A Review of the Troglobitic Decapod Crustaceans of the Americas

HORTON H. HOBBS, JR., H. H. HOBBS III, and MARGARET A. DANIEL

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Horton H. Hobbs, Jr., H. H. Hobbs III, and Margaret A. Daniel



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ABSTRACT

Hobbs, Horton H., Jr., H. H. Hobbs III, and Margaret A. Daniel. A Review of the Troglobitic Decapod Crustaceans of the Americas. Smithsonian Contributions to Zoology, number 244, 183 pages, 70 figures, 1 table, 1977.-Eight families comprising 18 genera and 55 species and subspecies of troglobitic and anchialine decapod crustaceans are recorded from the Americas. The family Atyidae is represented by two genera: Palaemonias, with two species occurring in the United States, and Typhlatya, encompassing seven species found in the West Indies, Yucatán, and the Galapagos Islands. Among the six genera of the family Palaemonidae are the Mexican monotypic Bithynops in Chiapas, Creaseria in Yucatán, and Neopalaemon in Oaxaca; in addition, one species of the genus Macrobrachium occurs in Oaxaca, two species of the genus Palaemonetes trequent subterranean habitats in the United States, and six members of the genus Troglocubanus occur in Cuba, Jamaica, and San Luis Potosí, Mexico. Only one troglobitic species of the genus Alpheopsis, a member of the largely marine family Alpheidae, occurs in the area, that in Oaxaca, Mexico. Two genera of the also primarily marine family Hippolytidae, Barbouria and Calliasmata, are each represented by a single species occurring in anchialine habitats in the West Indies, the latter only in the Dominican Republic. Of the three endemic American groups, the Cambarinae comprises the largest number of troglobites: there are eight species of Cambarus, six species and subspecies of Orconectes, and 13 species and subspecies of Procambarus; the former two are confined to the United States and the latter is present also in Cuba and Mexico; the monotypic *Troglocambarus* is restricted to peninsular Florida. The other two endemic groups, the families Aeglidae and Pseudothelphusidae, are represented, respectively, by a single species of the genus Aegla occurring in Brazil and one of Potamocarcinus in Chiapas, Mexico. The remaining widespread family Grapsidae encompasses a member of the genus Sesarma in Jamaica. Following a presentation of the composition of the fauna and a historical account of investigations leading to our present knowledge of it is a discussion of the evolution of the several groups and a key to aid in the identification of members of the fauna. The systematic section includes synonymies for the genera, subgenera, species, and subspecies. Each of the supraspecific taxa is diagnosed, its range defined, and the numbers of species and troglobitic or anchialine representatives noted. For each species and subspecies, as complete a synonymy as we have been able to obtain is provided. Also a diagnosis, the maximum size, disposition of the types, type-locality, and range (including locality records) are followed by a summary of available ecological and life-history data; illustrations are provided for each. Appended to this study is a list of the non-troglobitic decapods that are known to occur in subterranean habitats, a glossary of terms employed in the text, and a list of the symbionts of American troglobitic decapods.

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A Review of the Troglobitic Decapod Crustaceans of the Americas

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Introduction

More than one hundred and thirty years have elapsed since the first troglobitic decapod, a crayfish, was described from the Americas, and since that time 54 additional species and subspecies, including representatives of four families of shrimps, other crayfishes, and anomuran, and two crabs have been reported. In addition, almost 40 nontroglobitic decapods have been observed in spelean environments.

Included herein is a summary of our knowledge of all of the troglobitic decapods known to occur in the Western Hemisphere, together with the anchialine Barbouria cubensis and Calliasmata rimolii. Although two decapods, Caridinopsis brevinaris Holthuis (1956a:56) from French Guiana and Euryrhynchus burchelli Calman (1907:297) from Para (Belém), Brazil, are each known only from a subterranean locality, neither exhibits any modification suggesting a troglobitic habit. Furthermore, a congener of the latter, E. wrzesniowskii Miers (1877:662), has been found both in subsurface and epigean waters in Guyana, Surinam, and French Guiana, leading Holthuis (1956a:68) to treat both of them as "incidental visitors of subterranean waters." These three species have been included in the list of non-troglobitic decapods reported from American hypogean waters.

Following a presentation of the composition of the troglobitic fauna of the Americas is a history of the discovery of its components and of studies leading to our knowledge of it. A brief section devoted to the decapod fauna of American karst areas precedes a discussion of the evolution of several of the troglobitic groups, and this is followed by notes on certain adaptations of these crustaceans to a troglobitic existence and a key to aid in their identification. Most of the characters used in the key are illustrated in Figures 1 and 2. Appended to the systematic section are a list of the non-troglobitic decapods that are known to occur in subterranean habitats, a list of the symbionts of American troglobitic decapods, and a glossary of terms employed in the text.

DIAGNOSES.—To make the diagnoses of the supraspecific taxa more readily usable in the identification of the troglobites, they have been based primarily on the troglobitic fauna. As a result, some are not applicable to all epigean members assigned to them.

SIZE.—For each species the size noted represents the maximum (usually carapace) length, which, if

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FIGURE 1.—Diagrammatic shrimp and pleopods of crayfishes: *a*, diagrammatic shrimp showing terms used in key and diagnoses; *b*, mesial view of distal portion of diagrammatic first pleopod of crayfish, genus *Procambarus*; *c*, lateral view of same; *d*, mesial view of distal portion of diagrammatic first pleopod of crayfish, genus *Cambarus*; *e*, lateral view of same. (ai = appendix interna, am = appendix masculina, as = antennal spine, b = basis or basipodite, bg = branchiostegal groove, bs = branchiostegal spine, c = coxa or coxopodite, cp = carpus or carpopodite, d = dactyl or dactylopodite, end = endopod or endopodite, ep = epipod or epipodite, ex = exopod or exopodite, hs = hepatic spine, i = ischium or ischiopodite, m = merus or meropodite, p = propodus or propodite, ps = pterygostomian spine, sc = scaphocerite or antennal scale, ss = supraorbital spine.)

previously recorded, is followed by a reference to its source. For the shrimps, unless otherwise indicated, the length of the carapace is given as the distance between the caudal margin of the orbit and the mid-caudodorsal margin of the carapace. For the crayfishes, two lengths are employed: carapace length (= distance from tip of rostrum to midcaudodorsal margin of carapace) and postorbital



FIGURE 2.—Diagrammatic crayfish showing terms used in key and diagnoses: a, ventral view of male; b, dorsal view of same.

carapace length (= distance from orbit to midcaudodorsal margin of carapace).

DISPARITY IN TREATMENT OF THE SPECIES.—A casual perusal of the synonymies provided for the species will reveal readily the cause of the disproportionate amount of space devoted to them. In general, not only have the crayfishes been more frequently mentioned in the literature, but also they have attracted a greater number of investigators. This is particularly noticeable in the summaries of information offered for the two longestknown American troglobites, Orconectes inermis inermis and Orconectes pellucidus. At the same time, however, it should be realized that the number of references do not necessarily reflect the amount of information available concerning the animals, for a good majority of the citations are to articles which contribute nothing in the way of new data.

Only in the brief historical account of the study of the troglobites have we alluded to investigations other than those devoted to distribution, ecology, and life histories, and attention is called to the considerably more detailed discussion of the cave ecosystem in Barr (1967a, 1967b), Barr and Kuehne (1971), Mitchell (1969), Poulson (1964), and Poulson and White (1969).

LOCATION OF TYPES .- The location of the types

of each of the troglobites is indicated by the following.

- ANSP Academy of Natural Sciences of Philadelphia, Pennsylvania, U.S.A.
- HHH Collection of H.H.H. III, Wittenberg University, Springfield, Ohio, U.S.A.
- IBM Instituto de Biología de la Universidad Nacional Autónoma de México, Mexico City, Mexico
- ISER Institut de Speologie "Emile Racovitza," Bucharest, Romania
- ISNB Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium
- MCZ Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A.
- MNHA Alabama Museum of Natural History, Tuscaloosa, Alabama, U.S.A.
- NMG Naturhistorisches Museum Genf, Museum d'Histoire Naturelle, Geneva, Switzerland
- RNHL Rijksmuseum van Natuurlijke Historie, Leiden, The Netherlands
- RR Collection of Rendell Rhoades, Ashland College, Ashland, Ohio, U.S.A.
- TTM Texas Tech Museum, Lubbock, Texas, U.S.A.
- TU Department of Zoology, Tulane University, New Orleans, Louisiana, U.S.A.
- USNM Specimen labels using the acronym "USNM" for the former United States National Museum are deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D. C., U.S.A.
- ZBM Zoologisches Museum der Humboldt-Universitat, Berlin, East Germany
- ZIAS Zoological Institute, Academy of Sciences, Leningrad, U.S.S.R.

ACKNOWLEDGMENTS .- This review of the troglobitic decapod crustaceans of the Americas had its inception in an invitation to one of us (Hobbs, Jr.) from Professor C. Delamare Deboutteville of the Laboratoire d'Ecologie Générale, Brunoy, France, to prepare a summary of the American subterranean decapods for inclusion in the Annales de Spéléologie. In compliance with this request, we began compiling available information and discovered that there existed a far more extensive bibliography than we had realized; thus, the preliminary treatments of the species were expanded to such a degree in progressive drafts that the inclusion of this review in the Annales de Spéléologie did not seem suitable. We extend our apologies to Professor Deboutteville for our over-enthusiastic approach to this project, and, at the same time, wish to express our appreciation to him for suggesting that a summary of the American troglobitic decapods would be timely.

Without the aid and encouragement given us by our Smithsonian colleagues, Fenner A. Chace, Jr., Raymond B. Manning, and Isabel Pérez Farfante, throughout the preparation of the manuscript, this study would have been far less complete. For their interest, advice, and criticisms of the manuscript we are most grateful, as we are also for the invaluable critical reading of the penultimate draft by Martha R. and John E. Cooper of the State Museum of Natural History, Raleigh, North Carolina.

Especial thanks also go to Lipke B. Holthuis of the Rijksmuseum van Natuurlijke Historie in Leiden, Holland, and James R. Reddell of Texas Tech University in Lubbock, both for aid in certain bibliographic problems and for providing us with specimens. We are indebted to Richard Franz, of the Florida State Museum in Gainesville, for permitting us to include a number of unpublished locality records for several of the troglobitic crayfishes from Florida. Dr. H.-E. Gruner of the Zoologisches Museum in Berlin was most helpful in locating the types of Barbouria cubensis. For their persistent efforts in obtaining a number of hard-to-find references, we extend our appreciation to Carolyn S. Hahn and Jack F. Marquardt of the Smithsonian Library. A number of redrawn illustrations are the work of Carolyn B. Gast, also a member of the Smithsonian staff, and the photographs of Aegla cavernicola were kindly provided us by Michael Türkay of the Senckenberg Natur-Museum in Frankfurt am Main; to both of them we extend our thanks. For her interest and painstaking efforts in converting a tedious manuscript into this publication, we are deeply grateful to Joan B. Horn of the Smithsonian Institution Press.

Many persons have assisted us in obtaining specimens, the locality records for which are included in this report. Among the many to whom we are indebted are Thomas C. Barr, Jr., of the University of Kentucky in Lexington, John E. and Martha R. Cooper, John R. Holsinger of Old Dominion University in Norfolk, Virginia, Stewart B. Peck of Carlton University in Ottawa, and James R. Reddell. The latter two are responsible for accumulating much, if not most, of the materials available to us from tropical and subtropical areas. Finally, to Georgia B. and Susan K. Hobbs we extend our thanks for their patience in assisting us in proofing synonymies, locality records, and the bibliographic citations.

Composition of the Fauna

The known elements of the troglobitic fauna of the Americas include 55 described species and subspecies distributed among 18 genera and eight families.¹ These are systematically arranged in Table 1 in which the range of each taxon in the Americas is broadly defined, and, if occurring elsewhere (introductions indicated by stars), so noted; also indicated is whether or not non-troglobitic members of each of the supraspecific taxa exist and the type of aquatic habitat that has been invaded by each of the troglobites.

The family Atyidae is represented by two genera, *Palaemonias* and *Typhlatya*. The former, comprising two species, is restricted to subterranean waters of the United States. The latter, encompassing seven American species, is much more widespread, ranging from Ascension Island through the West Indies, Yucatán, and the Galapagos Islands.

The troglobitic Palaemonidae are distributed among six genera, three of which are monotypic and restricted to southern Mexico: Bithynops occurring in Chiapas, Creaseria in Yucatán, and Neopalaemon in Oaxaca. The genus Macrobrachium embraces a number of epigean American representatives, but only one troglobitic species has been described, that from the State of Oaxaca, Mexico. A second undescribed species is known to occur in the State of Tabasco. The genus Palaemonetes likewise contains a number of epigean species many of which live almost exclusively in fresh water; its only American troglobitic members, however, occur in the United States. Two species are treated herein, and a third is being described from Texas by Strenth (1976:3). The palaemonid genus with the largest number of troglobitic species is the American genus *Troglocubanus*. Its six members are restricted to subterranean waters of Cuba, Jamaica, and Mexico.

The family Alpheidae is represented by a single genus *Alpheopsis*, which is widespread in marine habitats in the tropics. Only three species are known to frequent fresh water, and the single American freshwater species is unique in being troglobitic, having been found only in one cave in Oaxaca.

Two genera of the largely marine family Hippolytidae possess members that have invaded anchialine habitats or subterranean waters in the Americas. The genus *Barbouria* is endemic in the West Indies, and one of its two members, the anchialine *B. cubensis*, occurs on several of the islands. The genus *Calliasmata* is also composed of two species, one of which occurs in slightly brackish waters in the Dominican Republic.

The family Cambaridae is represented in the troglobitic fauna of the Americas by four genera, three of which also have epigean members. The genera *Cambarus* and *Orconectes* (excluding introductions) are confined to North America where eight and six species and subspecies, respectively, have become adapted to a troglobitic existence. *Procambarus*, the largest genus of the family, occurring in North and Middle America and in Cuba, encompasses 13 described members that are restricted to hypogean waters. The remaining monotypic genus *Troglocambarus*, found only in Florida, is perhaps the most remarkable of the entire decapod fauna.

The three remaining families that have troglobitic members in the Americas include one anomuran, the South American Aeglidae with one Brazilian cave inhabitant, *Aegla cavernicola*; and two brachyurans, the Pseudothelphusidae, represented by a single species in Chiapas belonging to the genus *Potamocarcinus*; and the Grapsidae of which a Jamaican member of the large genus *Sesarma* is a troglobite.

As may be gleaned from Table 1, two of the families (the Aeglidae and Pseudothelphusidae), 11 of the genera (Aegla, Barbouria, Bithynops, Cambarus, Creaseria, Neopalaemon, Orconectes, Palaemonias, Procambarus, Troglocambarus, and Troglocubanus), and all 55 species are American endemics.

¹ In addition to the species listed here as troglobites, the following new species are known to exist or are being described from the Americas: a species of the genus *Bithynops* and another belonging to the genus *Macrobrachium* from Mexico (L. B. Holthuis); specimens of another member of the latter genus from Oaxaca, Mexico, collected by James R. Reddell, to be described by us when an adequate series becomes available; and two crayfishes of the subgenus *Aviticambarus* (genus *Cambarus*) from Alabama (John E. and Martha R. Cooper). Descriptions of a new shrimp, *Palaemonetes holthuisi* Strenth (1976:3) from Texas, and a new crayfish, *Procembarus* (*Ortmannicus*) franzi Hobbs and Lee (1976, *Proceedings of the Biological Society of Washington*, 89(32): 384) from Florida appeared too late for these species to be included in this review.

