 (Cave Science) of *Speleo Digest,* William T. Plummer, editor.

1969b. Cave-Associated Herpetozoa II: Salamanders of the genus *Gyrinophilus* in Alabama Caves. *Bulletin of the National Speleological Society,* 30(2): 19–24, 1 figure.

Cooper, J. E., and Thomas L. Poulson

1968. A Guide for Biological Collecting in Caves. *NSS News,* 26(9):127–138, 25 figures.

Cooper, Martha Riser

1969. Sensory Specialization and Allometric Growth in Cavernicolous Crayfishes. *Actes Du IV*^{e} *Congres International de Spéléologie en Yugoslavie (12–26 IX 1965),* 4–5:203–208, 1 figure.

Cope, Edward Drinker

1871a. Wyandotte Cave and Its Life. *The Indianapolis Journal,* 5 Sept. 1871, page 4.

1871b. Life in the Wyandotte Cave. *Annals and Magazine of Natural History,* series 4, 8(47):368–370 [reprinted from *Indianapolis Journal,* 5 Sept. 1871].

1872a. On the Wyandotte Cave and Its Fauna. *American Naturalist,* 6(7):406–422, figures 109–116.

1872b. Report on the Wyandotte Cave and its Fauna. *Third and Fourth Annual Report of the Geological Survey of Indiana,* pages 157–182, figures 109–116. [Reprinted from *American Naturalist,* 6(7):406–422.]

1872c. [In minutes of meeting of the Academy, 28 November 1871.] *Proceedings of the Academy of Natural Sciences of Philadelphia,* part I, new series, pages 297–298.

1879. Observations on Wyandotte Cave and its Fauna. *Eighth, Ninth, and Tenth Annual Reports of the Geological Survey of Indiana,* pp. 489–506, figures 109–116. [Reprinted from American Naturalist, 6(7):406–422.]

1881. *Orconectes hamulatus.* Pages 881–882, plate 7, figure 1, in The Fauna of the Nickajack Cave, by E. D. Cope and A. S. Packard, Jr. *American Naturalist,* Volume 15.

Cope, E. D., and A. S. Packard, Jr.

1881. The Fauna of the Nickajack Cave. *American Naturalist,* 15:877–882, plate 7.

Creaser, Edwin P.

1931. Three New Crayfishes (*Cambarus*) from Puebla and Missouri. *Occasional Papers of the Museum of Zoology, University of Michigan,* number 224, 10 pages, 17 figures.

1932. The Decapod Crustacea of Wisconsin. *Transactions of the Wisconsin Academy of Sciences, Arts and Letters,* 27:321–338, 13 figures.

1962. Notes on Homologies and Genetic Relationships in the Cambarinae Crayfishes. 7 pages, 22 figures. Privately printed.

Crocker, Denton W.

1957. The Crayfishes of New York State (Decapoda, Astacidae). *New York State Museum and Science Service Bulletin,* number 335, 97 pages, 5 plates, 6 figures.

Crocker, D. W., and David W. Barr

1968. *Handbook of the Crayfishes of Ontario.* ix + 158 pages, 87 figures. University of Toronto Press.

Croizat, Leon

1958. *Panbiogeography, or an Introductory Synthesis of Zoogeography, Phytogeography and Geology; with Notes on Evolution, Systematics, Ecology, Anthropology, etc.* Volume I (The New World), xxxi + 1018 pages, 119 figures. Distributed by Wheldon and Wesley, Ltd., Nr. Hitchin, Herts, England.

Cunningham, J. T.

1893. Blind Animals in Caves. *Nature,* 47:439.

Dana, James D.

1852. Crustacea, Part 1. Volume 13, 685 pages, in *United States Exploring Expedition During the Years 1838, 1839, 1840, 1841, 1842 Under the Command of Charles Wilkes, U.S.N.* Philadelphia, C. Sherman.

Darwin, Charles

1859. *On the Origin of Species, by Means of Natural Selection, or the Preservation of Favored Races in the Struggle for Life.* ix+502 pages. London, J. Murray.

Dearolf, Kenneth

1942. Report of a Biological Reconnaissance of the New Discovery in Mammoth Cave, Kentucky, January 7–11, 1941. *Bulletin of the National Speleological Society,* number 4, pages 48–52.

1953. The Invertebrates of 75 Caves in the United States. *Proceedings of the Pennsylvania Academy of Science,* 27:225–241.

Eberly, William R.

1954. The Use of Crayfish to Illustrate some Ecological Principles. *Turtox News* (General Biological Supply House, Inc.), 32(3):58–60.

1955. Summary of the Distribution of Indiana Crayfishes, Including New State and County Records. *Proceedings of the Indiana Academy of Science,* 65:281–283.

1958. *Competition and Evolution in Cave Crayfishes of Southern Indiana.* Mimeographed, 7 pages.

1960. Competition and Evolution in Cave Crayfishes of Southern Indiana. *Systematic Zoology,* 9:29–32.

Eigenmann, Carl H.

1899. Explorations in the Caves of Missouri and Kentucky. *Proceedings of the Indiana Academy of Science*, 1898, pages 58–61.

1903. The Eyes of the Blind Vertebrates of North America. V. The History of the Eye of the Blind Fish *Amblyopsis* from its Appearance to its Disintegration in Old Age. Pages 167–204, 4 plates, in *Mark Anniversary Volume*, George H. Parker, editor. New York, Henry Holt and Company. 4 plates.

Erichson, W. F.

1846. Uebersicht der Arten der Gattung *Astacus*. *Archiv für Naturgeschichte*, Berlin, 1:86–103.

Fage, Louis

1931. Crustaces Amphipodes et Decapodes. Pages 361–374, 21 figures, in Biospeologica LVI. Campagne spéologique dans l'Amérique du nord en 1928, by C. Bolívar and R. Jeannel. *Archives de Zoologie Expérimentale et Générale*, 71:361–374, 21 figures.

Faxon, Walter

1884. Descriptions of New Species of *Cambarus:* to Which is Added a Synonymical List of the Known Species of *Cambarus* and *Astacus*. *Proceedings of the American Academy of Arts and Science*, 20:107–158.

1885a. A Revision of the Astacidae. Part I. The Genera *Cambarus* and *Astacus*. *Memoirs of the Museum of Comparative Zoology at Harvard College*, volume 10, number 4, vi+186 pages, 10 plates.

1885b. A List of the Astacidae in the United States National Museum. *Proceedings of the United States National Museum*, 8(23):356–361.

1889. *Cambarus setosus*. Page 237, figures 1, 2, 3, 7 in Cave Animals in Southwestern Missouri, by Harrison Garman. *Bulletin of the Museum of Comparative Zoology at Harvard College*, volume 17, number 6.

1890. Notes on North American Crayfishes, Family Astacidae. *Proceedings of the United States National Museum*, 12(785):619–634.

1898. Observations on the Astacidae in the United States National Museum and in the Museum of Comparative Zoology, with Descriptions of New Species. *Proceedings of the United States National Museum*, 20(1136):643–694, plates 62–70.

1914. Notes on the Crayfishes in the United States National Museum and the Museum of Comparative Zoology, with Descriptions of New Species and Subspecies. *Memoirs of the Museum of Comparative Zoology at Harvard College*, 40(8):351–427, 13 plates.