	DI	DISTRIBUTION			HABITATS			гs		
							Tro	glob	itic	
	North America	Middle America	South America	West Indies	Extra-limital	Non-troglobitic	Lentic	Lotic	Anchialine	
Atyidae	•		•	•	•	•	•	•	•	Cambarus
Palaemonias	•						•	٠		Jugicamba
alabamae	•						٠	•		cryptody
ganteri	•						•	•		setosus
Typhlatya	•	•	•	•	•		•	•	•	tartarus
campecheae		•					?			zophonas
consobrina				•			•			Puncticam
galapagensis			•						•	nerterius
garciai				•			•			Orconectes
mitchelli		•					٠			a. austral
monae				•			•			a. packara
pearsei		•					?			incomptus
D.1										i. inermis
Palaemonidae	•	•	•	•	•	•	•	•	•	i. testii
Bithynops luscus	-	•		-			-	•		pellucidu
Creaseria		•	-	-				•		Procambarus
		•		-	-		•	-	-	Austrocam
morleyi Macrobrachium	•	•		-			•	-	-	niveus
villalobosi		•	•	•	•	•	•	•	•	o. oaxaca
Neopalaemon		-	-	-	-	-	-		-	o. reddel
nahuatlus		•	-	-	-	-	-		-	rodriguez
Palaemonetes	•		•	•	•	•	•		-	Leconticam
antrorum	•	-	-	-	-	-	-		-	milleri
cummingi		+	-	-	-	-	•	-	+	Lonnbergi
Troglocubanus		•	+	•	-	-	•	•	+-	acheront
calcis		-	1		1	-		-	+	Ortmannicu
eigenmanni		+	+	•	+	-		+	+	erythrops
gibarensis		-	1		-	-	-	•	-	horsti
inermis		-	+		+	-	•	1	+	l. lucifug
jamaicensis		-	+	•			-	•	+	l. alach
perezfarfanteae		•	+	-	1			-	1	orcinus
		1	+	+	+		1	1	+	pallidus
Alpheidae	•	•	٠	•	•	•	٠	•	•	Remoticam
Alpheopsis	•	•	•	•	•	•	•	•		pecki
stygicola		•						•		Troglocambe maclane
Hippolytidae										maciane
Barbouria		-	-	•	•	-	-	+	•	Aeglidae
cubensis		-	+-		+	-	-	-	•	Aegla
Calliasmata		-	+		•	-	-	-		cavernico
rimolii		+	+		-	-	-	+	-	
Cambaridae	-	-	1	-				1	-	Pseudothelph Potamocarcir
Cambarus	•	•	-	•	•*	-	-	•	+	Typhlopseu
Aviticambarus	•	-	-		+	•	•	•	+	mocinoi
hamulatus		-	+	+	+	+	•	•	+	
jonesi			+	+	-	-	•	•	+	Grapsidae
Erebicambarus	•		+		-	•	•	•	-	Sesarma
hubrichti			+	-	+	-			-	Sesarma
		-	1	1	1					verlevi

	DI	STR	IBU	UTI	H	ABITATS			
							Troglobitic		
	North America	Middle America	South America	West Indies	Extra-limital	Non-troglobitic	Lentic	Lotic	Anchialine
Cambarus	•					•	•	•	
Jugicambarus	•					٠	•	٠	
cryptodytes	•						•	•	
setosus	•							•	
tartarus	•							٠	
zophonastes	•							•	
Puncticambarus	•					•	•	٠	
nerterius	•						-	•	
Orconectes	•				*	•	•	•	-
a. australis	•						•	•	
a. packardi	•				-		•	•	-
incomptus	•		-					•	
i. inermis	•	-				-		•	
i. testii	•				-			•	-
pellucidus	•	-	-	-	-	-	-	•	-
Procambarus	•	•		•	*	•	•	•	
Austrocambarus niveus		•	-	•	-	•	•	•	
o. oaxacae		-	-	•	-			•	
o. oaxacae o. reddelli	-	•			-	-	-	•	
o. redaetti rodriguezi	-	•	-	-	-	-	-	•	
Leconticambarus		•	-		-	-		•	-
milleri	•		-	-	-	•	•	•	-
Lonnbergius		-	-		-	-	1	•	-
acherontis		-	-	-	-	-	-		-
Ortmannicus		•	-	-	*		•		-
erythrops		-	-	-	-	-		-	
horsti		-	-	-		\vdash	-	•	-
l. lucifugus		-	-	+	-	-	•	-	-
l. alachua		-	-	-	-	-	•	+	-
orcinus		+		+	-		•	•	
pallidus		+	-	-		-			-
Remoticambarus		1		+	+			?	-
pecki		1		-	+			17	-
Troglocambarus	•	1		+	1			t	-
maclanei	•	1		1	1			1	1
	1			1	1		t	1	-
Aeglidae	1		•			•	•	•	
Aegla	-	-	•		-	•	•	•	-
cavernicola		-	•	-	-	-	-	•	
Pseudothelphusidae		•	•	•		•	•	•	
Potamocarcinus		•	•	•		•	•	•	
Typhlopseudothelphusa		•						•	
mocinoi		•			-			•	
Grapsidae	•	•	•		•	•	•	•	•
Sesarma	•	•	•	•	•	•	•	•	
Sesarma		•	•	•	•	•	•	•	
verleyi									

 TABLE 1.—Summary of distribution and habitats (stars indicate introduction outside of Western Hemisphere)

Brief History of Investigations

While the bibliographic citations included in the account of each species or subspecies may provide a detailed historical summary of that taxon, they do not furnish an integrated history of the contributions to our knowledge of all of the currently recognized troglobitic decapods of the Western Hemisphere. The list below notes the components of the fauna in the sequence in which their existence was made known. The date of the publication precedes the name of the taxon (original combination) and its author, followed by the family and the geographic source of the original material on which the description of the species or subspecies was based. The narrative following the list by no means encompasses every isolated contribution that has been made, but we have endeavored to call attention to most original studies as well as to monographic and summary articles.

Date	Taxon	Family	Locality
1844	Astacus pellucidus Tellkampf	Cambaridae	Kentucky, U.S.A.
1871	Orconectes inermis Cope	Cambaridae	Indiana, U.S.A.
1872	Hippolyte Cubensis von Martens	Hippolytidae	La Habana, Cuba
1881	Orconectes hamulatus Cope	Cambaridae	Tennessee, U.S.A.
1889	Cambarus setosus Faxon	Cambaridae	Missouri, U.S.A.
1891	Cambarus pellucidus var. testii Hay	Cambaridae	Indiana, U.S.A.
1894	Cambarus acherontis Lönnberg	Cambaridae	Florida, U.S.A.
1896		Palaemonidae	Texas, U.S.A.
1901	Palaemonias ganteri Hay	Atyidae .	Kentucky, U.S.A.
1903	Palaemonetes eigenmanni Hay	Palaemonidae	Pinar del Río, Cuba
1912	Palaemonetes calcis Rathbun	Palaemonidae	La Habana, Cuba
1914	Sesarma (Sesarma) verleyi Rathbun	Grapsidae	St. Elizabeth, Jamaica
1936	Typhlatya pearsei Creaser	Atyidae	Yucatán, Mexico
1936	Palaemon morleyi Creaser	Palaemonidae	Yucatán, Mexico
1940	Cambarus pallidus Hobbs	Cambaridae	Florida, U.S.A.
1940	Cambarus lucifugus lucifugus Hobbs	Cambaridae	Florida, U.S.A.
1940	Cambarus lucifugus alachua Hobbs	Cambaridae	Florida, U.S.A.
1941	Cambarus pellucidus australis Rhoades	Cambaridae	Alabama, U.S.A.
1941	Cambarus (Cambarus) cryptodytes Hobbs	Cambarida e	Florida, U.S.A.
1942	Typhlatya garciai Chace	Atyidae	Oriente, Cuba
1942	Troglocambarus maclanei Hobbs	Cambaridae	Florida, U.S.A.
1943	Palaemonetes gibarensis Chace	Palaemonidae	Oriente, Cuba
1943	Palaemonetes inermis Chace	Palaem onid ae	La Habana, Cuba
1943	Procambarus rodriguezi Hobbs	Cambaridae	Veracruz, Mexico
1944	Orconectes pellucidus packardi Rhoades	Cambaridae	Kentucky, U.S.A.
1952	Cambarus hubrichti Hobbs	Cambaridae	Missouri, U.S.A.
1953	Typhlopseudothelphusa mociñoi Rioja	Pseudothelphusidae	Chiapas, Mexico
1954	Typhlatya monae Chace	Atyidae	Isla Mona, West Indies
1954	Palaemonetes (P.) cummingi Chace	Palaemonidae	Florida, U.S.A.
1960	Cambarus jonesi Hobbs and Barr	Cambaridae	Alabama, U.S.A.
1961	Palaemonias alabamae Smalley	Atyidae	Alabama, U.S.A.
1963	Troglocubanus jamaicensis Holthuis	Palaemonidae	Saint Mary, Jamaica
1 964	Cambarus zophonastes Hobbs and Bedinger	Cambaridae	Arkansas, U.S.A.
1964	Cambarus nerterius Hobbs	Cambaridae	West Virginia, U.S.A.
1964	Procambarus niveus Hobbs and Villalobos F.	Cambaridae	Pinar del Río, Cuba
1967	Construction of the second	Cambaridae	Alabama, U.S.A.
1970	Typhlatya consobrina Botosaneanu and Holthuis	Atyidae	Camagüey, Cuba
1970	Typhlatya galapagensis Monod and Cals	Atyidae	Galapagos Islands, Ecuador

Date	Taxon	Family	Locality
1971	Procumbarus milleri Hobbs	Cambaridae	Florida, U.S.A.
1972	Cambarus (Jugicambarus) tartarus Hobbs and Cooper	Cambaridae	Oklahoma, U.S.A.
1972	Orconectes incomptus Hobbs and Barr	Cambaridae	Tennessee, U.S.A.
1972	Procambarus horsti Hobbs and Means	Cambaridae	Florida, U.S.A.
1972	Procambarus orcinus Hobbs and	Cambaridae	Florida, U.S.A.
	Means		
1972	Aegla cavernicola Türkay	Aeglidae	São Paulo, Brazil
1973	Macrobrachium villalobosi Hobbs	Palaemonidae	Oaxaca, Mexico
1973	Neopalaemon nahuatlus Hobbs	Palaemonidae	Oaxaca, Mexico
1973	Alpheopsis stygicola Hobbs	Alpheidae	Oaxaca, Mexico
1973	Procambarus (Austrocambarus) oaxacae oaxacae Hobbs	Cambaridae	Oaxaca, Mexico
1973	Procambarus (Austrocambarus) oaxacae reddelli Hobbs	Cambaridae	Oaxaca, Mexico
1974	Bithynops luscus Holthuis	Palaemonidae	Chiapas, Mexico
1974	Troglocubanus perezjarjanteae Villalobos F.	Palaemonidae	San Luis Potosí, Mexico
1975	Calliasmata rimolii Chace	Hippolytid ae	Puerto Rico, Dominican Republic
1975	Procambarus (Ortmannicus) erythrops Relyea and Sutton	Cambaridae	Florida, U.S.A.
1976	Typhlatya campecheae Hobbs and Hobbs	Atyidae	Campeche, Mexico
197 6	Typhlatya mitchelli Hobbs and Hobbs	Atyidae	Yucatán, Mexico

The first notice of an American troglobitic decapod crustacean that has come to our attention appeared "in the minutes of the 'Stated Meeting of May 24, 1842' of the Academy of Natural Sciences at Philadelphia (Anonymous, 1843b), 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, . . . both taken from a small stream called the 'River Styx' in the Mammoth Cave, Kentucky, about 21/2 miles from the entrance'" (Hobbs and Barr, 1972: 1). This crayfish was designated Astacus pellucidus by Tellkampf in 1844a.

Almost 30 years elapsed before Cope (1871a) described the second troglobitic species. Rendell Rhoades (1959:399–400) commented:

... Cope, though an eminent zoologist, was not a student of crustacea. When he visited the Indiana caves with Professor E. T. Cox, the state geologist, public announcements were expected from this well-known scientist. *The Indianapolis Journal* of September 5, 1871 carried his "off-the-cuff" remarks regarding the mysterious denizens of the subterranean depths. The account specifically mentioned the blind crayfish, "Astacus pellucidus" given him by the state geologist. Cope's position as a carcinologist was hardly enhanced by his use of a generic name then nearly twenty-five years out of date! He did not even edit the error out of the account before it appeared in the Annals and Magazine of Natural History (1871[b]:368-370). In spite of his unfamiliarity with the field and apparently without consulting authorities on the group, he proceeded to name a new genus and a new species [Orconectes inermis] a few months later based upon a single second form male from Wyandotte Cave (Cope, 1872a:419). [Cope also relegated Tellkampf's Astacus pellucidus to his new genus.]

The publication had no sooner appeared than Dr. Hermann Hagen, who had revised and monographed the crayfishes the year before, published a stinging satire (Hagen, 1872) on the "hard-driving evolutionist" and his "inhumane treatment of Mother Nature's kindred creatures." Dr. A. S. Packard, Jr., well known zoologist and authority on cave animals, also challenged Cope's new taxonomic creation (Packard, 1872b). The words of these two authorities brought an avalanche of adverse criticism that buried the name, Orconectes inermis, for seventy years.

The year following the description of O. inermis, von Martens (1872) described the anchialine Hippolyte Cubensis [= Barbouria cubensis] from Cuba, and in 1881, Cope named the third member of his genus Orconectes, O. hamulatus, from Nickajack Cave, Tennessee.

In 1880, Joseph reported a nine-centimeter blind crayfish from Krain (= Carniola, now in northern Yugoslavia), which he designated *Cambarus typhlobius*. A year later, he referred to presumably the same crayfish as *Cambarus coecus* (1881:237) and as

Cambarus stygius (1881:241, 248). As pointed out by Holthuis (1974b:42), the latter two names, utilized without description or "indication," must be considered nomina nuda. In a third paper dealing with this crayfish, Joseph (1882:12) presented an expanded description of it, citing more precise locality data ["Recca (= Reka) River in St. Kanzian Cave (= St. Canzian Cave, = Skocijanska Jama) near Mataún (= Matavunje) not far from Divazza (= Divaca), east of Trieste in Carniola (at present province of Slovenija, N. Jugoslavia)" (Holthuis, 1964:43-44)], and designating it Cambarus stygius. Inasmuch as this combination had been applied previously to an epigean crayfish by Bundy (1876:3), Joseph's name was a homonym. In a clear presentation of available information relating to the confusion arising from Joseph's work, Holthuis (1964:45) reached the conclusion that "Joseph's type specimen actually was an American specimen of Orconectes pellucidus (Tellkampf), which had been incorrectly labeled as to locality."

Before the turn of the century, four additional troglobitic decapods had been added to the American list: Cambarus setosus Faxon (1889) from Missouri, C. pellucidus var. testii Hay (1891) from Indiana, C. acherontis Lönnberg (1894) from Florida, and Palaemonetes antrorum Benedict (1896) from Texas. The subgenus Cambarus Erichson (1846:97), encompassing all of the American crayfishes then assigned to the genus Astacus, was elevated to generic rank by Girard (1852:88).

Packard (1888), in his treatise on the North American cave fauna, summarized the state of our knowledge of the decapods, including a review of the observations of Newport (1855) on the eye of "Astacus pellucidus" and added his own notes on the eye and brain of this crayfish and of the eye of Cambarus (A.) hamulatus. Packard also presented a summary of the work of Leydig (1883), Wright (1884), and Faxon (1885a) on the olfactory organs of the Mammoth and Nickajack cave crayfishes. Auditory organs in these troglobitic crayfishes were also discussed by Packard.

During the first two decades of the present century, a shrimp, Palaemonias ganteri Hay (1901), was described from Mammoth Cave, and two additional ones, Palaemonetes eigenmanni Hay (1903) [= Troglocubanus eigenmanni] and P. calcis Rathbun (1912) [= T. calcis], were reported from Cuba. Cambarus ayersii Steele (1902) [= C. (J.) setosus] was described from Missouri, and the crab, Sesarma (Sesarma) verleyi Rathbun (1914), was named on the basis of a single specimen collected in Jamaica.