Fingerman, Milton, and W. C. Mobberly, Jr.

1960. Trophic Substances in a Blind Cave Crayfish. *Science*, 132(3418):44–45.

Fitzpatrick, Joseph F., Jr.

1963. Geographic Variation in the Crawfish *Faxonella clypeata* (Hay) with the Definition and Defense of the Genus *Faxonella* Creaser (Decapoda, Astacidae). *Tulane Studies in Zoology*, 10(1):57–79, 20 figures.

1967. The Propinquus Group of the Crawfish Genus *Orconectes* (Decapoda: Astacidae). *The Ohio Journal of Science*, 67(3):129–172, 27 figures.

Fitzpatrick, J. F., Jr., and Rudolph Prins

1965. The First-Form Male of *Orconectes bisectus* Rhoades, a Poorly Known Kentucky Crawfish. *American Midland Naturalist*, 74(1):141–147, 12 figures.

Fleming, Robert S.

1939. The Larger Crustacea of the Nashville Region. *Journal of the Tennessee Academy of Science*, 13(4):296–314; 14(2):261–264; 14(3):299–324; 22 plates.

Frey, David G.

1965. Other Invertebrates—an Essay in Biogeography. Pages 613–631 in *The Quaternary of the United States*, VII Congress of the International Association for Quaternary Research. Princeton University Press.

Garman, Samuel

1889. Cave Animals from Southwestern Missouri. *Bulletin of the Museum of Comparative Zoology at Harvard College*, 17(6):225–259, 2 plates.

1924. A Little Known Cave Crayfish. *Transactions of the Kentucky Academy of Science*, Seventh Annual Meeting, 1 (1914–1923): 87–94, 20 figures.

Gibbes, L. R.

1850. On the Carcinological Collections of the United States, an Enumeration of the Species Contained in Them, with Notes on the Most Remarkable and Descriptions of New Species. *Proceedings of the American Association for the Advancement of Science*, 3:167–201.

Giovannoli, Leonard

1933a. Invertebrate Life of Mammoth and Other Neighboring Caves. Pages 600–623, figures 86–90, in Cave Life of Kentucky, by Vernon Bailey. *American Midland Naturalist*, volume 14, number 5.

1933b. Invertebrate Life of Mammoth and Other Neighboring Caves. Pages 218–241, 4 figures, in *Cave Life of Kentucky Mainly in the Mammoth Cave Region*, by Vernon Bailey. Notre Dame University Press.

Girard, Charles

1852. A Revision of the North American Astaci, with Observations on Their Habits and Geographical Distribution. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 6:87–91.

Graeter, E.

1909. Die Zoologische Erforschung der Höhlengewässer seit dem Jahre 1900 mit Ausschluss der Vertebraten. *Internationale Revue der Gesamten Hydrobiologie und Hydrographie*. Dr. Werner Klinkhardt, Leipzig, 2:457–479.

Graham, Dick

1969. Indian Rock Cave. *Alabama Caving '68 '69*, page 4.

Hagen, Hermann A.

1870. Monograph of the North American Astacidae. *Illustrated Catalogue of the Museum of Comparative Zoology at Harvard College,* number 3, 109 pages, 11 plates.

1872. The Blind Crayfish. *American Naturalist,* 6:494–495.

Harris, J. Arthur

1903a. The Habits of *Cambarus. American Naturalist,* 37:601–608.

1903b. An Ecological Catalogue of the Crayfishes Belonging to the Genus *Cambarus. Kansas University Science Bulletin,* 2(3):51–187, 4 plates.

Hart, C. W., Jr., and Dabney G. Hart

1966. Four New Entocytherid Ostracods from Kentucky, with Notes on the Troglobitic *Sagittocythere barri. Notulae Naturae,* number 388, 10 pages, 13 figures.

1969. The Functional Morphology of Entocytherid Ostracod Copulatory Appendages, with a Discussion of Possible Homologues in other Ostracods. Pages 154–167, 12 figures, in *The Taxonomy, Morphology and Ecology of Recent Ostracoda,* John W. Neale, editor. Edinburgh, Oliver and Boyd.

Hart, C. W., Jr., and Horton H. Hobbs, Jr.

1961. Eight New Troglobitic Ostracods of the Genus *Entocythere* (Crustacea, Ostracoda) from the Eastern United States. *Proceedings of the Academy of Natural Sciences of Philadelphia,* 113(8): 173–185, figures 1–32.

Hay, William Perry

1891. The Crustacea of Indiana. *Proceedings of the Indiana Academy of Science,* 1891, pages 147–151.

1893. Observations on the Blind Crayfishes of Indiana, with a Description of a New Subspecies; *Cambarus pellucidus testii. Proceedings of the United States National Museum,* 16(935):283–286, plates 64–65.

1896. The Crawfishes of the State of Indiana. *Twentieth Annual Report of the Department of Geology and Natural Resources of Indiana,* pages 475–507, 15 figures.

1897. On a Collection of Crustaceans from Indiana Caves. Pages 206–210 in Indiana Caves and their Fauna, by W. S. Blatchley. *Twenty-first Annual Report of the Department of Geology and Natural Resources of Indiana.*

1899. Synopsis of North American Invertebrates—The Astacidae of North America. *American Naturalist,* 33(396):957–966.

1902a. Observations on the Crustacean Fauna of the Region about Mammoth Cave, Kentucky. *Proceedings of the United States National Museum,* 25 (1285):223–236.

1902b. Observations on the Crustacean Fauna of Nickajack Cave, Tennessee, and Vicinity. *Proceedings of the United States National Museum,* 25(1292): 417–439, sketch map, figures I, II, 1–8.

Hobbs, Horton H., Jr.

1940. Seven New Crayfishes of the Genus *Cambarus* from Florida, with Notes on Other Species. *Proceedings of the United States National Museum,* 89(3097):387–423, figures 14–22.

1941. Three New Florida Crayfishes of the Subgenus *Cambarus* (Decapoda, Astacidae). *American Midland Naturalist,* 26(1):110–121, 2 plates.

1942a. A Generic Revision of the Crayfishes of the Subfamily Cambarinae (Decapoda, Astacidae) with the Description of a New Genus and Species. *American Midland Naturalist,* 28(2):334–357, 3 plates.

1942b. The Crayfishes of Florida. *University of Florida Publications, Biological Science Series,* volume 3, number 2, 179 pages, 24 plates.

1943. Two New Crayfishes of the Genus *Procambarus* from Mexico (Decapoda, Astacidae). *Lloydia,* 6:198–206, 26 figures.

1948a. On the Crayfishes of the Limosus Section of the Genus *Orconectes. Journal of the Washington Academy of Science,* 38(1):14–21, 28 figures.

1948b. A New Crayfish of the Genus *Orconectes* from Southern Tennessee. *Proceedings of the Biological Society of Washington,* 61:85–92, 9 figures.

1952. A New Albinistic Crayfish of the Genus *Cambarus* from Southern Missouri with a Key to the Albinistic Species of the Genus (Decapoda, Astacidae). *American Midland Naturalist,* 48(3):689–693, 8 figures.

1958. The Evolutionary History of the Pictus Group of the Crayfish Genus *Procambarus* (Decapoda, Astacidae). *Quarterly Journal of the Florida Academy of Sciences,* 21(1):71–91, 20 figures.

1959. [Key to Crayfishes.] Pages 869–901, figures 31. 18–31.41, in *Ward and Whipple's Freshwater Biology,* ed. 2, W. T. Edmondson, editor. New York, J. Wiley & Sons, Inc.

1962. Notes on the Affinities of the Members of the Blandingii Section of the Crayfish Genus *Procambarus* (Decapoda, Astacidae). *Tulane Studies in Zoology,* 9(5):273–279, 72 figures.

1965. A New Crayfish of the Genus *Cambarus* from Tennessee with an Emended Definition of the Genus (Decapoda, Astacidae). *Proceedings of the Biological Society of Washington,* 78:265–273, 12 figures.

1967a. The Current Status of the Crayfishes Listed by Girard (1852) in His "A Revision of the North American Astaci . . ." (Decapoda, Astacidae). *Crustaceana,* 12(2):124–132.

1967b. A New Crayfish from Alabama Caves with Notes on the Origin of the Genera *Orconectes* and *Cambarus* (Decapoda, Astacidae). *Proceedings of the United States National Museum,* volume 123, number 3621, 17 pages, 21 figures.

1969. On the Distribution and Phylogeny of the Crayfish Genus *Cambarus.* Pages 93–178, 20 figures, in *The Distributional History of the Biota of the*

Southern Appalachians, Part I, Invertebrates, Perry C. Holt, Richard L. Hoffman, and C. Willard Hart, Jr., editors. Virginia Polytechnic Institute, Research Division Monograph.

1970. A New Crayfish from the Nashville Basin, Tennessee. *Proceedings of the Biological Society of Washington,* 83(14):161–169, 1 figure.

1971a. The Entocytherid Ostracods of Mexico and Cuba. *Smithsonian Contributions to Zoology,* number 81, 55 pages, 31 figures.

1971b. A New Troglobitic Crayfish from Florida. *Quarterly Journal of the Florida Academy of Sciences,* 34(2):114–124, 19 figures.

Hobbs, H. H., Jr., and Thomas C. Barr, Jr.

1960. The Origins and Affinities of the Troglobitic Crayfishes of North America (Decapoda, Astacidae). I. The Genus *Cambarus. American Midland Naturalist,* 64(1):12–33, 57 figures.

Hobbs, H. H., Jr., and M. S. Bedinger

1964. A New Troglobitic Crayfish of the Genus *Cambarus* (Decapoda, Astacidae) from Arkansas with a Note on the Range of *Cambarus cryptodytes* Hobbs. *Proceedings of the Biological Society of Washington,* 77:9–15, 11 figures.

Hobbs, H. H., Jr., and J. F. Fitzpatrick, Jr.

1962. A New Crayfish of the Propinquus Group of the genus *Orconectes* from the Ohio Drainage System in West Virginia (Decapoda, Astacidae). *Proceedings of the Biological Society of Washington,* 75:207–214, 15 figures.

Hobbs, H. H., Jr., and Alejandro Villalobos F.

1964. Los Cambarinos de Cuba. *Anales del Instituto de Biología de la Universidad Nacional Autónoma de México,* 34(1–2):307–366, 50 figures.

Holthuis, L. B.

1956. Proposed Addition to the "Official List of Generic Names in Zoology . . . ." *Bulletin of Zoological Nomenclature,* 12(4):107–119.

1964. On the Status of Two Allegedly European Crayfishes, *Cambarus typhlobius* Joseph, 1880, and *Austropotamobius pallipes bispinosus* Karaman, 1961 (Decapoda, Atacidae). *Crustaceana,* 7(1): 42–48, 1 plate.

Hovey, Horace C.

1882. *Celebrated American Caverns, Especially Mammoth, Wyandot, and Luray, Together with Historical Scientific and Descriptive Notices of Caves and Grottoes in other Lands; with Maps and Illustrations.* xii+288 pages, illustrated. Cincinnati, Robert Clarke and Company.

1891. *Guide Book to the Mammoth Cave of Kentucky; Historical, Scientific and Descriptive.* 75 pages, illustrated. Cincinnati, Robert Clarke and Company.

1912. *Mammoth Cave of Kentucky, with an Account of Colossal Cavern.* 131 pages, illustrated. Louisville, John P. Morton and Company.

Hubbard, H. G.

1880. Two Days' Collecting in the Mammoth Cave, with Contributions to a Study of its Fauna. *American Entomologist,* 3:34–40, 79–86, figures 8–10, 18–24.

Huheey, James E.

1961. A Cyclical Evolutionary Process. *Systematic Zoology,* 10(1):43–45.

Jackson, George F.

1942. Animal Life of Caverns. *Bulletin of the National Speleological Society,* number 4, pages 3–7.

1953. *Wyandotte Cave.* 66 pages, illustrated. Narberth, Pennsylvania, Livingston Publishing Company.

1955. Caves of Indiana. *Bulletin of the National Speleological Society,* 16:55–64.

Jegla, Thomas C.

1964. Reproductive and Molt Periods in a Cave Crayfish. *Bulletin of the National Speleological Society,* 26(2):81.

1965a. Studies of the Eyestalks of Cave Crayfish. *American Zoologist,* 5(4):647.

1965b. Studies of the Eyestalk, Metabolism, and Molting and Reproductive Cycles in a Cave Crayfish [*Orconectes pellacious*]. *Dissertation Abstracts,* 25 (2):1421.

1966. Reproductive and Molting Cycles in Cave Crayfish. *Biological Bulletin,* 130(3):345–358, 4 figures.

1969. Cave Crayfish: Annual Periods of Molting and Reproduction. *Actes du IV*^{e} *Congres International de Speleologie en Yugoslavie (12–26 IX 1965),* 4–5: 135–137.

Jegla, T. C., and Thomas L. Poulson

1968. Evidence of Circadian Rhythms in a Cave Crayfish. *Journal of Experimental Zoology,* 168(2): 273–282, 5 figures.

1970. Circannian Rhythms—I. Reproduction in the Cave Crayfish, *Orconectes pellucidus inermis. Comparative Biochemical Physiology,* 33:347–355, 4 figures.

Jegla, T. C., T. L. Poulson, and M. R. Cooper

1965. Interpopulation Variations in a Cave Crayfish (*Orconectes pellucidus*). *American Zoologist,* 5(4):639.

Jeannel, R., and H. Henrot

1949. Les coléoptères cavernicoles de la région des Appalaches. *Notes Biospéoléogiques, Muséum National d'Histoire Naturelle,* 4(12):7–116.

Jillson, Willard Rouse

1954. *Geology of Crystal Cave.* 39 pages. Frankfort, Kentucky, Roberts Printing Co.

Jones, Walter B., and William W. Varnedoe, Jr.

1968. Caves of Madison County, Alabama. *Geological Survey of Alabama,* Circular 52, 177 pages, 128 figures, 1 plate.

Joseph, Gustav

1880. Demonstration eines neuen zur Familie der Astaciden gehorenden blinden Grottenkrebses aus Krain. *Jahres-Bericht der Schlesische Gesellschaft für vaterlandische Kultur,* 57:202.

1881. Erfahrungen im wissenschaftlichen Sammeln und Beobachten der den Krainer Tropfsteingrotten eigenen Arthropoden. *Berliner Entomologische Zeitschrift,* 25:233–282.