Possibly reflecting the effect of World War I on scientific expeditions, the Jamaican crab was the last troglobite to be described from the Americas until after the expeditions sponsored by the University of Michigan to the cenotes of Yucatán in the middle 1930s. Creaser (1936) described the then monotypic atyid *Typhlatya pearsei* and the fourth known troglobitic palaemonid, *Palaemon morleyi* [= *Creaseria morleyi*], specimens of both of which were discovered during the expeditions.

Between 1940 and 1944, 11 American troglobitic decapods were named. Of these, three are Cuban shrimps: Typhlatya garciai Chace (1942), Palaemonetes inermis Chace (1943) [= Troglocubanus inermis], and P. gibarensis Chace (1943) [= T.gibarensis]. The remaining forms were crayfishes, five of which were described from Florida: Cambarus pallidus Hobbs (1940) [= Procambarus (O.) pallidus], C. lucifugus lucifugus Hobbs (1940) [= P. (O.) l. lucifugus], C. lucifugus alachua Hobbs (1940) = P. (O.) l. alachua, C. (C.) cryptodytesHobbs (1941b) and Troglocambarus maclanei Hobbs (1942a). The new Cambarus pellucidus australis R. Rhoades (1941) [= O. a. australis] was reported from Alabama caves, Orconectes pellucidus packardi R. Rhoades (1944) [= O. australis packardi] was described from Kentucky, and the first report of a troglobitic crayfish from Mexico appeared in 1943 with the description of Procambarus rodriguezi Hobbs.

In summation, of the 25 troglobites described prior to 1950, three were shrimps belonging to the family Atyidae (one each from Cuba, Mexico, and the United States); six were shrimps of the family Palaemonidae (four from Cuba and one each from Mexico and the United States); another was a member of the Hippolytidae (Cuba); 14 were crayfishes (all, except one Mexican species, from the United States); and one was a Jamaican crab belonging to the family Grapsidae.

During the first half of the current century, comparatively few additions were made to our knowledge of the biology of these troglobites. There were a limited number of new locality records, observations on habits and responses of the crayfishes to light and sound, and expressions of opinions regarding relationships and migrations of primitive stocks. Studies of the crayfish eye were continued with the work of Spurgeon (1915), and Turner (1935) made observations on aberrant secondary sexual characteristics of the Mammoth Cave crayfish. Park (1938) and Park, Roberts, and Harris (1941), investigating periodicity of activity, found this crayfish to be arhythmic. Burbanck, Edwards, and Burbanck (1948) were the first to shed light on the metabolic rate of a troglobitic crayfish, comparing the oxygen consumption of Cambarus (J.)setosus with that of an epigean species. Perhaps the most important single work of the last decade of the half-century was that of Jeannel (1943), in which he presented a classical review and synthesis of biology of cave dwelling organisms, including references to the American troglobites.

Between 1950 and 1959, the presence of four additional troglobites in the Americas was made known: the crayfish, *Cambarus hubrichti* Hobbs (1952), from Missouri; the crab, *Typhlopseudothelphusa mociñoi* Rioja (1953b), from Chiapas; and two shrimps, *Typhlatya monae* Chace (1954) from Isla Mona, and *Palaemonetes* (*Palaemonetes*) cummingi Chace (1954) from Florida.

Eberly (1958, 1960) wrote primarily concerning the evolution of Orconectes pellucidus [= 0. i. inermis] and the competition existing between it and the troglophilic Cambarus bartoni leavis Faxon (1914:391) [= C. (Erebicambarus) laevis]; and Hobbs (1958b), in discussing the evolution of the members of the Pictus Group of the crayfish genus Procambarus, included remarks on the origin of the Floridian troglobitic crayfishes. A brief treatment was accorded the albinistic members of the genus Orconectes in Indiana by R. Rhoades (1959) in an attempt to clarify the identity of O. inermis. Interest in the perception of light by troglobitic crayfishes continued with the studies of Wells (1952, 1957a, 1959). For the shrimps, the most noteworthy contribution of the decade was Holthuis' (1956a) compilation and summary of available information on all Natantia known to have invaded subterranean waters.

During the next decade, 1960–1969, the presence in the Americas of five additional troglobitic crayfishes was revealed: *Cambarus jonesi* Hobbs and Barr (1960) from Alabama, *C. zophonastes* Hobbs and Bedinger (1964) from Arkansas, *C. nerterius* Hobbs (1964) from West Virginia, *Procambarus* niveus Hobbs and Villalobos F. (1964) from Cuba, and P. pecki Hobbs (1967b) from Alabama. In addition, two shrimps were named: Palaemonias alabamae Smalley (1961) from Alabama, and Troglocubanus jamaicensis Holthuis (1963a) from Jamaica.

Our knowledge of the troglobitic members of the crayfish genus Cambarus was summarized by Hobbs and Barr (1960), and in the nine years to follow there were a number of studies of the American decapod troglobites, most of them relating to the crayfishes. Huheey (1961), on the data provided by Eberly (1960), constructed a model for a cyclical evolutionary process in a spelean habitat frequented by a troglobitic and a troglophilic crayfish. R. Rhoades (1962) sketched in some detail his concepts of the evolution of the troglobitic members of the genus Orconectes and their allies. Outstanding during the decade was the work of Jegla (1964b, 1965, 1966, 1969), Jegla, Poulson, and Cooper (1965), Jegla and Poulson (1968, 1970), and M. R. Cooper (1969), dealing with variations, life history, biological rhythms, olfaction, and other facets of the biology of troglobitic Orconectes. Fingerman and Mobberly (1960) and Fingerman, et al. (1964) initiated work on the endocrine system involving the eye and brain of troglobitic Orconectes and Cambarus. Larimer (1966) investigated the caudal photoreceptor of C. (J.) setosus, and Larimer, Trevino, and Ashby (1966) compared this receptor in O. a. australis with that of epigean species.

Chace and Hobbs (1969), in reviewing the freshwater and terrestrial decapods of the West Indies, included the troglobitic species, and in his list of "los Crustaceos Dulceacuicolas," Straskraba (1969) briefly treated the troglobitic fauna of Cuba. An infrageneric classification of the crayfishes of the genus *Cambarus* was proposed by Hobbs (1969b) in his discussion of the distribution and phylogeny of species comprising it. Particularly significant among the contributions of the 1960s was Vandel's (1964) *Biospéologie: La Biologie des Animaux Cavernicoles.*

Increased interest in the cave fauna during the current and previous decades has resulted in a third of the known American troglobitic decapods having been described since 1969. Typhlatya consobrina was reported by Botosaneanu and Holthuis (1970) from Cuba, and T. galapagensis Monod and Cals (1970) was found in the Galapagos Islands. Four

crayfishes were added to the faunal list from Florida: Procambarus milleri Hobbs (1971b), P. horsti Hobbs and Means (1972), P. orcinus Hobbs and Means (1972), and P. (O.) erythrops Relyea and Sutton (1975c). From Oklahoma, Hobbs and Cooper (1972) described Cambarus (J.) tartarus, and from Tennessee, Hobbs and Barr (1972) introduced Orconectes incomptus. Aegla cavernicola Türkay (1972) was described from Brazil and Calliasmata rimolii Chace (1975) from the Dominican Republic.

The nine remaining species described since 1969 are from Mexico. Particularly noteworthy in accelerating our knowledge of the Mexican fauna were the Italian expeditions to Mexico and the efforts of the Association for Mexican Cave Studies group in Texas. The palaemonids include Macrobrachium villalobosi Hobbs (1973b), Neopalaemon nahuatlus Hobbs (1973a), Bithynops luscus Holthuis (1974a), and Troglocubanus perezfarfanteae Villalobos F. (1974); the cambarids are Procambarus (A.) oaxacae oaxacae Hobbs (1973a) and P. (A.) oaxacae reddelli Hobbs (1973a); the atyids are Typhlatya campecheae Hobbs and Hobbs (1976) and T. mitchelli Hobbs and Hobbs (1976); and finally, the only known troglobitic alpheid is Alpheopsis stygicola Hobbs (1973b), which was found in the State of Oaxaca.

Among the summary articles that have appeared since 1969 is the contribution of Botosaneanu and Holthuis (1970) providing a synopsis of the subterranean shrimps from Cuba; complementing and extending this work is Silva T.'s (1974) "Sinopsis de la Espeleofauna Cubana." Studies of the decapod fauna in the United States include a monograph of the troglobitic Orconectes by Hobbs and Barr (1972) and a zoogeographic discussion of the Floridian troglobitic crayfishes by Caine (1974a). In the area of ecology, the work of Barr and Kuehne (1971) on the troglobites inhabiting Mammoth Cave is particularly important, as are the unpublished dissertations of Caine (1974b), J. E. Cooper (1975), and Hobbs III (1973e), containing much new ecological, behavioral, and populational data on the decapod inhabitants of several Florida caves, Shelta Cave in Alabama, and Pless and Mayfield's caves in Indiana, respectively. Strenth's (1976) review of the systematics and zoogeography of the freshwater Palaemonetes places the two previously known troglobitic species and a new one from Texas in perspective with their epigean relatives. Reddell (in press) provides an excellent summary of our knowledge of all the Mexican troglobitic fauna.

Smaller in scope, but no less important are the contributions of many others. For example, the excellent morphological study of *Typhlatya galapagensis* by Monod and Cals (1970) is presented in great detail, and the ideas for estimating the antiquity of some troglobites expressed by Wilkens (1973c) are interesting. Also worthy of note is the study by Monod (1975) implying correlation between continental drift and the distribution of subterranean Atyidae.

Karst Regions Supporting Troglobitic Decapods

The various karst regions of the Americas are each characterized by a particular assemblage of organisms. Summarized here are the families and species of troglobitic decapod crustaceans populating each region. Those regions in North and Middle America are designated by physiographic areas or geological formations; in contrast, because of our meager knowledge of the troglobitic fauna of South America, and because of the limited size of the islands of the West Indies, we have employed geographic designations for them.

NORTH AMERICA

United States	
Greenbrier Valley (West Virginia)	Cambaridae: Cambarus (P.) nerterius
Cumberland Plateau and Eastern Highland Rim	Atyidae: Palaemonias alabamae
(Alabama to Kentucky)	Cambaridae: Cambarus (A.) hamulatus, C. (A.) jonesi, Orconectes australis aus- tralis, O. a. packardi, O. incomptus, Procambarus (R.) pecki
Pennyroyal Plateau—	Atyidae: Palaemonias ganteri
Mitchell Plain (Indiana,	Cambaridae: Orconectes
Kentucky)	inermis inermis, O. i. testii, O. pellucidus
Dougherty Plain (Georgia, Florida)	Cambaridae: Cambarus (J.) cryptodytes
Tertiary Karst in Eastern Panhandle and Peninsula	Palamonidae: Palaemonetes cummingi
Florida	Cambaridae: Procambarus
	(L.) acherontis, P. (O.)
	erythrops, P. (O.) horsti,
	P. (O.) lucifugus lucifugus,
	P. (0.) <i>l. alachua</i> , P. (0.)
	orcinus, P. (O.) pallidus, Troglocambarus maclanei
	a rogiocamourus macianei

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Miami Oolite (Florida)	Cambaridae: Procambarus (L.) milleri
Ozark Uplift (Arkansas, Missouri, Oklahoma)	Cambaridae: Cambarus (E.) hubrichti, C. (J.) setosus, C. (J.) tartarus, C. (J.) zophonastes
Balcones Escarpment (Texas)	Palaemonidae: Palaemonetes antrorum

MIDDLE AMERICA

Mexico (Physiographic Regions recognized by West, 1964, fig. 3) Sierra Madre Oriental Palaemonidae: Troglo-(Eastern slope in San cubanus perezfarfanteae Luis Potosi) Chiapas Highlands Palaemonidae: Bithynops luscus Pseudothelphusidae: Potamocarcinus (T.) mocinoi Gulf Coastal Lowlands and Palaemonidae: Macro-Isthmus of Tehuantepec brachium villalobosi, Neopalaemon nahuatlus Alpheidae: Alpheopsis stygicola Cambaridae: Procambarus (A.) oaxacae oaxacae, P. (A.) o. reddelli, P. (A.) rodriguezi Yucatán Platform Atyidae: Typhlatya campecheae, T. mitchelli, T. pearsei Palaemonidae: Creaseria morleyi SOUTH AMERICA Brazil (São Paulo) Aeglidae: Aegla cavernicola Atyidae: Typhlatya gala-Galapagos Islands pagensis WEST INDIES Atyidae: Typhlatya con-Cuba sobrina, T. garciai roglo-T. eigen. rensis,

	Palaemonidae: Troglo-
	cubanus calcis, T. eigen-
	manni, T. gibarensis,
	T. inermis
	Hippolytidae: Barbouria cubensis
	Cambaridae: Procambarus (A.) niveus
Hispaniola (Dominican	Atyidae: Typhlatya monae
Republic)	Hippolytidae: Calliasmata rimolii
Jamaica	Palaemonidae: Troglo- cubanus jamaicensis
	0

ogloensis Grapsidae: Sesarma (S.) verleyi

Puerto Rico (including Isla Mona)	Atyidae: Typhlatya monae
Lesser Antilles	Atyidae: Typhlatya monae
Bahama Islands	Atyidae: Typhlatya garciai Hippolytidae: Barbouria cubensis
Cayman Islands	Hippolytidae: Barbouria cubensis

Evolution of the Troglobitic Decapods

Comments and discussions on the evolution of the troglobitic decapods of the Americas date back to Cope (1872a) in his account of the occurrence of Orconectes inermis in "Wyandotte Cave" in Indiana. Some authors have made no more than a passing statement pertaining to the evolution of these animals; others have proposed rather broad generalizations as to the place and time of origin as well as to migratory paths, and a few have briefly discussed adaptations by one or more of the species to spelean habitats. For the West Indian portion of the decapod fauna, the present review relies basically on the comprehensive account by Chace and Hobbs (1969:17-28). Their postulates on origins are summarized in light of more recent, and occasionally earlier, contributions. For the other geographic regions of the Americas, the works of various authors are utilized, as indicated in the discussion of each family.² The crayfishes have received considerably more attention than have the other decapods, and the account devoted to them utilizes the works of Caine (1974a), Hobbs (1958b, 1962, 1965, 1969b), Hobbs and Barr (1960, 1972), and R. Rhoades (1962).

Of the eight families represented in the troglobitic decapod fauna of the Americas, only three, the Aeglidae, Cambaridae, and Pseudothelphusidae, include no species which require brackish or salt water to complete their life cycles. Thus it seems reasonable to assume that the troglobitic aeglid, the crayfishes, and the single pseudothelphusid crab have had their origin in stocks that were already adapted to a freshwater environment.

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² Subsequent to the completion of this manuscript, an interesting and pertinent treatise on Caribbean Biogeography has appeared: Donn E. Rosen, "A Vicariance Model of Caribbean Biogeography," Systematic Zoology, 24(4):431-464, 21 figures (1976).

ATYIDAE

Chace and Hobbs (1969:21) noted that the members of the genus Typhlatya

represent relicts of a once much more widespread epigean stock of which no other trace is known to exist. The ancestral stock must have been a primitive one, retaining exopods on all of the pereiopods Perhaps the absence of epigean species signifies an inability of the surface members to compete with faunas that later invaded the ancestral range; however, it is not inconceivable that had the ancestral stock become adapted for a freshwater existence, as have their spelean descendents [sic], one or more Pleistocene inundations of their ranges could have had effects similar to those postulated by Hobbs (1958b[:87]) in considering the evolutionary history of certain troglobitic crayfishes in Florida. Were there sufficient land remaining in Yucatán, Cuba, and on Mona during such an inundation to serve as recharge areas for the subterranean streams, or if adequate underlying aquifers were available to feed them, those forms that had invaded subsurface waters could have survived, even if the epigean stock were annihilated by salt water. On the basis of the present distribution of the members of Typhlatya, there seems no reason to doubt that the Antillean members have been derived from stocks that reached the islands from the Central American-Mexican region, probably in Miocene or Pliocene times.