1882. Systematisches Verzeichniss der in der Tropfstein-Grotten von Krain einheimischen Arthropoden nebst Diagnosen der vom Verfasser entdeckten und bisher noch nicht beschriebenen Arten. Schluss der Abhandl.: Erfahrungen im wissenschaftlichen Sammeln und Beobachten der den Krainer Tropfsteingrotten eigenen Arthropoden. *Berliner Entomologische Zeitschrift,* 26:1–50.

Larimer, James L., Daniel L. Trevino, and Eberts A. Ashby

1966. A Comparison of Spectral Sensitivities of Caudal Photoreceptors of Epigeal and Cavernicolous Crayfish. *Comparative Biochemical Physiology,* 19 (2):409–415, 1 figure.

Leydig, Franz

1883. *Untersuchungen zur Anatomie und Histologie der Thiere.* 174 pages, 8 plates. Bonn, Verlag von Emil Strauss.

Lönnberg, Einar

1894. Cambarids from Florida, A New Blind Species. *Zoologischer Anzeiger,* 17:125–127.

1895. Cambarids from Florida, a New Blind Species. *Bihang till Koniglische Svenska Vetenskaps-Akademiens Handlingar,* 22(4):3–14, 6 figures.

Lucas, H.

1864. [Note on *Astacus pellucidus.*] *Bulletin Société Entomologique de France,* 4:iv.

Meredith, W. G., and F. J. Schwartz

1960. *Maryland Crayfishes.* Maryland Department of Research and Education, Educational Series, number 46, 32 pages, 17 figures.

Minckley, W. L.

1963. The Ecology of a Spring Stream, Doe Run, Meade County, Kentucky. *Wildlife Monographs,* number 11, 124 pages, 30 figures.

Mohr, Charles E.

1964. Exploring America Underground. *National Geographic,* 125(6):803–837, illustrated.

Mohr, Charles E., and Thomas L. Poulson

1966. *The Life of the Cave.* Our Living World of Nature series. 232 pages, illustrated. New York, McGraw Hill Book Company.

Newport, George

1855. On the Ocelli of the Genus *Anthophorabia. Transactions of the Linnean Society of London,* 21:161–165, figures 10–15.

Nicholas, Brother G.

1960. Checklist of Macroscopic Troglobitic Organisms of the United States. *American Midland Naturralist,* 64(1):123–160.

1969. Troglobites of Alabama—The Beetles. Pages 18–25 in Section 2, Cave Science, of *Speleo Digest,* William T. Plummer, editor.

1970. Life in the Underground World. *National Wildlife,* 8(6):21–24, illustrated.

Ortmann, A. E.

1892. Decapod Crustacea in Strassburger Museums. *Zoologische Jahrbücher abteilung für Systematik, Ökologie und Geographie der Tiese,* 6:1–13.

1902. The Geographical Distribution of Freshwater Decapods and its Bearing Upon Ancient Geography. *Proceedings of the American Philosophical Society,* 41(171):267–400, 8 figures.

1905a. The Mutual Affinities of the Species of the Genus *Cambarus* and Their Dispersal over the United States. *Proceedings of the American Philosophical Society,* 44(180):91–136, plate 3.

1905b. *Procambarus,* a New Subgenus of the Genus *Cambarus. Annals of the Carnegie Museum,* 3(3):435–442, 3 figures.

1906. The Crayfish of the State of Pennsylvania. *Memoirs of the Carnegie Museum,* 2(10):343–534, plates A, B, 39–43.

1918. Higher Crustaceans (Malacostraca). Pages 828–850, figures 1303–1318, in *Freshwater Biology,* by H. B. Ward and G. C. Whipple, New York, John Wiley and Sons, Inc.

1931. Crawfishes of the Southern Appalachians and the Cumberland Plateau. *Annals of the Carnegie Museum,* 20(2):61–160.

Osborn, R. C.

1912. The Crayfish. *Zoological Society Bulletin,* 16 (54):921–927.

Packard, A. S., Jr.

1871. On the Crustaceans and Insects. In The Mammoth Cave and Its Inhabitants, by A. S. Packard and F. W. Putnam. *American Naturalist,* 5(12): 744–761, figures 122–133.

1872a. [Note on Cope 1871b.] *American Naturalist,* 6: 30.

1872b. In *The Mammoth Cave and its Inhabitants; or Descriptions of the Fishes, Insects and Crustaceans Found in the Cave; wtih Figures of the Various Species, and an Account of Allied Forms, Comprising Notes upon their Structure, Development and Habits, with Remarks upon Subterranean Life in General,* by A. S. Packard, Jr., and F. W. Putnam. [Consists largely of reprints of articles by Packard (*American Naturalist,* 1871) and Putnam (*Annual Report of the Peabody Academy,* 1871, and *American Naturalist,* 1872).] 62 pages, 8 figures, 2 plates. Salem, Massachusetts, Salem Press.

1873. On the Cave Fauna of Indiana. *Fifth Annual Report of the Peabody Academy of Science,* July 1873, pages 93–97.

1874. [Remarks] in Minutes of the Section of Entomology Meeting of the Boston Society of Natural History, January 1, 1874. *Proceedings of the Boston Society of Natural History,* 16:209.

1879. *Zoology for Students and General Readers.* vi+ 719 pages, 545 figures. New York, Henry Holt and Company.

1888. The Cave Fauna of North America, with Remarks on the Anatomy of the Brain and Origin of the Blind Species. *Memoirs of the National Academy of Sciences,* volume 4, 156 pages, 21 figures, 27 plates.

1890. The Effect of Cave Life on Animals, and its Bearing on the Evolutionary Theory. *Popular Science Monthly,* 36(3):389–397.

1894. On the Origin of the Subterranean Fauna of North America. *American Naturalist,* 28:727–751.

Park, Orlando

1938. Studies in Nocturnal Ecology, VII. Preliminary Observations on Panama Rain Forest Animals. *Ecology,* 19(2):208–223.

Park, O., T. W. Roberts, and S. J. Harris

1941. Preliminary Analysis of Activity of the Cave Crayfish, *Cambarus pellucidus. American Naturalist,* 75(757):154–171, 5 figures.

Parker, G. H.

1890. The Eyes in Blind Crayfishes. *Bulletin of the Museum of Comparative Zoology at Harvard College,* 20(5):153–162, 1 plate.

Pearse, A. S.

1910. The Crawfishes of Michigan. *Michigan State Biological Survey,* Publication 1:9–22, 8 plates.

Penn, George H., Jr.

1952. A New Crayfish of the Virilis Section of the Genus *Orconectes. Natural History Miscellanea, Chicago Academy of Sciences,* number 109, 7 pages, 12 figures.

Penn, G. H., Jr., and J. F. Fitzpatrick, Jr.

1963. Interspecific Competition Between Two Sympatric Species of Dwarf Crawfishes. *Ecology,* 44(4): 793–797, 1 figure.

Pennak, Robert W.

1953. *Freshwater Invertebrates of the United States.* ix+769 pages, 470 figures. New York, The Ronald Press Company.

Pope, T. E. B.

1926. Blind Fishes and Crayfishes. *Yearbook of the City of Milwaukee,* 6:163–171, figures 156, 157.

Poulson, Thomas L.