We are much puzzled by the remarkable occurrence of T. monae on [both] Mona and Barbuda. This disjunct distribution of the troglobite seems almost inconceivable; however, careful comparison of specimens from the two islands reveals no differences worthy of note. That parallel evolution should have resulted in apparently identical populations on the two islands hardly seems possible, but the alternative proposal that a continuous spelean corridor exists or has existed between the islands seems ridiculous. Of course, if it could be shown that the troglobitic facies of T. monae are actually nothing more than ecophenotypic expressions, then the apparent parallelism is precisely what might be expected in the troglobitic adaptation of an old, stable species. The fact that T. garciai differs from T. monae in comparatively minor details lends some credence to the latter possible interpretation.

In their recent critique of the concepts of centers of origin, Croizat, Nelson, and Rosen (1974:275– 276) briefly referred to the distribution of *Typhlatya*, using it and the crab genus, *Gecarcinus*, to illustrate their "track," stating that "similar distributions are shown by other groups, and sometimes even by single species." If we interpret this discourse correctly, they view the ancestral range of the genus as encompassing the tract connecting the ranges of the modern species, all of which have arisen through "vicariance."

In remarking on the origin of *Typhlatya rogersi*, the only known member of the genus from outside the Americas, Chace and Manning (1972:5) noted that the estimated age of Ascension Island suggested an ancestral stock of *Typhlatya* derived from "free-living marine forms that could have colonized the island in relatively recent times." They concluded that colonization took place in the late Pliocene or Pleistocene and indicated that if

true, and assuming that the directions of oceanic currents during that time were similar to those of existing currents, then the Ascension Typhlatya precursor possibly was an amphi-Atlantic marine shrimp, perhaps pelagic, which existed at least into the Pleistocene but did not survive in the oceanic habitat into the present; living atyids are confined almost entirely to fresh water. The close similarities of the known species of Typhlatya suggest a common origin, but their relationship may be obscured by convergence.

The discoveries of T. monae of Puerto Rico and in the Dominican Republic do not alter the state of our understanding. The presence of T. galapagensis on an eastern Pacific island suggests an extension of the range of the ancestral Typhlatya stock prior to the closing of the Middle American isthmus.

Peck (1974a:28), "suggest[ing] the sequence of adaptive events" attendant upon the occupancy of fresh water by the members of the genus *Typhlatya*, noted that

T. rogersi on Ascension lives in salt-water pools which have subterranean extensions. This situation suggests that the marine ancestors associated with shorelines and had an affinity for associating with marine interstitial or subterranean environment, and sought out these situations in many places. All known species except T. rogersi then proceeded to a greater subterranean dependence. A mechanism may have been to seek and to occupy an environment with fewer competitive interactions with other crustaceans. Perhaps simultaneously a tolerance and then dependence for fresh water was established. The subterranean fresh-water habitat is greater in volume than the subterranean salt-water habitat. The tolerance for fresh water may have occurred at first in the adults. The later loss of a possible requirement of marine conditions for larval development should have been only a minor physiological adjustment and may be genetically very simple for species in which the adults already have the ability to cope with problems of fresh water (Hutchison, 1960).

In considering the colonization of Isla Mona, he concluded that it must have occurred in the late Pliocene or early Miocene.

The North American atyids belonging to the genus *Palaemonias* perhaps reached the subterranean waters of the Cumberland and Pennyroyal plateaus at an earlier date than did the crayfishes with which they now share the same aquatic environment. If their surface-dwelling precursors were a marine stock rather than one that had become adapted to epigean fresh waters, they could well have been in spelean habitats long before the crayfish stock gained access to them. The atyids differ from the crayfishes in that there are no epigean atyids occupying fresh water east of the Continental Divide that are even remotely related to these relicts. As Hobbs and Barr (1972:10) have postulated for some of the crayfishes occupying the same subterranean waters, it is suggested that the two atyid species have arisen independently from an epigean stock that ranged over the two areas.

Monod (1975:103), in referring to the origins of the "typhlatyienne" atyids, stated that, in spite of our incomplete knowledge of the subterranean aquatic fauna of the world and the absence of fossils, in his opinion

D'autre part, les genres de la série typhlatyienne sont à ce point voisins les uns des autres qu'il semble difficile d'imaginer entre eux une simple convergence plutôt qu'une communauté d'origine, à la fois phylétique et géographique, avec légère divergence ultérieure.

PALAEMONIDAE

The troglobitic palaemonids include some species that seem to have taken their origin from stocks already adapted, at least in part, to fresh water, whereas the ancestors of the others could well have been salt-water inhabitants. Among the latter are the three monotypic genera, Bithynops, Creaseria, and Neopalaemon, frequenting subterranean waters in the southern part of Mexico. Also, of probable marine origin is the troglobitic genus Troglocubanus, which is represented in Cuba by four species and in Jamaica and Mexico by one each, constituting a group remotely related to other members of the family. According to Chace and Hobbs (1969:22), "since all are cavernicolous, they should perhaps be looked upon as relicts of a stock of the family that reached the Antilles comparatively early, perhaps as early as the Miocene, populating the freshwater systems of at least Cuba and Jamaica and gaining access to the underground water systems on both. For some reason the supposed epigean derivatives from the original stock were unsuccessful and became extinct, leaving albinistic relicts as the only evidence of their existence." As they pointed out, it is highly improbable that subterranean freshwater connections ever existed between Cuba and Jamaica, and we may now add, between either and Mexico; consequently no fewer than three independent invasions of subsurface waters by this stock must have occurred. Strenth (1976:23) has suggested competitive exclusion involving the genus Macrobrachium being at least in part responsible for the absence of Palaemonetes from the lowland (below 500 feet = approximately 152m) regions of Mexico. The extinction of the epigean segments of the ancestral Troglocubanus dwelling in fresh water may well have resulted from their being unsuccessful competitors of members of either or both Macrobrachium and Palaemonetes. This marine stock was almost certainly present in the Gulf-Caribbean area prior to the Pleistocene and was very likely there as early as Miocene times.

Strenth (1976:15), in a careful analysis of the morphology, distribution, and limited fossil records of the genus Palaemonetes in North America, concluded that the American freshwater species of the genus had a monophyletic origin, and he recognized three species groups based on the condition of the movable spine on the exopod of the uropod. Two of these groups include troglobitic members. Palaemonetes cummingi represents that which ranges from south central Texas eastward in the United States, and P. antrorum and a previously undescribed species are members of the second group occurring from central Texas into Mexico. Strenth offered several alternative hypotheses to explain the origin of the two groups, one of which, in view of our convictions concerning the relationships of several crayfish stocks, is favored by us: the isolation of eastern and western segments of a wide ranging stock by epeiric seas covering large segments of the central United States during the late Mesozoic and early Cenozoic. Subsequently a part of the eastern segment gave rise to the Floridian troglobitic P. cummingi, and the western one to the two troglobitic species frequenting the subterranean waters of Texas. For reasons stated below involving the origin of the Floridian crayfishes, Troglocambarus and certain troglobitic members of the genus Procambarus, a pre-Pleistocene origin is postulated for Palaemonetes cummingi. The time

en tous les cas, sur un schéma paléogéographique du Trias (fig. 1 [see Figure 3]), la distribution des Atyidés cavernicoles actuellement connus peut s'expliquer par une origine marine ancienne....



FIGURE 3.—Distribution of atyid shrimps as depicted by Monod (1975:99) (triangles = "Phreatoicoidés"; circles = subterranean atyids of the "série typhlatyienne"; squares = other subterranean atyids: 1 = Typhlatya pearsei Creaser, 2 = Typhlatya garciai Chace, 3 = Typhlatyaconsobrina Botosaneanu and Holthuis, 4 = Typhlatya monae Chace, 5 = Typhlatya galapagensis Monod and Cals, 6 = Typhlatya rogersi Chace and Manning, 7 = Antecaridina lauensis Holthuis, 8 = Typhlopatsa pauliani Holthuis, 9 = Spelaeocaris pretneri Matjasic, 10 = Stygiocaris stylifera Holthuis, <math>11 = Stygiocaris lancifera Holthuis, 12 = Palaemonias ganteri Hay, 13 = Palaemonias alabamae Smalley, 14 = Caridinopsis brevinaris Holthuis, <math>15 = Caridinaloboensis Roth-Woltereck, 16 = Troglocaris inermis Fage, 17 = Troglocaris anophthalmus (Kollar), 18 = Troglocaris kutaissiana (Sadovsky), 19 = Parisia microphthalma (Fage), 20 =Parisia macrophthalma Holthuis, 21 = Parisia edentata Holthuis, 22 = Parisia fowleri Gordon, 23 = Caridina japonica sikokuensis Kubo, 24 = Halocaridina rubra (Holthuis) (Hawaiian Islands).

of origin of the Texas species is probably at least as early.

In considering the more southern segment of the freshwater stock, Strenth (1976:23) postulated an

early (implying no later than Miocene) widespread range of *Palaemonetes* in the Mexican-Central American area. This was followed by an incursion of *Macrobrachium* prior to the most recent emergence of the transcontinental landmass, at least as early as the Pliocene, causing competitive exclusion of freshwater Palaemonetes at lower elevations and in the southern parts of Mexico, leaving only relict populations at higher elevations. If this hypothesis is extended, the appearance and domination of Macrobrachium in the region of the Isthmus of Tehuantepec could have been responsible for the annihilation of the ancestral stocks of the monotypic palaemonid genera occurring in Chiapas, Oaxaca, and Yucatán. Assuming this sequence to be tenable, then the presence of Macrobrachium villalobosi in the subterranean waters of Oaxaca probably represents a more recent conquest of the spelean environment than that of Bithynops, Creaseria, and Neopalaemon. The other members of the genus Macrobrachium (a large majority of which are primarily freshwater dwellers) for which data are available, require a brackish or marine habitat during at least part of the life cycle; thus, there seems little reason to assume that M. villalobosi has had an origin markedly unlike its congeners, which, while departing from an ancestral marine habitat, have not been able to become entirely free of it. Perhaps the troglobite will be shown to have broken the last tie with the primitive habitat and can complete its life cycle in a freshwater environment (see "Adaptations" under Macrobrachium).

ALPHEIDAE

In this predominantly marine family, the genus *Alpheopsis* includes only three known freshwaterinhabiting species: two from epigean waters in Africa and the uniquely troglobitic *Alpheopsis* stygicola from Oaxaca. This species assuredly has been derived directly from a marine stock that ranged the sea in the vicinity of the Tehuantepec isthmus during the late Pliocene or early Pleistocene.

HIPPOLYTIDAE

The two hippolytid species included here are inhabitants of salt (*Barbouria cubensis*) or brackish (*Calliasmata rimolii*) water habitats having connections, at least for the former, with the sea, and are thus virtually still marine species.

According to Chace and Hobbs (1969:18), the

then monotypic genus Barbouria "is the only one [in the West Indies] that has possibly been derived from a marine ancestor in situ, on the Island of Cuba." Now that the anchialine B. cubensis has been discovered on additional islands in the Caribbean (p. 70) and a second, marine as opposed to anchialine, species, B. antiguensis Chace (1972:107), has been found on Antigua, their statement must be reconsidered. In fact, the affinities demonstrated by the latter cast some doubt concerning even the present range of the genus. The features shared in common by B. antiguensis and the Mediterranean and Indo-Pacific members of the genus Ligur led Chace (1972:110) to conclude that "it is possible that Barbouria eventually will be relegated to the synonomy of Ligur or perhaps Barbouria will revert to its previous monotypic status and that B. antiguensis will be transferred to Ligur." Regardless of the source of the ancestral stock, B. cubensis must have had a West Indian origin, and, in view of its salt-water habitat, its dispersal in the Caribbean region could well have been accomplished through migrations of the larval and/or adult stages. The combination of reduced eyes and its occurrence in salt-water pools that maintain a connection with the sea suggests, as has been pointed out by others, a step in the evolution of B. cubensis toward a troglobitic habit.

Decidedly more restricted in its known range than Barbouria cubensis is the recently described Calliasmata rimolii, which is known from a single brackish pool in the Dominican Republic. Its origin, although certainly marine, is clouded by the fact that the only other species of the genus, C. pholidota Holthuis (1973:37), occurs in the Sinai Peninsula, Ellice Islands, and Hawaiian Islands. Either the genus is a polyphyletic one, or the ancestral stock must have reached the Gulf of Mexico-Caribbean region prior to the most recent emergence of the isthmus joining North and South America, which occurred no later than the Pliocene (Schuchert, 1968, and others; see Strenth, 1976).

CAMBARIDAE

The origins and migrations of few invertebrates have furnished the background for so much speculation as have those of the crayfishes! No attempt will be made here to enumerate, review, or evalu-

ate all of the many hypotheses that have been proposed; however, some of the more recent ones are considered in expressing certain of our views. The earliest and perhaps most notable contributions were those of Ortmann (1902, 1905a, 1913), and among the many others that have followed are those of Caine (1974a), Croizat (1958), Fitzpatrick (1967), Hobbs (1942b, 1958b, 1962, 1967b, 1969b, 1971a), Hobbs and Barr (1960, 1972), Hobbs and Villalobos F. (1964), Holt (1968), and R. Rhoades (1962). Drawing freely from these works, the following summary is offered.

For reasons pointed out by Ortmann and elaborated upon by Hobbs, the American crayfishes that are believed to have retained the most generalized characteristics are members of the genus Procambarus. Both workers expressed conviction that during the early Cenozoic this highly variable stock became widespread in the southern part of the United States and Mexico, forming a number of species groups, four of which gave rise to descendants found in the present troglobitic fauna of the Americas. No later than Miocene times, the crayfish stock from which the Mexican and Cuban troglobites arose was separated from others by the uplift of the Cordillera Volcanica Transversal north of the Isthmus of Tehuantepec. From this stock that became isolated in southern Mexico, migrants reached Cuba to become ancestral to P. (A.) niveus and its Cuban allies. The remaining stock in the area of the Isthmus gave rise to the other members of the subgenus Austrocambarus, three of which are troglobites, two occurring in Oaxaca (P. (A.) oaxacae oaxacae and P. (A.) o. reddelli) and one in Veracruz (P. (A.) rodriguezi). As to when the spelean environments in Mexico and Cuba were invaded, no more restrictive a time can be postulated than post-Miocene (perhaps as late as Pleistocene) for the isolation of the ancestral troglobites.

More specific timing has been offered for the North American *Procambarus* stock, and Caine (1974a:490-491) has correlated the origin of most of the Floridian members with fluctuations in the Pleistocene inundations of the State. He postulated one or more of the saltwater inundations at or near the 50-ft. level, and purportedly accounted for the widespread Lucifugus group of the subgenus Ortmannicus . . . The third invasion may have been from causes other than sea level fluctuations . . . As *P. milleri* appears to be not nearly so old as the other troglobilic procambarids . . . this species may have been isolated after the aquifer was lowered in southern Florida in the 1920's.

Although Caine may be more nearly correct than are we in his assessment of the isolations involving the troglobitic Procambarus of Florida, one of us (Hobbs, 1958b) suggested other possibilities that were not discussed by Caine. Three stocks are represented in the present troglobitic fauna of Florida by the subgenera Lonnbergius, Leconticambarus, and Ortmannicus. The fact that Lonnbergius is a monotypic subgenus with no close allies among hypogean or epigean crayfishes suggests its position in the fauna as a relict. The obvious strong affinities between P. (L.) milleri and P. (L.) alleni were pointed out by Hobbs (1971b:121-122) and Caine (1974a:490-491), and, while these crayfishes assuredly share a recent common ancestry, we are not convinced of an isolation of the two stocks of only approximately 50 years.

The remaining troglobitic Procambarus occurring in Florida, and probably Troglocambarus as well, share a common origin with the more generalized members of the subgenus Ortmannicus, assuredly not with P. (Pennides) spiculifer (LeConte, 1856), as implied by Caine, which is among the more specialized members of the subgenus Pennides. Perhaps the reason Caine referred to Hobbs' (1958b) remarks on the origin of the Ortmannicus segment of the troglobitic crayfishes of Florida as having been "mentioned" is due to their being buried among others relating to the evolution of their epigean relatives. The remarks (Hobbs, 1958b):85– 88) which seem pertinent to us are quoted here.

Although it is highly probable that much of the evolutionary history of the Pictus Group [= more generalized members of the subgenus Ortmannicus mentioned above] was accomplished during the Pleistocene Period, the invasion of the freshwaters of the area that is now within the boundaries of the Piedmont Province by freshwater crayfishes must have occurred during the late Cretaceous or perhaps during the Tertiary. As has been stated above, the lack of fossils prohibits any accurate temporal assignments in the evolutionary history of the group.

It is postulated that the Propictus Stock had gained a foothold in at least some of the streams of the southeast not later than the Pliocene—probably much earlier—and that

three separate "invasions" into the subterranean environment . . . in Florida. The first took place as the sea level rose above the 50-ft. [approximately 15 m] level (Early Pleistocene terrace), effectively isolating the ancestor of *P. acherontis* The second invasion occurred during

their migrations from one river system to another were largely dependent upon stream piracy or short migrations across very narrow land barriers between the dove-tailing headwaters of adjacent drainage systems. (This assumption is made because none of the modern species thought to be similar to the ancestral stock has been found on land or in ponds, lakes, or any other type of lentic habitat). In this manner the stock invaded most of the major systems in the area between the Pee Dee River in South Carolina and the Altamaha River in Georgia, and during the middle Pliocene, when "the Gulf of Mexico extended farther to the north than now, and Florida was a short, stubby peninsula that ended at about the level of Tampa . . .' (Hubbell. 1954:46), the stock gained an entrance into the peninsula [as well as to those streams of the panhandle lying east of the Choctawhatchee River]. Almost certainly by this time the porous Eocene limestone underlying the eastern portion of the peninsula [and panhandle] had begun to be honeycombed and there was developing a system of subterranean pools and streams. There is no reason to doubt that some of the surface waters were being deflected from their [surface] coastal routes into these subterranean channels, just as is the case at the present time. Certainly such a setting was at least conducive to the invasion of these hypogean waters by members of the stream-dwelling Propictus Stock, and it is postulated that in taking advantage of this opportunity this Stock successfully invaded these waters-perhaps in two areas [probably in several areas] . . . In the southern area either two already differentiated stocks independently entered the underground waters, which seems most probable, or there was a subsequent marked dicotomous [sic] divergence in members of a single stock, resulting subsequently in the evolution of the sympatric Troglocambarus maclanei and Procambarus lucifugus [Figure 4], the latter consisting of two geographic races. [At about the same time, to the north and west, the ancestors of P. (O.) pallidus, P. (O.) erythrops, P. (O.) horsti, and P. (O.) orcinus found their way underground in at least two (perhaps four) separate hypogean invasions.] The presence of these troglodyte species in the subterranean waters of [peninsular] Florida almost demands an assumed insular landmass throughout the Pleistocene. Hubbell's (loc. cit., p. 48) statements regarding insular Florida are particularly apropos. "Not so long ago the geologists would have none of this [land in central Florida since the Pliocene] at least for the highest Pleistocene level of the sea, but in his latest maps [C. Wythe] Cooke has left a tiny island exposed just about where it is needed. If it were only a little larger!" In this I heartily concur!

The question arises as to what became of the original surface stock from which the cavernicoles took their origin. Only a small fragment of it is to be found in Florida at the present time—the relict, *P. pictus* [and the more highly specialized *P.* (0.) youngi]. This species [P. (0.) pictus], presumably the one most closely approximating the ancestral stock of the group, has been found in only one stream tributary of the St. Johns River in northeastern Florida. Geographically disjunct in relation to its epigean relatives, its presence here can be explained only by the assumption that it is a relict form left on an insular landmass that persisted throughout the submergences of the landmass to the



FIGURE 4.—Diagrammatic representation of Squirrel Chimney showing the habitats of the crayfishes.

north during the Pleistocene. In support of this hypothesis, it is remarkable that in northeastern Florida Cooke left a sizable island in precisely the right place for the ancestral *P. pictus* to have persisted, and the creek in which it now occurs lies largely within an area of the Duplin marle [sic], an exposed Miocene formation, apparently occupying the cite [sic] of Cooke's island!

Although Procambarus (O.) youngi, the range of which overlaps that of P. (O.) orcinus, is probably a descendant from the same Propictus stock, its antecedents were distinctly remote from those believed to have been the more recent forerunners of P. (O.) orcinus. This must have been a stock that strongly resembled P. (O.) lepidodactylus Hobbs (1947:25) and one which ranged through the eastern part of the Florida panhandle between (but not in) the Apalachicola and Suwannee rivers prior to the Pleistocene inundations; during these inundations, except for ancestral P. (O.) horsti and P. (O.)orcinus, the stock became extinct.

Invading the northern part of the peninsular region were two separate stocks, one that was closely allied to the northern subspecies, P. (O.) *lucifugus alachua*, giving rise to P. (O.) *erythrops*, and the other to the rather distinctive *Procambarus* (O.) *pallidus*, which in some respects is the most disjunct of the troglobitic Ortmannicus.

Troglocambarus maclanei probably had a remote common ancestry with several members of the subgenus Ortmannicus, the ranges of which it overlaps. It appears, however, to have been derived from an ecologically more tolerant stock (Seminolae Subgroup, Hobbs, 1958b:78, 80) than did those members of Ortmannicus. The secondary sexual characters are remarkably similar to those of Procambarus (O.) ancylus Hobbs (1958a:164) (= Procambarus sp. D, Hobbs, 1958b), which occupies the northernmost part of the range of the subgroup. Is it coincidental that P. (O.) horsti and P. (O.) orcinus seem to be most closely allied to the northernmost epigean member of the Pictus Subgroup, P. (O.) lepidodactylus (North Carolina and South Carolina), the range of which is sympatric with that of P. (O.) ancylus?

We should like to propose that three epigean stocks were ancestral to the troglobitic crayfishes frequenting the northern part of Florida east of the Apalachicola River. Two of them were stream dwellers, one, resembling the epigean P. (O.) pictus, which is believed to have given rise to P. (O.) erythrops, P. (O.) l. lucifugus, and P. (O.) l. alachua, and the other, resembling P. (O.) lepido-dactylus, to P. (O.) horsti, P. (O.) orcinus, and perhaps to P. (O.) pallidus. The third, less ecologically restricted, and resembling P. (O.) ancylus, was ancestral to Troglocambarus maclanei.

Inasmuch as the range of the seemingly highly evolved *Troglocambarus maclanei* virtually envelops that of several troglobitic members of the subgenus *Ortmannicus* inhabiting the northern part of peninsular Florida, we believe it likely that the invasion by its ancestors into the subterranean waters of the state occurred no later than Pliocene times. This incursion must have happened about the same time or shortly after the time the ancestors of the spelean *Ortmannicus* reached the same waters.

To accept a Pliocene advent of surface stocks into hypogean waters, one must assume a continuous submarine freshwater environment to have been present in at least limited areas throughout the Pleistocene.

It seems reasonable to us that the invasion of a separate subterranean system by the primitive Lonnbergius stock might also date to the Pliocene. Its epigean forebearer, unlike that of P. (O.) pictus, having no persistent island within the boundary of its range which might serve as a refuge, became confounded with the Pleistocene inundations. Only *Procambarus* (L.) acherontis remains to attest to the existence of the primitive ancestral stock.

In the absence of epigean relatives within the range of the troglobites (and only one epigean nearrelative close by) and with almost no knowledge about the subterranean watersheds, one can do little more than guess as to the ties of the troglobites to their epigean predecessors. Does each species represent a separate conquest of the subterranean environment as has been suggested above and postulated for *Orconectes* by Hobbs and Barr (1972:10), or has subsurface migration and isolation been effected by fewer stocks after each became adapted to a spelean environment?

Procambarus (Remoticambarus) pecki seems to have been derived from a primitive stock of the genus Procambarus that was also ancestral to the genera Orconectes, Cambarus, Fallicambarus, Faxonella, and Hobbseus. As was stated by Hobbs (1967b:7) when the species was described, this crayfish "seems equally closely related to the troglobitic members of the genus Orconectes and to the members of the Mexicanus Section [= subgenus Austrocambarus] of the genus Procambarus, and there are good reasons for assigning it to either of the two." Consequently, as pointed out by him, this ancestral stock is believed to have been present in and along the margin of the Cumberland Plateau during the Miocene. Inasmuch as this area was one in which several presumably more advanced stocks (Orconectes and Cambarus) became widespread in epigean habitats and also invaded spelean waters, it is likely that the ancestors of P. (R.) pecki had sought refuge in the latter in pre-Pleistocene times.

R. Rhoades (1962:77-79) was the first to propose in any detail a hypothesis as to the origin of the troglobitic members of the genus Orconectes.

There can be little doubt that the Group *rafinesquei* [in his view, the stock ancestral to the troglobitic *Orconectes*] has occupied the streams of the Cumberland Plateau since very ancient times. Perhaps the Pliocene surface species, that oc-

cupied the trenching streams, entered rock-fissure springs and lived in subterranean water courses . . .

Selection pressures to which surface crayfishes are subjected are very different from those of caves. In caves, weather has a minimum effect; predators are lacking. Light, which governs some motor reactions and rhythmic behavior, is absent. The eye, a high metabolic organ, would seem to have negative survival value in a habitat where food is so scarce. Cave crayfishes feed largely upon decayed wood and bat manure. Both of these items are devoid of Vitamin A and Vitamin B12 which are regarded as essential in photoperception (Wright, 1939). It may be that crayfish living under cave conditions may not form the visual purple associated with the formation of optic images. As a consequence, crayfishes may have been physiologically blind before they become morphologically blind (Duke-Elder, 1958). Since the functioning eye continues to require energy difficult to obtain from the spelean environment, a crayfish bearing a genetic mutation which suppresses eye development has a distinct advantage over the eyed individuals. Since cave populations are always small, such a mutation could survive and the frequency of the mutant gene may be greatly increased by selection in a relatively short period of time. Individuals of the new type in which less calories of energy are required are no longer limited in the areas that they may occupy. They may penetrate deeply into caves beyond the hordes of bats or the influx of organic material through sink holes. This would serve to intensify isolation and contribute to greater homozygosity in the blind population. In the generosity of geological time could come the increase in tactile sense of the appendages, the expansion of the olfactory sense to all joints of the antennae and other cave adaptations by the integration of genetic mutations and environmental pressures

It would be difficult to say where rafinesquei stock first entered the subsurface drainage under the Cumberland Plateau. It appears that a specific population of Orconectes pellucidus [= Pellucidus Section of Orconectes according to Hobbs and Barr (1972)] was established and 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 corrasion 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. While the Ohio River flowed upon a channel bottom scoured in the cavernous Mitchell limestone in the Fort Knox area during the immediate pre-Pleistocene, blind crayfish might presumably emerge from passageways opening into the river bottom on the south side of the river and enter other passageways beneath the opposite bank. With glacial filling of the 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. This fraction of blind crayfishes north of the Ohio River is still heterogeneous with respect to its lack of armature which is diagnostic of Orconectes pellucidus inermis [= O. inermis testii, according to Hobbs and Barr, 1972] of Mayfield Cave. Most of the blind crayfishes from southern Indiana counties still possess the spinosity and other features of the Kentucky O. pellucidus. This may be the result of late Pleistocene isolation. It may also be that relatively uninterrupted passageways lie under the Ohio River permitting a limited contact between the northern Kentucky O. pellucidus [= O. inermis inermis] and those of southern Indiana.

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, and this population is now designated Orconectes pellucidus packardi [= O. australis packardi]. The blind Orconectes in the subterranean channels of the Mussel Shoals region were similarly isolated and have been described as Orconectes pellucidus australis [= O. australis australis]. The surface streams have been at least partial barriers to aquatic cave animals.

With a different concept of the affinities of the troglobitic members of the genus, Hobbs and Barr (1972) offered an alternative interpretation of the evolutionary history of the troglobitic Orconectes.

R. Rhoades (1962)	Hobbs and Barr (1972)
Orconectes pellucidus inermis	Orconectes inermis inermis Orconectes inermis testii
Orconectes pellucidus pellucidus	Orconectes pellucidus
Orconectes pellucidus australis	Orconectes australis australis
Orconectes pellucidus packardi	Orconectes australis packardi
(Unknown to Rhoades)	Orconectes incomptus

Preceded by a long discussion, Hobbs and Barr (1972:10) recapitulated

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 . . . [They] postulated that the ancestral stock of the Pellucidus Section was derived from a primitive Procambarus stock [the same as that from which Procambarus (R.) pecki arose] 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 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* . . . 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.

Slightly modifying and updating the account of the origin of the troglobitic members of the genus Cambarus as recounted by Hobbs and Barr (1960: 14-16), these crayfishes are now assigned to four subgenera: Aviticambarus consists of only two species occurring in northern Alabama and southern Tennessee, C. hamulatus and C. jonesi, both of which are troglobitic; Erebicambarus is represented by a single troglobite restricted to southeastern Missouri, C. hubrichti; troglobitic members of the subgenus Jugicambarus exhibit a disjunct distribution, with C. cryptodytes occurring in Florida and Georgia, and C. setosus, C. tartarus, and C. zophonastes in the Ozark regions of Missouri, Oklahoma, and Arkansas, respectively; and Puncticambarus is represented by a single troglobite, C. nerterius, in West Virginia.

The resemblances of the two species belonging to the subgenus *Aviticambarus* to the more generalized members of *Puncticambarus* suggest origins from a stream-dwelling stock on the southern part of the Cumberland Plateau. There are no data to our knowledge that would restrict a dating of their invasion into subterranean waters more accurately than subsequent to late Miocene times.

Among members of the subgenus *Erebicambarus*, at least two could well be designated troglophiles, so it is not surprising that C. (E.) hubrichti has become limited to a hypogean existence.

It is suggested that sometime during the Tertiary the range of the ancestral stock of the Tenebrosus Group [= subgenus *Erebicambarus*] extended westward from Kentucky and Tennessee to the eastern edge of the Ozark Plateau. What events occurred in the Pleistocene or Recent to bring about an annihilation of the epigean stock from the Mississippi Valley and the area to the west are not known, but it seems clear that a segment of it, *C. hubrichti*, was preserved in the subterranean waters [Hobbs and Barr, 1960:15].

Typically the members of . . . [the subgenus Jugicambarus] frequent cool riffles or mountain streams [nevertheless, several are burrowing species]. Although the range is a discontinuous one, most of the species occur in streams

of the Western and Eastern Highland Rims of Tennessee, the Cumberland Plateau, and ... [Appalachian Mountains] [The troglobitic members] are here considered to be relicts of a previously much more widely distributed stock. The Florida species, located several hundred miles south of the most southern limit of the range of presently existing epigean species of the group, suggests that its ancestors moved southward into southern Alabama or northern Florida during one or more glacial epochs of the Pleistocene. Assuming, tentatively, that such dispersal occurred, the epigean members may have been unable to survive the warming trend following glacial retreat. But a segment of this stock, the progenitors of C. cryptodytes, found a combination of tolerable environmental conditions in the subterranean waters of the northern portion of the Florida Panhandle [and southeastern Georgia]. Perhaps it was also during the Pleistocene that the ancestors . . . [of the three more western species] became established in the Ozark Plateau. It does not seem unreasonable to suppose that the ancestral stock attained the interior of the Ozark Plateau at the southern highly dissected margin of the Springfield upland by dispersal up the White River and into the James [Gasconade, and Neosho]. Furthermore, if this route was followed, it seems probable that the stock moving into the area from the east would have had to cross what is now the Mississippi Valley before the river and the lower reaches of its tributaries became mud-bottomed streams, a type of habitat in which no [epigean stream-dwelling] member of the group is found at the present time.