1964. Animals in Aquatic Environments: Animals in Caves. Pages 749-771 in *Handbook of Physiology,* D. B. Dill, editor. Washington, American Physiological Society.

Poulson, T. L., and Thomas C. Jegla

1966. Circadian Rhythms and Seasonal Cycles in Cave Fishes and Crayfish. *Bulletin of the National Speleological Society,* 28(2):98.

Poulson, T. L., and William B. White

1969. The Cave Environment. *Science,* 165(3897): 971–981, 3 figures.

Powell, Richard L.

1961. Caves of Indiana. *Indiana Department of Conservation, Geological Survey,* Circular 8, 127 pages, 58 figures, 4 plates.

Pratt, Henry Sherring

1916. *A Manual of the Common Invertebrate Animals Exclusive of Insects.* 737 pages, illustrated. A. C. McClurg and Company.

Price, F. M.

1900. The Eyes of *Cambrus pellucidus* [Title, without text, of a paper presented to the Academy]. *Proceedings of the Indiana Academy of Science,* 1899, page 155.

Prins, Rudolph

1968. Comparative Ecology of the Crayfishes *Orconectes rusticus rusticus* and *Cambarus tenebrosus* in Doe Run, Meade County, Kentucky. *Internationale Revue der gesamten Hydrobiologie,* 53(5):667–714, 13 figures.

Putnam, F. W.

1872. The Blind Fishes of Mammoth Cave and Their Allies. *American Naturalist,* 6:6–30, 2 plates.

1875a. Remarks on Living Fishes and Crayfishes of Mammoth Cave. (In Minutes of the Meeting of the Boston Society of Natural History, December 2, 1874.) *Proceedings of the Boston Society of Natural History,* 17:222–225.

1875b. Remarks on the Mammoth Cave and Some of its Animals. (In Minutes of the Meeting of the Essex Institute, Salem, Massachusetts, November 25, 1874.) *Bulletin of the Essex Institute,* 6(2):190–200.

1877. On Some of the Habits of the Blind Crawfish, *Cambarus pellucidus,* and the Reproduction of Lost Parts. *Proceedings of the Boston Society of Natural History,* 18:16–19.

Rabé, Felix

1890. *La Question de L'Ecrevisse.* 83 pages. Imprimerie de Sezanne, H. Patoux.

Rhoades, Rendell

1941. Notes on Some Crayfishes from Alabama Caves, with the Description of a New Species and a New Subspecies. *Proceedings of the United States National Museum,* 91(3129):141–148, 2 figures.

1944. The Crayfishes of Kentucky with Notes on Variation, Distribution and Descriptions of New Species and Subspecies. *American Midland Naturalist,* 31(1):111–149, 10 figures.

1959. A Review of the Status of *Orconectes inermis* Cope and a Suggested Nomenclatorial Change. *American Midland Naturalist,* 61(2):399–402.

1962. The Evolution of Crayfishes of the Genus *Orconectes* Section *Limosus.* (Crustacea, Decapoda). *Ohio Journal of Science,* 62(2):65–96, 8 figures.

Semper, Karl

1881. *Animal Life as Affected by the Natural Conditions of Existence.* xvi+472 pages, 106 woodcuts. New York, D. Appleton and Company.

Shaler, N. S.

1875. On the Antiquity of the Caverns and Cavern Life of the Ohio Valley. *Memoirs of the Boston Society of Natural History,* 2:355–363. [Republished, 1876, in *Memoirs of the Kentucky Geological Survey,* 1(1):1–13.]

Silliman, B., Jr.

1851. On the Mammoth Cave of Kentucky. [From a letter addressed to Prof. Guyot, Cambridge; dated November 8, 1950, Louisville.] *American Journal of Science and Arts,* series 2, 11:332–339.

Sloan, John

1888. Letters to Packard Written in 1873. *In* Packard, A. S., The Cave Fauna of North American, with Remarks on the Anatomy of the Brain and Origin of the Blind Species. *Memoirs of the National Academy of Sciences,* 4:15, 16.

Smith, S. I.

1873. The Crustacea of the Freshwaters of the United States. *Report of the United States Commission of Fish and Fisheries, (1872–1873),* pages 637–665.

1875. The Crustaceans of the Caves of Kentucky and Indiana. *American Journal of Science and Arts,* series 3, 9:476–477.

Spandl, Hermann

1926. *Die Tierwelt der Unterirdischen Gewässer.* xi+235 pages, 116 figures. Speläologische Monographien herausgegeben vom Speläologischen Institut der Bundeshöhlen-kommission, Wien, 11.

Spurgeon, C. H.

1915. The Eyes of *Cambarus setosus* and *Cambarus pellucidus. Biological Bulletin,* 28:385–396, 9 figures, 1 plate.

Stammer, H. J.

1932. Die Fauna des Timavo. Ein Beitrag sur Kenntnis der Höhlen Gewässer, des Suss-und Brackwässers im Karst. *Zoologische Jahrbücher abteilung für Systematik, Ökologie und Geographie der Tiese,* 63:521–656, 16 figures.

Stebbing, Thomas R. R.

1893. *A History of Crustacea, Recent Malacostraca.* viii+466 pages, illustrated. New York, D. Appleton and Company.

Steele, Mary Isabelle

1902. Crayfish of Missouri. *Publications of the University of Cincinnati,* series 2, volume 2, bulletin 10, 33 pages, 5 plates.

Stenuit, Robert, and Marc Jasinski

1964. *Marveilleux monde souterrain.* 95 pages, illustrated. Western Publishing-Hachette International.

1966. *Caves and the Marvelous World Beneath Us.* [Translated from the French by Harry Pearman.] 95 pages, illustrated. New York, A.S. Barnes and Company.

Stiles, C. W., and Albert Hassall

1927. Key-Catalogue of the Crustacea and Arachnoids of Importance in Public Health. *Hygienic Laboratory Bulletin,* number 148, pages 197–289.

Tarkington, Terry W., William W. Varnedoe, Jr., and John D. Veitch

1965. *Alabama Caves.* iv+81 pages and maps. Huntsville, Alabama, Huntsville Grotto of the National Speleological Society.

Tellkampf, Theodor G.

1844a. Ausflug nach der Mammuthhöhle in Kentucky. *Das Ausland,* (168):671–672, (169):675–676, (170):679–680, (171):683–684, (172):687–688, (173):691–692, (174):695–696, (175):699–700.

1844b. Ueber den blinden Fisch der Mammuthhöhle in Kentucky, mit Bemerkungen über einige andere in dieser Höhle lebende Thiere. *Archiv für Anatomie, Physiologie und wissenschaftliche Medicin,* Heft IV, pages 381–394, Tafel IX.

1845. Memoirs on the Blind Fishes and some other Animals Living in the Mammoth Cave in Kentucky. *New York Journal of Medical and Collateral Science,* pages 84–93, 1 plate.

Thompson, David H.

1967. A Comparison of Visual Acuity between Cave and Epigeal Crayfish. *Wisconsin Speleologist,* Summer-Fall, 1967, page 45.

Thompson, W. M.

1844. Notice of the Blind Fish, Cray-fish and Insects from the Mammoth Cave, Kentucky. *Annals and Magazine of Natural History,* 13:111–113.

Torode, William

1968. Alabama 1000. *Huntsville Grotto Newsletter,* 9 (10):152–153.

1969. Alabama 1000. *Alabama Caving '68–'69,* Special Publication of the Huntsville Grotto of the National Speleological Society, page 16.

Turner, C. L.

1935. The Aberrant Secondary Sex Characters of the Crayfishes of the Genus *Cambarus. American Midland Naturalist,* 16(6):863–882.

Underwood, Lucien M.

1886. List of the Described Species of Freshwater Crustacea from America, North of Mexico. *Bulletin of the Illinois State Laboratory of Natural History,* 2(5):323–386.

Vandel, Albert

1964. *Biospeologie. La Biologie des Animaux Cavernicoles.* xviii+619 pages, 80 figures, 11 plates. Paris, Gauthier-Villars.

Van Straelen, Victor

1942. A propos de la distribution des ecrevisses, des homards et des crabes d'eau douce. *Bulletin Musée Royal d'Histoire des Sciences Naturelles de Belgique,* 18(56):1–11.

Villalobos, Alejandro F.

1953. Distribución geografica y notas ecologicas de los cambarinos mexicanos. *Memoria del Congresso Científico Mexicano, IV Centario de la Universidad de Mexicano,* 7:343–374, 4 plates.

1954. Estudios de los cambarinos mexicanos XII. Parte 1. Revisión de las especies afines a *Procambarus mexicanus* (Erichson) con Descripción de formas nuevas. *Anales del Instituto de Biologia, Universidad Autónoma de México,* 25(1,2):299–379, 19 plates.

1955. Cambarinos de la fauna mexicana (Crustacea Decapoda). Tesis, Facultad de Ciencias, xvi+290 pages, 62 plates. Universidad Nacional Autónoma de México.

Wells, P. H.
1959. Response to Light by Cave Crayfishes. *Occasional Papers of the National Speleological Society,* number 4, 15 pages, 10 figures.

Wolf, Benno
1934–1938. Volume 3, pages 103–105, in *Animalium Cavernarum Catalogus,* by Dr. W. Junk. Verlag für Naturwissenschaften, 's-Gravenhage.

Wolfe, Douglas A., and David G. Cornwell
1964. Carotenoids of Cavernicolous Crayfish. *Science,* 144:1467–1469.

Wright, R. Ramsey
1884. Leydig's Researches in Anatomy and Histology. [A review of Leydig's work (1893) and a comparison of the olfactory organs of *O. pellucidus* with those of *O. propinquus.*] *American Naturalist,* 18(3):272–273.

Appendix

LIST OF CAVES.—The caves listed below are those from which troglobitic crayfishes of the genus *Orconectes* have been reported. An asterisk indicates those from which we have examined no specimens; for these the earliest reference to the occurrence of crayfish in them is cited. More precise locations for most of the caves may be found under the Specimens Examined section of the species treatments.

The number in parentheses following most of the cave names identifies the troglobitic crayfish inhibiting it, as listed below:

1. *Orconectes australis australis* (Rhoades)
2. *Orconectes australis packardi* Rhoades
3. *Orconectes incomptus,* new species
4. *Orconectes inermis inermis* Cope
5. *Orconectes inermis testii* (Hay)
6. *Orconectes pellucidus* (Tellkampf)

Also enclosed in these parentheses are letters referring to the associated commensal entocytherid ostracods listed below (these ostracod records have been extracted from Hart and Hobbs (1961) and Hart and Hart (1966), with corrections and emendations in locality records and in the identities of the crayfish hosts):

A. *Dactylocythere prionata* (Hart and Hobbs)
B. *Dactylocythere steevesi* (Hart and Hobbs)
C. *Dactylocythere ungulata* (Hart and Hobbs)
D. *Donnaldsoncythere donnaldsonensis* (Klie)
E. *Donnaldsoncythere hiwasseensis* (Hobbs and Walton)
F. *Donnaldsoncythere tuberosa* (Hart and Hobbs)
G. *Sagittocythere barri* (Hart and Hobbs)
H. *Sagittocythere stygia* Hart and Hart
I. *Uncinocythere simondsi* (Hobbs and Walton)
J. *Uncinocythere zancla* Hobbs and Walton

ALABAMA
Jackson County
Bell Spring Cave (1)
Borderline Cave (1)
Canyon Cave (1)
Doodlebug Hole [=Blowing Cave] (1)
Doug Green Cave (1)
Fern Cave (1 G)
Guess Creek Cave (1)
Indian Rock Cave (Graham, 1969)
Jess Elliott Cave (1)
Kennamer Cave (1)
Larkins Cave (1)
Limrock Blowing Cave (1)
McFarland Cave (1)
Paint Rock Cave (1)
Saltpeter Cave (1)
Salt River Cave (1)
Sauta Cave [=Blowing Cave] (1 G)
Madison County
Aladdin Cave (1)
Big Spring [=Huntsville] Cave (1)
Burwell Cave (1)
Byrd Spring Cave (1)
Cold Spring Cave (1)
Fuqua Spring Cave (1)
*Grayson Spring Cave (Jones and Varnedoe, 1968)
Hering Cave [=Cave Spring Cave] (1)
Matthews Cave (1)
Sadler Spring Cave (1)
Shelta Cave (1 G)

INDIANA
Bartholomew County: Clifty Caves incorrectly cited by Hay, 1893; see Washington County. Rhoades, 1959, mentioned crayfish from the County but cited no localities.
Brown County: Rhoades, 1959; no specific localities were mentioned.
Crawford County
Archibald Cave (4)
*Binkleys Cave (Sight record, T.C.B.)
*Carter Byrnes Cave (Sight record, T.C.B.)
Crawfish Spring (4)