Why C. hubrichti should occur only in the eastern part of the plateau and . . . [the three western members of Jugicambarus] in the west cannot be explained on the basis of available data. Various hypotheses may be advanced; for example . . . [the latter] may have colonized the caves earlier than hubrichti, the ancestors of which were unable to compete successfully with an established cavernicole species in the western part of the White River drainage, but were able to occupy a similar vacant niche in the eastern part of the plateau. There is little evidence to favor this over several alternative hypotheses [Hobbs and Barr, 1960:15-16].

The subterranean waters of the Elk and Greenbrier watersheds probably represent a Pleistocene refugium sought by the ancestors of *Cambarus* (P.) *nerterius*. This stock is believed to be the same as that which also gave rise to the epigean C. (P.) *robustus* Girard (1852:90), a crayfish with a wide range that encompasses the Greenbrier basin (see Hobbs, 1969b:134-135).

GRAPSIDAE

This family, represented in the troglobitic fauna by the Jamaican Sesarma (S.) verleyi, encompasses a number of species that have invaded fresh water, and, in the Antillean region alone, some 10 species have been reported from nonmarine habitats (Chace and Hobbs, 1969). Whether or not the larvae of all of these crabs may complete their metamorphosis in fresh water, as does *Metopaulias depressus* Rathbun (1896:144) (see Hartnoll, 1964a:154-159), is not known, but it seems likely that the troglobitic S. (S.) verleyi, which must have had its origin from a freshwater stock that ventured into hypogean waters of Jamaica, might well be able to do so.

Adaptations

There are few data upon which to base a discussion of adaptations made by the various stocks, the descendants of which have become modified for a troglobitic existence; and the advantages that have accrued from such modifications are poorly understood. Whether the troglobite be shrimp, crayfish or crab, all must trace their ancestry to a marine origin, and such anchialine derivatives as *Barbouria cubensis* that remain in a saline environment have had to make different sorts of, if not also fewer, adjustments than those species that moved into fresh water.

The most obvious character that pervades virtually all of the troglobites is a strong reduction in pigmentation, frequently a total loss. Only one among the troglobites included here, C. (P.) nerterius, characteristically has body pigment, but even this crayfish may be very pale in color. Only slightly less conspicuous are the reduced eyes. A number of the troglobitic decapods have retained pigment in the eyes and a few of them have faceted corneae, but the number of facets in the eyes of the latter forms is obviously fewer than in their epigean counterparts.

Hardly less noticeable than the reduced pigmentation is the attenuate appendages of many, if not most, troglobitic decapods. Many troglobites are conspicuously smaller, or at least more delicately constructed, than their epigean relatives. As in epigean waters, however, the sizes of individuals in populations of the same species exhibit considerable variations in different localities. At times these differences in size seem to reflect the productivity of the body of water in which the animals are living. Such differences observable in spelean waters may well prove to be correlated with available energy; unfortunately, there are too few data on the environmental conditions existing in the localities from which available decapods were collected to document such a correlation.

Almost certainly a metabolic rate lower than that of epigean relatives exists in the troglobitic decapods, even though data that would corroborate such a supposition are lacking for the majority of the species. Cooper (1975) provides evidence for a considerably longer life span in the troglobites Orconectes a. australis and Cambarus (A.) jonesi than has been reported for any other crayfish. This would correlate with an assumed lowered metabolism. Unfortunately, the only information available on the life history of most troglobitic decapods is limited to one or two observations made by collector(s) whose primary interests were not in the biology of the species and who consequently failed to record the presence of ovigerous females or breeding males when the specimens were obtained. Only the studies of Jegla (1964b, 1969), Hobbs III (1973e), and J. E. Cooper (1975) have been directed toward understanding the biology of the species pertaining to their life history. Even with their contributions, we still do not know with certainty the life span of a single American troglobitic decapod!

Perhaps correlated with the lesser available energy in some species is the production of fewer eggs than one might expect in related epigean species of comparable size. There is some evidence that with the production of fewer eggs there is an increase in the size of the egg, suggesting that the young might hatch in a more advanced stage than do relatives that produce more but smaller eggs. Unfortunately, to our knowledge, the development of newly hatched young has not been observed in any troglobitic decapods except *Palaemonetes cummingi*, and its early larval development does not seem to differ in any conspicuous way from that of its epigean freshwater relatives.

Insofar as we are aware a part of the larval development of members of the genus *Macro*brachium must occur in salt or at least brackish water. Assuming that larval stages are characteristic of these shrimps, the question arises as to whether or not there is a period in the development of the larvae of *M. villalobosi* during which the young must dwell in a saline environment. If the latter environment is not essential in the life history of this shrimp, what physiological or developmental

modifications has it undergone?³ Some, if not most, of the non-troglobitic atyids also have larvae that characteristically return to the sea, but it seems highly improbable that the young of the troglobitic members of the family have maintained this tie with their ancestral environment.

There are reasons to suspect that annual egg production in individuals belonging to some spelean decapod species might be much rarer (if it exists at all) than in epigean relatives. For example, ovulation appears to be seasonal, as judged by the enlargement of the ovarian eggs in Orconectes inermis (Jegla, 1965, 1969; Hobbs III, 1973e). Paradoxically, extremely few ovigerous females have been observed in a population at any time. Whether the paucity of such females is due to their secretive habit or to resorption of the enlarged ova, thus failure to produce a clutch of eggs each year, has not been determined, although J. E. Cooper (1975) presents observations that support the latter possibility.

The scarcity of food in spelean waters has fortified an already probable opportunistic type of feeding. Most of the decapods frequenting freshwater habitats may be termed euryphagous, but are primarily scavengers and detritivores. There are perhaps no basically new inventive feeding techniques among the troglobites; however, we are not aware of reports of surface feeding by shrimps other than that reported for Troglocubanus jamaicensis by Hartnoll (1964b:78) and for Palaemonias alabamae by J. E. Cooper (1975). The third maxilliped of Troglocambarus maclanei appears modified to function in a filter capacity, a task that could not be accomplished by its cambarid ancestors or by other crayfishes, including those which share its habitat. The use of these appendages to strike at potential food on the surface of the water (Mohr and Poulson, 1966:138) also is a unique innovation in the cambarids, all the others of which rely on the chelate legs for grasping food rather than a "setal net" on the third maxillipeds.

Most certainly there are other adaptations that are characteristic of some, if not all, troglobitic decapods (see Hobbs, 1976); however, comparative data are too few to be convincing. We might point out that subjectively the troglobitic crayfishes appear to move about less frequently than do epigean forms, but whether or not this behavior is in the interest of energy economy or due to one of several extrinsic factors, such as lack of photostimuli, remains to be demonstrated.

Key to Species of American Troglobitic Decapods

- Body compressed; rostrum often with dorsal margin serrate; first abdominal segment not much smaller than others; if first and second pereiopods unequal in size, second larger or carpus of second subdivided; pereiopods often with exopods, fifth not conspicuously smaller than fourth; pleopods natatory, some usually provided with appendices internae, first never modified for sperm transfer ______2
- 1'. Body depressed or not strongly compressed; rostrum, if distinct, always flattened dorsoventrally and often with lateral (marginal) spines; first abdominal segment always much smaller than others; first pereiopod always larger than second, carpus of second never subdivided; pereiopods never with exopods, fifth occasionally conspicuously smaller than fourth; pleopods never natatory nor provided with appendices internae; first or first and second pleopods of male modified for sperm transfer or fifth pereiopod much smaller than fourth 26
- 2(1). Carpus of second pereiopod multiarticulate, consisting of 5 or more articles 3

³ After this manuscript had gone to press, Fenner A. Chace, Ir., called to our attention a recent study on the early life history of Macrobrachium hendersodayanum (Tiwari, 1955) by D. R. Jalihal and K. N. Sankolli (On the Abbreviated Metamorphosis of the Freshwater Prawn Macrobrachium hendersodayanum (Tiwari) in the Laboratory, Karnatak University Journal: Science, 20(1975):283-291, 5 figures). According to them, this shrimp has only one larval stage before metamorphosing to the post larva. "Hatching . . . is very slow and gradual The larvae were yellowish brown, large, about 7.0 mm in length, and were observed to crawl rather than swim unlike the zoeal stages of other caridean prawns . . . immediately on hatching, [they] were observed to be clinging to the body of the mother on various parts like pleopods, abdomen, carapace, rostrum etc. This tendency of clinging to the mother continued for some time, after which they were observed to dart away either on their own accord or when disturbed The first stage larva took 3-4 days to moult to the next which is the postlarval stage. The postlarva, however, took about 10 days to moult to the next instar, the juvenile stage," (1975:284-285). Perhaps a similar adaptation has occurred in the postembryonic development of Macrobrachium villalobosi.

2′. 3(2).	Carpus of second pereiopod undivided 5 Carpus of second pereiopod consisting of fewer than 20 articles; dactyli of third, fourth, and fifth pereiopods without spines on flexor margin; mandible with in- cisor process (Alpheidae) Alpheopsis stygicola
3′.	Carpus of second pereiopod consisting of at least 25 articles; dactyli of third, fourth, and fifth pereiopods with spines on flexor margin; mandible without incisor process (Hippolytidae) 4
4(3').	Rostrum armed with 4 to 6 dorsal teeth and 2 to 4 ventral teeth; mandible with palp Barbouria cubensis
4'. 5(2').	Rostrum unarmed; mandible without palp
5′.	some perciopods with exopods
6(5).	all pereiopods lacking exopods
6′.	Carapace without spines; rostrum never overreaching antennular peduncle
7(6).	(Typhlatya) 8 Rostrum with ventral teeth and with more than 15 dorsal teeth; flexor surface of distal podomere of third maxilliped bearing more than 12 rows of plumose setae Palaemonias ganteri
7 ' .	Rostrum usually without ventral teeth and with fewer than 15 dorsal teeth; flexor
	surface of distal podomere of third maxilliped bearing fewer than 12 rows of plumose setae
8(6′).	Rostrum extending anteriorly beyond eyes 9 Rostrum not extending anteriorly beyond eyes 12
8′. 9(8).	Eyes with pigment; first pereiopod with extensor surface of carpus shorter than palm of chela; flagellar lobule of first maxilliped vestigial (extra-limital: saltwater pools on Ascension Island)
9′.	Eyes without pigment; first pereiopod with extensor surface of carpus longer than palm; flagellar lobule of first maxilliped well developed (not set off from remainder of exopod in T. galapagensis) 10
1 0(9').	Dactyl of fifth pereiopod with fewer than 40 denticulate spines on flexor surface; male with appendix masculina not extending so far distally as appendix interna Typhlatya consobrina
1 0′.	Dactyl of fifth pereiopod with more than 40 denticulate spines on flexor surface; male with appendix masculina extending farther distally than appendix interna
11 (10′) .	Rostrum reaching, at most, only slightly beyond articulation between first 2 podomeres of antennular peduncle; peduncle extending beyond lateral spine on antennal scale,
	sometimes almost to distal margin of latter; exopod of fifth pereiopod barely sur- passing distal extremity of basis or sometimes reaching midlength of ischium Typhlatya campecheae
11′.	Rostrum reaching at least midlength of second podomere of antennular peduncle;
	latter extending no farther than level of lateral spine on antennal scale; exopod of fifth pereiopod, at most, barely surpassing distal extremity of basis Typhlatya pearsei
12(8′).	Eyes with pigment; dactyl of fourth pereiopod with 5 or more denticles on flexor sur- face13
12'.	Eyes without pigment; dactyl of fourth pereiopod with fewer than 5 denticles on flexor surface 14
13(12).	Exopod of fifth pereiopod extending much beyond ischiomeral articulation
1 3′.	Typhlatya garciai Exopod of fifth pereiopod, if present, much reduced, not nearly reaching ischiomeral articulation Typhlatya monae
1 4(12′) .	Telson less than twice as long as broad; first maxilliped with caridean lobe very broad; flagellar lobule not differentiated, and palp uniformly slender; distal podo- mere of third maxilliped with fewer than 8 rows of setae on basal portion of flexor surface and fewer than 7 spiniform setae in distal row

¹ This species is included here inasmuch as it is in the only non-American member of the genus (Chace and Manning, 1972:14).

14'.	Telson more than twice as long as broad; first maxilliped with flagellar lobule nar- row, distinctly set off from remainder of exopod, and palp broadened distally; distal podomere of third maxilliped with more than 8 rows of setae on proximal portion of flexor surface and more than 7 spiniform setae in distal row Typhlatya mitchelli
15(5').	Carapace with antennal and branchiostegal spines
15'.	Carapace lacking either antennal or branchiostegal spine
16(15).	Mandible with 2-jointed palp Creaseria morleyi
16'.	Mandible lacking palp (Palaemonetes) 17
17(16').	Rostrum with ventral teeth; eye with reduced cornea; lateral ramus of uropod with 2
	spines on lateral margin, more mesial one movable Palaemonetes cummingi
17'.	Rostrum without ventral teeth; eye without faceted cornea; lateral ramus of uropod
	with 1 spine on lateral margin Palaemonetes antrorum
18(15').	Carapace without hepatic spine 19
18'.	Carapace with hepatic spine 25
19(18).	Eye with faceted cornea; mandible with 3-jointed palp Bithynops luscus
19'.	Eye without faceted cornea; mandible without palp (Troglocubanus) 20
20(19').	Rostrum with 6 to 8 dorsal teeth and reaching distal margin of scaphocerite; antennal
	spine premarginal Troglocubanus eigenmanni
20′.	Rostrum without or with fewer than 6 dorsal teeth and never reaching distal margin
	of scaphocerite; antennal spine marginal or absent 21
21(20').	Rostrum overreaching antennular peduncle Troglocubanus calcis
21'.	Rostrum not overreaching antennular peduncle
22(21').	Rostrum not reaching distal end of first article of antennular peduncle; endite of sec-
. ,	ond maxilla unilobulate; 2 lateralmost spines on caudal margin of telson subequal
	in length Troglocubanus perezfarfanteae
22'.	Rostrum usually overreaching distal end of first article of antennular peduncle (some- times not doing so in T . jamaicensis); endite of second maxilla bilobed; more mesial of 2 lateralmost spines on caudal margin of telson at least twice as long as lateral
	0ne 98
98/994	one 28 Restrum with 2 or 2 dorest teath Tradocubanus gibarensis
	Rostrum with 2 or 3 dorsal teeth
23'.	Rostrum with 2 or 3 dorsal teeth
23'. 24(23').	Rostrum with 2 or 3 dorsal teeth Troglocubanus gibarensis Rostrum without or with no more than 1 tooth 24 Carapace with antennal spine Troglocubanus jamaicensis
23'. 24(23'). 24'.	Rostrum with 2 or 3 dorsal teeth Troglocubanus gibarensis Rostrum without or with no more than 1 tooth 24 Carapace with antennal spine Troglocubanus jamaicensis Carapace without antennal spine Troglocubanus inermis
23'. 24(23'). 24'.	Rostrum with 2 or 3 dorsal teeth Troglocubanus gibarensis Rostrum without or with no more than 1 tooth 24 Carapace with antennal spine Troglocubanus jamaicensis Carapace without antennal spine Troglocubanus inermis Propodus of fifth pereiopod without transverse rows of setae on distal flexor surface;
23'. 24(23'). 24'. 25(18').	Rostrum with 2 or 3 dorsal teeth Troglocubanus gibarensis Rostrum without or with no more than 1 tooth 24 Carapace with antennal spine Troglocubanus jamaicensis Carapace without antennal spine Troglocubanus inermis Propodus of fifth pereiopod without transverse rows of setae on distal flexor surface; mandibular palp 2-jointed
23'. 24(23'). 24'.	Rostrum with 2 or 3 dorsal teeth Troglocubanus gibarensis Rostrum without or with no more than 1 tooth 24 Carapace with antennal spine Troglocubanus jamaicensis Carapace without antennal spine Troglocubanus inermis Propodus of fifth pereiopod without transverse rows of setae on distal flexor surface; mandibular palp 2-jointed Propodus of fifth pereiopod with transverse rows of setae on distal flexor surface; mandibular flexor surface;
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23'. 24(23'). 24'. 25(18'). 25'.	Rostrum with 2 or 3 dorsal teeth Troglocubanus gibarensis Rostrum without or with no more than 1 tooth 24 Carapace with antennal spine Troglocubanus jamaicensis Carapace without antennal spine Troglocubanus inermis Propodus of fifth pereiopod without transverse rows of setae on distal flexor surface; mandibular palp 2-jointed Propodus of fifth pereiopod with transverse rows of setae on distal flexor surface; mandibular palp 3-jointed Second and third pereiopods chelate (Cambaridae) ² 27 Second and third pereiopods never chelate 54
23'. 24(23'). 24'. 25(18'). 25'. 26(1').	Rostrum with 2 or 3 dorsal teeth Troglocubanus gibarensis Rostrum without or with no more than 1 tooth 24 Carapace with antennal spine Troglocubanus jamaicensis Carapace without antennal spine Troglocubanus inermis Propodus of fifth pereiopod without transverse rows of setae on distal flexor surface; mandibular palp 2-jointed Propodus of fifth pereiopod with transverse rows of setae on distal flexor surface; mandibular palp 3-jointed Second and third pereiopods chelate (Cambaridae) ² 27 Second and third pereiopods never chelate 54 Third maxilliped conspicuously large and without teeth on opposable margin of
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² The identification of most crayfishes can be made only if first form males are available. Characters of the first pleopod are usually not recognizable in second form males.