*“Evaston” [=Everton] Cave (Blatchley, 1897)
Marengo Cave (4)
Sibert’s Well Cave (4 G)
*Wild Cat Cave (Hay, 1893)
Wyandotte Cave (4)
Harrison County
Bradford Cave (4 G)
*Cave near Mauckport (4)
King’s Cave (4)
Rhodes Cave (Collett, 1879)
Jefferson County
*Caves near Madison (Hay, 1893)
Lawrence County
*Bedford Cave (Packard, 1890)
Blue Spring Cave (4)
*“Connelly’s” [=Connerly’s] Cave (Hay, 1893)
Donaldson’s [Donaldson’s-Bronson’s] Cave (4 D)
Mitchell Cave (Eigenmann 1903, Banta 1907)
Shawnee Cave (Spurgeon, 1915)
*“Donnihue’s” [=Donnehue’s] Cave (Hay, 1893)
*Down’s Cave (Hay, 1893)
*Hamer’s Cave (Collett, 1874)
Harrison Cave (4)
Pless Cave (4)
Shiloh Cave (4)
Sullivan Cave (4)
Wagoner Cave (4)
Monroe County
Carmichael Cave (5)
Eller’s Cave (5 G)
*Goode’s Cave (Powell, 1961)
Mayfield’s Cave (5)
May’s Cave (5 G)
*Ranard School Cave (Powell, 1961)
Reeve’s Cave (5)
Salamander Cave (5)
Shaft Cave (5)
*“Truett’s” [=Truitt’s] Cave (Hay, 1891)
Orange County
*Cave in Orleans (Packard, 1888)
*Cave near Paoli (Hay, 1893)
*Lost River Cave (Packard, 1888)
Murray Spring Cave (4)
Washington County
Endless Cavern [=Clifty Cave] (4)
Fredericksburg Cave (4)
River [=Clifty] Cave (4)
KENTUCKY
Barren County
Cave City [=Railroad] Cave (6)
Diamond Cave (6 G)
Twyman Cave (6)
Breckenridge County
Bandy Cave (4)
Bat Cave (?Packard, 1888) (4)
Cave near Big Spring (4)
Lockard Cave (4 G)
*McCubbin’s Cave (Jegla and Poulson, 1968)
Thornhill Cave (4)
Christian County
Glover’s Cave (6)
Edmonson County
Blowing Spring Cave (6)
Cedar Sink Cave (6)
Floyd Collins Crystal Cave (6)
*?Ganter’s Cave [=“cave . . . down the Green River from Mammoth Cave”] (Putnam, 1875b)
Long Cave (6)
Mammoth Cave (6 G, H)
*Martin Cave (Sight record, T.C.B.)
Stillhouse Hollow Cave (6)
White Cave (6)
Green County
Brush Creek Cave (4)
Scott Cave (4)
Hardin County
Bland Cave (4 G, J)
Nelson Cave (4)
Hart County
Bald Knob Cave (6)
Buckner Hollow Cave (6 C, G)
Cave near Northtown (6)
Cooch Webb Cave (4)
Cub Run Cave (4)
Horse [=Hidden River] Cave (6)
Mammoth Onyx Cave (6)
Riders Mill Cave (4 G, J)
Turner Cave (4)
Logan County
Cooks Cave (6)
Mud River Cave (6)
McCreary County
Eureka Cave (2)
Steele Hollow Cave (2)
Meade County
Joe Jones Cave (4)
Lime Kiln Cave (4)
Rockhaven Cave (4 E, G)

Shackletts Cave (4)
Pulaski County
Baker Cave (2)
Cumberland Crystal [=Sloans Valley] Cave (2)
Hydens Cave (2 A, G, I)
Old Kentucky Cave (2)
Pourover Cave (2)
Wind Cave (2 A)
Rockcastle County
Duvalt Cave (2)
Fletchers Spring Cave (2)
Pine Hill Cave (2)
Teamers Cave (2 G)
Trigg County
Cool Spring Cave (6 G)
Warren County
By-Pass Cave (6)
Lost River Cave (6)
Pruitt Saltpeter Cave (6)
Wayne County
Blowing Cave (2)
Horse Hollow Cave (2 B, C, F)
Johnson Fork Cave (2)
Kogers Cave (2)
TENNESSEE
Fentress County
Buffalo Cave (1)
Sells Cave (1)
Wolf River Cave (1)
Franklin County
Caroline Cove Cave (1)
Putman Spring Cave (1)
Walker Spring Cave (1)
Wet Cave (1)
Grundy County
Bear Cave (1)
Big Mouth Cave (1 C)
Crystal Cave (1)
Wonder Cave (1)
Jackson County
Carter Cave (3 G)
Cherry Cave (3)
Haile Cave (3)
Montgomery County
Bellamy Cave (6)
Sinkhole Cave (6)
Overton County
*East Water Supply Cave (Sight record, T.C.B.)
Raven Bluff Cave (1)
Sheep Cave (1)
Putnam County
Blind Fish Cave (1 B, C, F, G)
Bridge Creek Cave (1 G)
Johnson Saltpeter Cave (1)
Warren County
*Blowing Cave (Sight record, T.C.B.)
Cumberland Caverns (1)
Turkeyscratch Cave (1)
White County
*Haskell Sims Cave (Sight record, T.C.B.)
Indian Cave (1)
Ross Cave (1)
Ward [=Dairy House] Cave (1)
Wildcat Cove Cave (1)

COLLECTORS.—Listed below, alphabetically by the initials used to identify them in the species treatments, are the collectors of the specimens studied:

A.F. A. Fiske
A.R.B Andrew R. Boone
A.R.C. A. R. Cahn
A.W.D. Arthur W. Dobson
B. J. C. Beakley
B.B. Bret Blosser
B.D. Bert Denton
B.D.V. B. D. Valentine
C.E.B. C. E. Bush
C.E.M. Charles E. Mohr
C.E.Mc. C. E. McCary
C.H. C. Harrel
C.M. Carl Melton
C.W.H. C. W. Hart, Jr.
D.A.E. D. A. Etnier
D.B. Donald Blair
D.E. D. Egbert
D.G.H. Dabney G. Hart
D.H.P. D. Hugh Puckett
D.P.B. David P. Beiter
E.C. Ellsworth Call
E.P.C. E. P. Creaser
F.N.B. F. N. Blanchard
G.H.E. G. H. Ehlers
H.H. H. Henrot
H.H.H. III H. H. Hobbs III
H.R.S. H. R. Steeves, Jr.
H.R.S. III H. R. Steeves III
H.S. Herbert Shadowen
H.T. Hugh Thomas
J.E.C. J. E. Cooper
J.E.Cr. J. E. Crouch
J.E.Y. John E. Younglove
J.F.F. J. F. Fitzpatrick, Jr.
J.H. J. Harris
J.H.C. Jerry H. Carpenter

J.M.V. J. M. Valentine
J.N.D. J. N. Dent
J.P. J. Purcell
J.P.V. J. P. Voigt
J.R. J. Rhines
J.R.H. J. R. Holsinger
J.R.R. James R. Reddell
J.S. Jerry Stade
K.B. Kenneth Burdsall
K.H. K. Haas
K.S. Kjell Sandved
L.G. Leonard Giovannoli
L.G.C. Lloyd G. Carr
L.G.Co. Lyle G. Conrad
L.H. Leslie Hubricht
L.M. L. Merkle
M.B. Mark Becker
M.E.M. M. E. Mann
M.R.C. Martha R. Cooper
M.T. Merlin Tuttle
O.D.L. O. D. Lee
P.P. Peter Parker
R.A.K. R. A. Kuehne
R.B. R. Baroody
R.B.C. R. B. Cumming
R.G. Richard Graham
R.M. R. McAdams
R.M.N. R. M. Norton
R.N. Raymond Nelson
R.P. Rudolph Prins
R.R. Rendell Rhoades
R.T. R. Taylor
R.W. R. Walker
S.B.P. Stewart B. Peck
S.M. Sherman Minton
S.R.G. S. R. Gorin
T.C.B. T. C. Barr, Jr.
T.C.B. III T. C. Barr III
T.C.J. Thomas C. Jegla
T.E.S. T. E. Simpson
T.G.M. Terrence G. Marsh
V.E.S. V. E. Shelford
W.B.J. Walter B. Jones
W.L.M. W. L. Minckley
W.M.A. W. M. Andrews
W.P.H. W. P. Hay
W.R.E. W. R. Eberly
W.T. William Torode

* U.S. GOVERNMENT PRINTING OFFICE: 1972—484-312/7

Publication in Smithsonian Contributions to Zoology

Manuscripts for serial publications are accepted by the Smithsonian Institution Press, subject to substantive review, only through departments of the various Smithsonian museums. Non-Smithsonian authors should address inquiries to the appropriate department. If submission is invited, the following format requirements of the Press will govern the preparation of copy.