30′.	First pleopods of first form male asymmetrical and bearing subapical setae; ischia of third and fourth pairs of pereiopods with simple hooks
31(30).	First pleopod of male lacking shoulder on cephalic surface; mesial process not nearly reaching level at apex of central projection; ischia of third and fourth pereiopods with bituberculate hooks Procambarus (Lonnbergius) acherontis
31' .	First pleopod of male with strong shoulder on cephalic surface; mesial process sur- passing level of apex of central projection: ischia of fourth pereiopods lacking hooks, those on third with simple hooks 32
32(31′).	Areola constituting 38 to 43 percent of total length of carapace; coxa of fourth pereiopod of first form male with prominent bulbous caudomesial boss; first pleopod with heavy, cephalically grooved, distolaterally directed mesial process obscuring central projection in caudal aspect, caudal element obsolete Procambarus (Remoticambarus) pecki
32'.	Areola constituting less than 38 percent of total length of carapace; coxa of fourth pereiopod of first form male lacking caudomesial boss; first pleopod with tapering or flattened mesial process never completely obscuring central projection in caudal aspect, caudal element always represented at least by caudal knob (Austrocambarus) 33
	Epistome produced laterally in small lobes; antennal scale broadest at midlength; first pleopod of first form male with caudal element bearing cushion-like prominence; central projection with accessory tooth; mesial process not tapering, directed more laterally than distally Procambarus (Austrocambarus) niveus
33'.	Epistome not produced laterally; antennal scale broadest distal to midlength; first pleopod of first form male with caudal element lacking cushion-like prominence; central projection lacking accessory tooth, and mesial process tapering distally, directed more distally than laterally
34(33′).	First form male with prominent sclerotized caudomesial boss on coxa of fifth pereiopod; mesial process somewhat flattened; annulus ventralis protruding prominently caudo- ventrally; postannular plate with transverse row of tubercles Procambarus (Austrocambarus) rodriguezi
34′.	First form male lacking prominent sclerotized caudomesial boss on coxa of fifth pereio- pod; mesial process not strongly flattened; annulus ventralis gently rounded caudo- ventrally; postannular plate lacking transverse row of small tubercles
	Areola constituting 35.8 to 37.8 percent of total length of carapace; cervical spine absent
35'.	Areola constituting 32.9 to 35.6 percent of total length of carapace; cervical spine present
	Mesial process of first pleopod of male sinuous and directed distally; cephalic process arising from cephalomesial side of appendage and never hooding central projection Procambarus (Leconticambarus) milleri
36′.	Mesial process of first pleopod never sinuous and always directed caudally or caudo- distally; cephalic process arising from lateral or cephalic side of appendage; if from latter often hooding central projection
	Eyes with pigment
37'. 38/87)	Eyes without pigment 40 Pigment in eyes black Procambarus (Ortmannicus) lucifugus alachua
38(37). 38′.	Pigment in eyes black Procambarus (Ortmannicus) tucijugus alachua Pigment in eyes red
	Several cervical spines present; postorbital ridge with spines caudally; male with hook on ischium of fourth pereiopod reaching basioischial articulation and opposed by tubercle on basis; cephalic process of first pleopod situated lateral to central pro- jection. Female with caudally directed tuberculiform prominences on caudal margin of sternum immediately cephalic to annulus ventralis
39'.	Procambarus (Ortmannicus) orcinus Only one cervical spine present; postorbital ridge without spines caudally; male with hook on ischium of fourth pereiopod neither reaching basioischial articulation nor opposed by tubercle on basis; cephalic process of first pleopod situated cephalic to and hooding central projection. Female without tuberculiform prominences on caudal margin of sternum immediately cephalic to annulus ventralis Procambarus (Ortmannicus) erythrops

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40(37′).	Rostrum narrower at base than along orbit. Male with central projection of first pleopod narrow and elongate; hook on ischium of fourth pereiopod not reaching basioischial articulation. Female without caudally directed tubercles on caudal mar- gin of sternum immediately cephalic to annulus ventralis <i>Procambarus (Ortmannicus) lucifugus lucifugus</i>
40′.	Rostrum tapering from base. Male with central projection of first pleopod beaklike; hook on ischium of fourth pereiopod overreaching basioischial articulation. Female with caudally directed tubercles on caudal margin of sternum immediately cephalic to annulus ventralis 41
41(40').	Postorbital ridges with spines or tubercles caudally; areola less than 20 times as long as broad. Male with cephalic process of first pleopod situated lateral to central pro- jection Procambarus (Ortmannicus) horsti
41′.	Postorbital ridges without caudally situated spines or tubercles; areola more than 20 times as long as broad. Male with cephalic process of first pleopod situated cephalic to and partially hooding central projection Procambarus (Ortmannicus) pallidus
	First pleopod without shoulder at cephalic base of central projection; distal portion of appendage much more slender than that proximal to it
42'.	First pleopod with shoulder at cephalic base of central projection; distal portion of appendage not conspicuously more slender than that proximal to it
43(42).	Cephalo-caudal thickness of first pleopod immediately proximal to base of central pro- jection less than half maximum cephalo-caudal thicknessOrconectes pellucidus
43'.	Cephalo-caudal thickness of first pleopod immediately proximal to base of central projection more than half maximum cephalo-caudal thickness
44(43').	Rostrum usually without marginal spines or tubercles, and areola constituting at least 43 percent of entire length of carapace
44′.	Rostrum with marginal spines and areola constituting less than 43 percent of entire length of carapace Orconectes inermis inermis
45(42′).	Rostrum without marginal spines or tubercles; mesial process of first pleopod compara- tively robust Orconectes incomptus
45'.	Rostrum with marginal spines or tubercles; mesial process of first pleopod compara- tively slender, never quite so robust as in O. incomptus
46(45').	Hooks usually present on ischiopodites of fourth pereiopods of male; shoulder at cephalic base of central projection of first pleopod angular; caudal process of first pleopod absent but caudal element prominently inflated
46' .	Orconectes australis packardi 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 Orconectes australis australis
	Eye without pigment
47'. 48(47).	Eye with pigment
	tubercles; areola less than 5 times as long as broad
48 ′.	Rostrum seldom tapering to apex, if so then short and subtriangular, usually with marginal spines or tubercles; areola more than 5 times as long as broad
49(48′).	Cervical spine absent although sometimes represented by small, occasionally acute, tubercle, little if at all larger than neighboring ones; areola more than 10 times as long as broad 50
49′.	Cervical spines well developed, or if reduced or absent, areola less than 10 times as long as broad
50(49).	First pleopod of first form male with central projection tapering distally to acute tip and lacking subapical notch; rostrum subtriangular <i>Cambarus (Jugicambarus) zophonastes</i>
50'.	First pleopod of first form male with central projection not conspicuously tapering and bearing distinct subapical notch; rostrum subacuminate Cambarus (Jugicambarus) tartarus
51 (49')	Areola more than 10 times as long as broad; chelae conspicuously setose
51′.	Cambarus (Jugicambarus) setosus Areola less than 10 times as long as broad; chelae not conspicuously setose

52(51'). Cervical spines often multiple; hepatic spines usually present; areola at least 7 times as long as broad; first pleopod of first form male with terminal elements bent no more than 90 degrees to shaft of appendage ... Cambarus (Aviticambarus) hamulatus

- 53(47'). Body with pigment; eye with faceted cornea Cambarus (Puncticambarus) nerterius 53'. Body without pigment; eye lacking faceted cornea

Cambarus (Erebicambarus) hubrichti

- 54(26'). Anteromedian part of carapace produced in narrow subacute rostrum; abdomen transversely arched, provided with well developed uropods, and not held flush against thoracic sternum (Aeglidae) Aegla cavernicola
- 54'. Anteromedian part of carapace almost truncate, never bearing subacute rostrum; abdomen quite flat, lacking uropods, and, except in ovigerous females, held flush against thoracic sternum. 55

Suborder NATANTIA

Section CARIDEA

Family ATYIDAE

Genus Palaemonias

Palaemonias Hay, 1901:179 [type-species: Palaemonias ganteri Hay, 1901:180].

Pataemonias.—Anonymous, 1904:691 [erroneous spelling]. Palemonias.—Roux, 1915:225 [erroneous spelling]. Palaemonies.—Giovannoli, 1933a:620 [erroneous spelling]. Poiotmonias.—Birstein, 1939:972 [erroneous spelling]. Paleomonetes.—Poulson, 1964:752 [lapsus for Palaemonetes]. palaemonias.—Barr and Kuehne, 1971:86 [lapsus calami].

DIAGNOSIS.—Eye without pigment or faceted cornea. Body without pigment. Carapace with supraorbital and antennal spines, lacking hepatic and branchiostegal spines. Rostrum, with dorsal teeth, overreaching antennular peduncle. Fingers of chelae of first and second pereiopods with setal tufts. First through fourth pereiopods bearing exopods, fifth lacking even rudiment of latter.

RANGE.—U.S.A. Disjunct: northern Alabama and central Kentucky.

NUMBER OF SPECIES.—Two, both of which are troglobitic.

Palaemonias alabamae Smalley

FIGURE 5

Palaemonias alabamae Smalley, 1961:127-130, fig. 1.-Vandel,

1964:178; 1965:139.—Barr, 1967a:162.—Cooper 1967:14; 1968a:34.—Nicholas, 1969:14.—Powell, 1970:228.—Cooper and Cooper, 1974:48.—Anonymous, 1975a:9; 1975b:117.— Hedgpeth, 1975:1.

Palaemonias .- Barr, 1967a:190; 1968:60.

Blind shrimp.—Anonymous, 1972b:2.

Palaemonias alabamea.-Monod, 1975:99, fig. 1 [erroneous spelling].

DIAGNOSIS.—Rostrum usually without ventral teeth and with fewer than 15 dorsal teeth. Third maxilliped with flexor surface of distal podomere bearing fewer than 12 rows of plumose setae followed by row of no more than 4 spiniform setae. First pleopod with mesial margin of endopod provided with row of fewer than 10 setae, usually absent. Appendix masculina studded with fewer than 15 spinelike setae.

SIZE.—Postorbital carapace length 5.9 mm (Smalley, 1961:129); total length 20 mm (Cooper, 1975).

Types.—Holotype (3) USNM 107028; paratypes, TU, USNM.

TYPE-LOCALITY.—Shelta Cave, SE 1/4, NE 1/4, Sec. 27, T. 3S, R. 1W, Madison County, Alabama, U.S.A.

RANGE.—U.S.A. Known only from: (1) typelocality; (2) a population occurring in Bobcat Cave, 8 mi (approximately 13 km) from Shelta Cave (Cooper and Cooper, 1974:48), is here assigned to this species.

ECOLOGICAL NOTES.—According to Smalley (1961: 129):


FIGURE 5.—Palaemonias alabamae, from type series: a, lateral view of cephalic region; b, mandible; c, d, first and second maxillae; e-g, first, second, and third maxillipeds; h-j, first, second, and third pereiopods; k, l, first and second pleopods of male. (Redrawn from Smalley, 1961.)

Most of the type series were found in a pool about 20 by 30 feet, with a bottom of up to eighteen inches [approximately 0.45 m] of fine silt. Water temperature was 16.5°C. During periods of high water, the room where the shrimp were collected is probably completely filled with water. In the same pool with the shrimp were blind cave fish, *Typhlichthys subterraneus* Girard, and blind crayfish, *Orconectes pellucidus* (Tellkampf) [= 0. australis australis (Rhoades)]. Behavior of *P. alabamae* is similar to that described by Hay (1902a:226-227) for *P. ganteri*; when disturbed, they swim toward the surface where they are easily collected...."

According to Cooper and Cooper (1974:48), "the shrimp inhabit standing pools, or a permanent lake, remaining after annual recedence of high water levels.... Known predators include *Typhlichthys* subterraneus." LIFE HISTORY NOTES.—From Cooper and Cooper (1974:48):

In Shelta Cave shrimp may be found from July through mid-January, with peak abundance in December; despite intensive searching they have not been found from February through June when the water table is high ... ovigerous females have been found in Shelta Cave in August and January, and [the population here assigned to this species] in Bobcat Cave in September and October. Individuals [of the genus] are smaller in Shelta Cave than in either [Bobcat or Mammoth caves], and females appear to produce fewer ova.

REMARKS.—Further data on the biology of this shrimp are available in J. E. Cooper (1975). Parts of this study are being prepared for publication.

Palaemonias ganteri Hay

FIGURE 6

- Palaemonias ganteri Hay, 1901:180; 1902a:226-230, fig. 1a-k.--Calman, 1909:93.--Kemp, 1912:115.--Ortmann, 1918:838, 845, fig. 1311.--Spandl, 1926:94, 141, 181.--Wolf, 1934:102.--Edmondson, 1935:15.--Woltereck, 1937:327.--Chace, 1943:30, 32; 1954:323; 1959:879, fig. 31.8.--Pennak, 1953:458, 466.--Dearolf, 1953:228.--Holthuis, 1955, fig. 8b; 1956a:50-51.--Nicholas, 1960:134.--Vandel, 1964:178; 1965:139.--Barr, 1967a:161, 162, 187, 192, pl. 47; 1968:60, 85, 95, fig. 15.--Poulson and Smith, 1969:199.--Anonymous, 1970:120.--Barr and Kuehne, 1971:81, 85.--Cooper and Cooper, 1974:48.--Burukovskii, 1974, fig. 84a.--Hedgpeth, 1975:1.--Monod, 1975:99, fig. 1.
- Palaemonias.—Hay, 1902a:227, 229, 230.—Bolivar and Jeannel, 1931:306, 307.—Fage, 1931:362, 372, 373; 1932:646, 649.— Chace, 1942:101.—Jeannel, 1943:271, 272.—Balss, 1955:1310. —Barr, 1967a:190.—Barr and Kuehne, 1971:85-87.
- Pataemonias ganteri.—Anonymous, 1904:691 [erroneous spelling].
- Palaemonias Ganteri.—Bouvier, 1925:74, figs. 120–127.—Chappuis, 1927:89, 152.—Fage, 1931:362–371, figs. 1–21; 1932: 646.—Jeannel, 1943:271.—Roth-Woltereck, 1955:197, 198.
- Palaemonies ganteri.—Giovannoli, 1933a:620 [erroneous spelling].
- Crevettes .- Jeannel, 1950:59.
- Paleomonetes ganteri.-Poulson, 1964:752 [lapsus calami].
- palaemonias ganteri.—Barr and Kuehne, 1971:86 [lapsus calami].
- Atyid shrimps .- Barr and Kuehne, 1971:94.