Copy must be typewritten, double-spaced, on one side of standard white bond paper, with 1½" top and left margins, submitted in ribbon copy with a carbon or duplicate, and accompanied by the original artwork. Duplicate copies of all material, including illustrations, should be retained by the author. There may be several paragraphs to a page, but each page should begin with a new paragraph. Number consecutively all pages, including title page, abstract, text, literature cited, legends, and tables. The minimum length is 30 pages, including typescript and illustrations.

The *title* should be complete and clear for easy indexing by abstracting services. Taxonomic titles will carry a final line indicating the higher categories to which the taxon is referable: "(Hymenoptera: Sphecidae)." Include an *abstract* as an introductory part of the text. Identify the *author* on the first page of text with an unnumbered footnote that includes his professional mailing address. A *table of contents* is optional. An *index,* if required, may be supplied by the author when he returns page proof.

Two *headings* are used: (1) text heads (boldface in print) for major sections and chapters and (2) paragraph sideheads (caps and small caps in print) for subdivisions. Further headings may be worked out with the editor.

In *taxonomic keys,* number only the first item of each couplet; if there is only one couplet, omit the number. For easy reference, number also the taxa and their corresponding headings throughout the text; do not incorporate page references in the key.

In *synonymy,* use the short form (taxon, author, date:page) with a full reference at the end of the paper under "Literature Cited." Begin each taxon at the left margin with subsequent lines indented about three spaces. Within an entry, use a period-dash (.—) to separate each reference. Enclose with square brackets any annotation in, or at the end of, the entry. For *references within the text,* use the author-date system: "(Jones, 1910)" and "Jones (1910)." If the reference is expanded, abbreviate the data: "Jones (1910:122, pl. 20: fig. 1)."

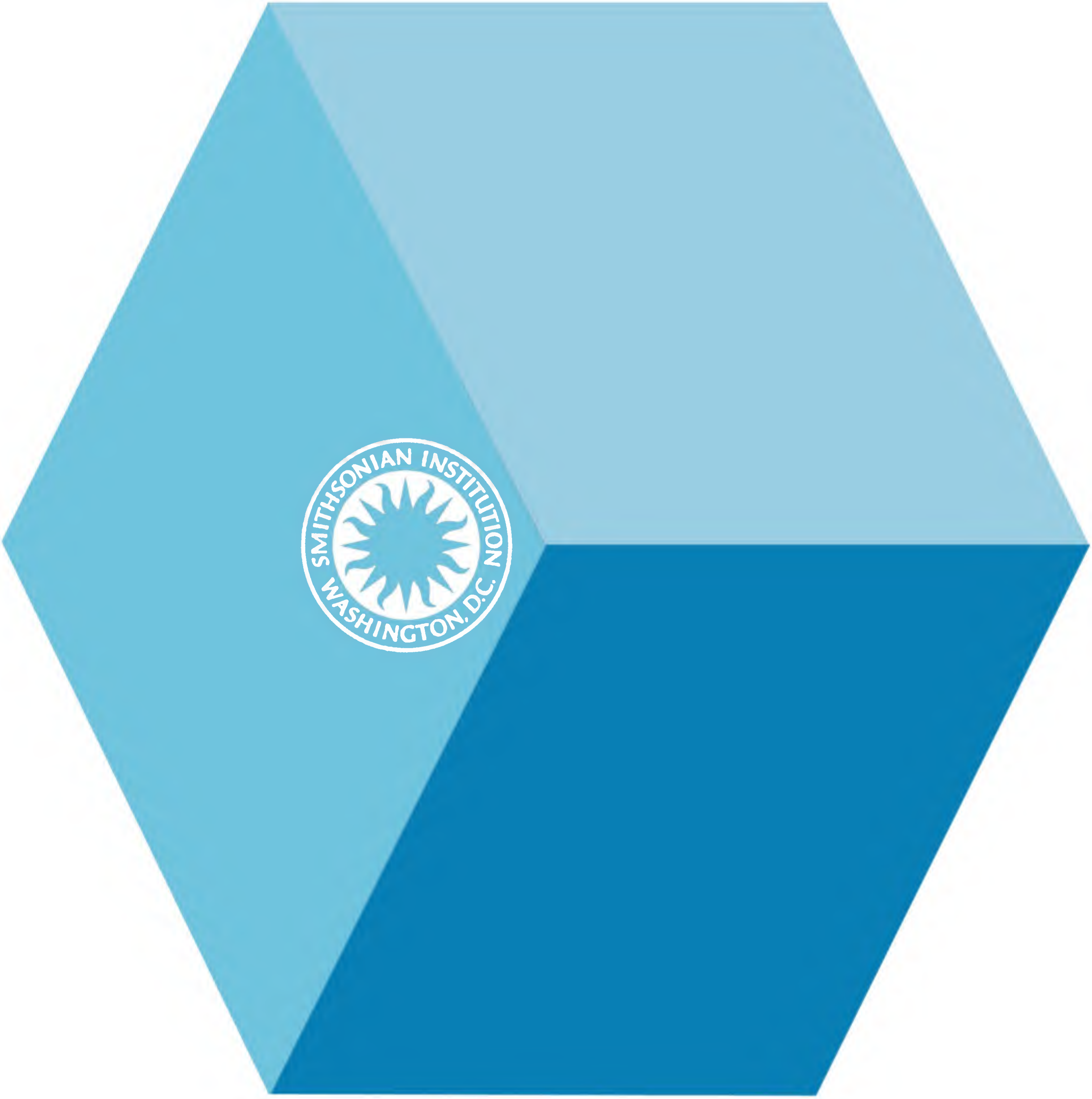
Simple *tabulations* in the text (e.g., columns of data) may carry headings or not, but they should not contain rules. Formal *tables* must be submitted as pages separate from the text, and each table, no matter how large, should be pasted up as a single sheet of copy.

Use the *metric system* instead of, or in addition to, the English system.

Illustrations (line drawings, maps, photographs, shaded drawings) can be intermixed throughout the printed text. They will be termed *Figures* and should be numbered consecutively; however, if a group of figures is treated as a single figure, the components should be indicated by lowercase italic letters on the illustration, in the legend, and in text references: "Figure 9*b*." If illustrations (usually tone photographs) are printed separately from the text as full pages on a different stock of paper, they will be termed *Plates,* and individual components should be lettered (Plate 9*b*) but may be numbered (Plate 9: figure 2). Never combine the numbering system of text illustrations with that of plate illustrations. Submit all legends on pages separate from the text and not attached to the artwork. An instruction booklet for the preparation of illustrations is available from the Press on request.

In the *bibliography* (usually called "Literature Cited"), spell out book, journal, and article titles, using initial caps with all words except minor terms such as "and, of, the." For capitalization of titles in foreign languages, follow the national practice of each language. Underscore (for italics) book and journal titles. Use the colon-parentheses system for volume, number, and page citations: "10(2):5-9." Spell out such words as "figures," "plates," "pages."

For *free copies* of his own paper, a Smithsonian author should indicate his requirements on "Form 36" (submitted to the Press with the manuscript). A non-Smithsonian author will receive 50 free copies; order forms for quantities above this amount with instructions for payment will be supplied when page proof is forwarded.



SMITHSONIAN INSTITUTION
WASHINGTON, D.C.