DIAGNOSIS.—Rostrum with ventral teeth and more than 15 dorsal teeth. Third maxilliped with flexor surface of distal podomere bearing more than 12 rows of plumose setae, followed by row of no fewer than 4 spiniform setae. First pleopod with mesial margin of endopod bearing fewer than 10 setae. Appendix masculina studded with more than 15 spinelike setae. SIZE.—Total length 23 mm (Barr and Kuehne, 1971:86); postorbital carapace length 6.7 mm (J. E. Cooper, 1975).

TYPES.—Syntypes, USNM 27000.

TYPE-LOCALITY.—Roaring River, Mammoth Cave, Edmonson County, Kentucky, U.S.A.

RANGE.—U.S.A. Known only from the typelocality and "the Golden Triangle area in the lower levels of Crystal Cave in Flint Ridge [Mammoth-Flint Ridge System]. The cave guides report that shrimps were formerly occasionally seen in a pool near the Fourth Landing on Echo River [Mammoth Cave]," (Barr, 1967a:162).

ECOLOGICAL NOTES.—Following the capture of the first specimen by Hay (1902a:226-227), he noted:

When first seen they were usually resting quietly or were slowly walking on the bottom of the pool, and were as insensible to the glare of my lantern as were the crayfish [Orconectes pellucidus]. They were so transparent that several times they were detected only by their shadows, and even when moving near the surface they were almost invisible. When disturbed they at once left the bottom, and by the rapid strokes of their subabdominal appendages came to the surface, where they remained for some time before sinking again to the bottom. All of their movements were unmistakably shrimp-like and very different from those of any of the other crustaceans in the cave. They were very easily captured, either in the net or by gently slipping my hand beneath them as they swam slowly on the surface; in fact, the latter method was used in nearly every case.

Giovannoli (1933a:620) noted that this shrimp is

one of the most spirit-like of all of Mammoth Cave's ghostly inhabitants . . . is all but transparent, and when in the water is almost invisible. One opaque spot in the anterior part of the body is all that can be seen. Usually these creatures remain at the bottom, resting or moving slowly. When disturbed they leave the bottom and swim in a deliberate and steady fashion up near the surface . . . if not disturbed again they soon sink to the bottom.

Similar observations were made by Barr and Kuehne (1971:85) who added that the population is such that to find a shrimp, one needs to examine from one to two square meters of the bottom of a pool. The pools are flooded annually, gradually diminishing during the dry season, and lasting until late fall or early winter before being recharged following heavy rains. They observed that the shrimp strained sediments in the pool with its mouth parts; its local occurrence in restricted parts of the cave was associated with seasonal sediment deposition in limited areas. A hypothetical food web involving *P. ganteri* is also depicted by them.



FIGURE 6.—Palaemonias ganteri, from Mammoth Cave: a, lateral view of cephalic region; b, antenna; c, second maxilla; d-f, first, second, and third maxillipeds; g-j, first, second, third, and fifth pereiopods; k, l, first and second pleopods of male; m, dorsal view of telson. (Redrawn from Fage, 1931.)

Barr (1968:60) noted that the sediments contain populations of protozoans including *Paramecium*, *Peranema*, *Halteria*, *Phacus*, and *Difflugia*.

LIFE HISTORY NOTES.—Poulson (1964:752) reported observing four ovigerous females in the fall. Later, he and Smith (1969:199) indicated that the "early egg" stage occurs from early May to mid-June and that "late egg-early young" are found from October to mid-November. Barr and Kuehne (1971:81), observing ovigerous females "between April and November," noted (p. 86) that in a collection made on 13 May 1962, 5 males and 7 ovigerous females were obtained; the latter were carrying 14 to 33 eggs each. An ovigerous female collected on 3 October 1961 was reported to have borne 15 eggs that were much larger than those

observed in May. Two males, five females, and three specimens, the sex of which was not determined, were collected with the latter female. Pointing out a lack of direct evidence, they suggested that the eggs hatch during the fall. Their smallest and largest specimens (measured from the base of the rostrum to the extremity of the telson) were 10 and 23 mm, respectively.

Genus Typhlatya

Typhlatya Creaser, 1936:128 [type-species: Typhlatya pearsei Creaser, 1936:128].

Typhlata.—Cardenas F., 1950:157 [erroneous spelling]. Typhatya.—Monod, 1975:99 [erroneous spelling].

DIAGNOSIS.—Eye with or without pigment spot, lacking faceted cornea. Body usually without dark pigment (occasionally present in T. mitchelli), sometimes yellowish orange, pinkish or reddish. Carapace without spines. Rostrum without dorsal teeth, never overreaching antennular peduncle. Fingers of chelae of first and second pereiopods with setal tufts. First through fifth pereiopods with exopods, that on fifth sometimes rudimentary.

RANGE.—Ascension Island, West Indies (Barbuda, Caicos Islands, Cuba, Dominican Republic, Mona, Puerto Rico), Mexico (Campeche, Yucatán), and Galapagos Islands.

NUMBER OF SPECIES.—Eight, all of which are troglobitic.

REMARKS.—Silva T. (1974:22) recorded an unidentified member of the genus from Cueva de los Murciélagos, Punta Pedernales, Isla de Pinos, Cuba.

Typhlatya campecheae Hobbs and Hobbs

FIGURES 7, 8

Typhlatya campecheae Hobbs and Hobbs, 1976:6-10, 14-16, 20-21, figs. 3-4.-Reddell, in press.

DIAGNOSIS.—Eyes without pigment. Rostrum extending anteriorly beyond eyes, at most only slightly beyond articulation between first 2 podomeres of antennular peduncle; latter extending beyond distolateral spine of scaphocerite. Flagellar lobule of first maxilliped well developed. Distal podomere of third maxilliped with 10 or 11 transverse rows of spatulate setae on basal portion of flexor surface and 4 to 6 spiniform setae in distal longitudinal row. Exopod of fifth pereiopod reaching between distal end of basis and midlength of ischium; dactyl of fourth pereiopod with 8 denticles on flexor surface; dactyl of fifth pereiopod with 45 to 50 denticulate spines on flexor surface. Appendix masculina extending much farther distally than appendix interna.

SIZE.—Postorbital carapace length 4.5 mm (Hobbs and Hobbs, 1976:8).

TYPES.—Holotype (3) USNM 151903; paratypes, IBM, TTM, USNM.

TYPE-LOCALITY.—Grutas de Xtacumbilxunam, Bolonchenticul, Campeche, Mexico.

RANGE.—Mexico. Known only from the typelocality.

ECOLOGICAL NOTES.—This shrimp was described by James R. Reddell, one of its discoverers, as occurring "in vast numbers in small pool containing amphipods and ostracods." He (in press) noted that the shrimp "was found to be extremely abundant on guano-floored pools . . . They were observed to rest on the floor of the pool and when disturbed would swim straight up or away at a slight angle."

LIFE HISTORY NOTES.—Representatives of the species have been collected on two occasions: 1_{0^3} , 4_{9} , 2 ovigerous 9 on 19 April 1973, and 40_{0^3} , 109_{9} , and 21 juveniles on 13 May 1973. The ovigerous females, both with a carapace length of 3.9 mm, were carrying 9 and 11 eggs; 2 additional unattached eggs were in the container. The eggs were approximately 0.8 by 1.1 mm.

REMARKS.—The preserved specimens were translucent to white, and within the cephalothorax was a yellowish orange mass, the identity of which could not be determined.

Typhlatya consobrina Botosaneanu and Holthuis

FIGURE 9

- Typhlatya consobrina Botosaneanu and Holthuis, 1970:123-128, figs. 1, 2.—Chace and Manning, 1972:17.—Botosaneanu, 1973:211.—Peck, 1974a:21.—Silva T., 1974:22, 45.—Hobbs and Hobbs, 1976:14-16.
- Typhatya consobrina.—Monod, 1975:99, fig. 1 [erroneous spelling].

DIAGNOSIS.—Eyes without pigment. Rostrum extending anteriorly beyond eyes. Flagellar lobule of first maxilliped well developed. Exopod of fifth pereiopod extending distinctly beyond ischiomeral articulation; dactyl of fourth pereiopod presumably

with 3 or 4 denticles on flexor surface; dactyl of fifth pereiopod with fewer than 40 denticulate

spines on flexor surface. Appendix masculina not extending so far distally as appendix interna.



FIGURE 7.—Typhlatya campecheae, all (except b) from holotypic male: a, lateral view; b, lateral view of abdomen of paratypic ovigerous female; c, dorsal view of cephalic region; d, antennule; e, base of antenna and scaphocerite; f, mandible; g, h, first and second maxillae; i, j, first and second maxillipeds (fl = flagellar lobule); k, l, first and second pleopods; m, appendices interna and masculina; n, dorsal view of telson and uropods; o, dorsal view of posterior part of telson. (Scales in mm; from Hobbs and Hobbs, 1976, fig. 3.)

SIZE.—Postorbital carapace length 4 mm (Botosaneanu and Holthuis, 1970:128).

TYPES.—Holotype (♂) ISER; paratypes, RNHL. TYPE-LOCALITY.—Cueva del Agua, Sierra de Cubitas, at foot of Cerro Tuabaquei, very near "Finca la Entrada," northeast of Camagüey, Provincia de Camagüey, Cuba.

RANGE.—Cuba. This shrimp is restricted to the Island of Cuba where it is known from only one locality in addition to the type-locality: Cueva del



FIGURE 8.—Typhlatya campecheae, holotypic male: a, third maxilliped; b, distal part of same; c-g, first through fifth pereiopods; h, distal end of dactyl of fifth pereiopod. (Scales in mm; from Hobbs and Hobbs, 1976, fig. 4.)



FIGURE 9.—Typhlatya consobrina, from type series: a, lateral view of cephalic region; b, dorsal view of same; c, scaphocerite; d, mandible; e, f, first and second maxillae; g-i, first, second, and third maxillipeds; j-m, first, second, third, and fifth pereiopods; n, o, first and second pleopods of male. (Redrawn from Botosaneanu and Holthuis, 1970, figs. 1, 2.)

Agua, Peninsula Guanahacabibes at "El Veral," Provincia de Pinar del Río (Botosaneanu and Holthuis, 1970:123).

ECOLOGICAL NOTES.—In both caves the specimens were found in a subterranean lake, from the typelocality in April, and from the other in June. Their color was described as pale pink. Occurring with this shrimp in the type-locality are two palaemonids: *Troglocubanus calcis* and *T. inermis*.

LIFE HISTORY NOTES .- Only four specimens have

been collected, one of which, the holotype, is a male. No other data have been recorded.

Typhlatya galapagensis Monod and Cals

FIGURE 10

 1974:275, fig. 2.-Monod, 1975:99, fig. 1.-Hobbs and Hobbs, 1976:1, 14-16.

Shrimp.-Peck, 1974b:35.

Typhlatya.-Croizat, Nelson, and Rosen, 1974:276 [in part].

DIAGNOSIS.—Eyes without pigment. Rostrum short, not extending anteriorly beyond eyes. Flagel-

lar lobule of first maxilliped not differentiated and palp uniformly comparatively slender. Exopod of fifth pereiopod reaching at least midlength of merus; dactyl of fourth pereiopod with 3 denticles on flexor surface; dactyl of fifth pereiopod with fewer than 40 denticulate spines on flexor surface.



FIGURE 10.—Typhlatya galapagensis, syntypes: a, lateral view; b, antennule; c, antenna; d, mandible; e, f, first and second maxillae; g-i, first, second, and third maxillipeds; j-n, first through fifth pereiopods; o, second pleopod of male; p, dorsal view of posterior part of telson. (Redrawn from Monod and Cals, 1970.)

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Distal podomere of third maxilliped with fewer than 8 transverse rows of spatulate setae on basal portion of flexor surface and fewer than 7 spiniform setae in distal longitudinal row.

SIZE.—Postorbital carapace length of juveniles 2 to 3 mm (Monod and Cals, 1970:60).

TYPES.—Syntypes, ISNB.

TYPE-LOCALITY.—Isla Santa Cruz "versant S-E, eau courante . . . dans une crevasse profonde de 15–20m, à 50 m d'altitude et à 2 km de la côte" of the Galapagos Islands (Monod and Cals, 1970:60).

RANGE.—Galapagos Islands. The following localities were cited by Monod and Cals (1970:60):

Isla Santa Cruz: (1) type-locality; (2) "côte S-E, eaux saumâtres souterraines, alt 5 m"; (3) "à 1 km de la plage de la Bahia de la Tortuga"; (4) "à 800 m de la Station Darwin . . . une crevasse de 10 m de prof." Isla Isabela: (5) "partie S . . . à proximité de la côte."

ECOLOGICAL NOTES.—The only specimens of which we have knowledge are those reported by Monod and Cals (1970). All were found in subterranean brackish water near the coast, and at least some were taken in localities where there was a current.

LIFE HISTORY NOTES.—The juvenile specimens described by Monod and Cals were collected in February, October, November, and December. No adult specimens have been recognized.

Typhlatya garciai Chace

FIGURE 11

Typhlatya garciai Chace, 1942:99–101, pl. 29; 1943:30, 32; 1954:319, 323; 1972:15; 1975:30.—Holthuis, 1955, fig. 8g; 1956a:52.—Balss, 1955:1310.—Nicholas, 1962:173.—Pino R., 1962:5.—Vandel, 1964:178; 1965:139.—Chace and Hobbs, 1969:5, 14, 19–21, 34, 38, 57, 80.—Straskraba, 1969:18.— Botosaneanu and Holthuis, 1970:122-123.—Monod and Cals, 1970:69, 73, 75, 78, 82, 84, 85, 93, 94, 101.—Chace and Manning, 1972:17.—Botosaneanu, 1973:211.—Croizat, Nelson, and Rosen, 1974:275, fig. 2.—Peck, 1974a:21.—Silva T., 1974:22, 44, 45.—Burukovskii, 1974, fig. 84 Zh.—Monod, 1975:99, fig. 1.—Hobbs and Hobbs, 1976:14–16.

Typhlatya.-Straskraba, 1969:25, 28.-Croizat, Nelson, and Rosen, 1974:276 [in part].

Typhlatya garciae.--Rioja, 1971:524 [erroneous spelling].

DIAGNOSIS.—Eyes with pigment spot. Rostrum not extending anteriorly beyond eyes. Flagellar lobule of first maxilliped well developed. Exopod of fifth pereiopod extending much beyond ischiomeral articulation; dactyl of fourth pereiopod with 5 or more denticles on flexor surface. SIZE.—Postorbital carapace length 6 mm (Botosaneanu and Holthuis, 1970:122); total length approximately 14 mm (Silva T., 1974:45).

TYPES.—Holotype (3) MCZ 12210; paratypes, MCZ.

TYPE-LOCALITY.—Potrero del Molino Cave, Las Cuatrocientas Rosas, Banes, Provincia de Oriente, Cuba.

RANGE.-West Indies. Known only from the vicinity of the type-locality and from the Caicos Islands. Botosaneanu and Holthuis (1970:122) reported it from "one of the 4 caves, isolated nowadays but formerly forming the system 'Las Cuatro Cientas Rosas,' in the place bearing the same name, E. from the town Banes, near the place known as 'Dolina de las Colmenas' (Prov. Oriente)." According to them, "our locality is almost certainly the same as the cave whence Chace's material . . . was collected." The only other locality is a cave pool about 0.75 mi (1.2 km) N of Blue Hills airstrip, Providenciales, Caicos Islands. Specimens were collected there by Donald W. Buden on 9 April 1975. This record was taken from the manuscript by Donald W. Buden and Darryl L. Felder; they have kindly permitted us to include it here.

ECOLOGICAL NOTES.—From Botosaneanu and Holthuis (1970:122–123):

Our specimens were taken by net in several 'lagos freaticos' connected to each other (it is more correct to say that we are concerned with a single 'lake' separated into several parts by fallen rocks); this is located in the rather large room of the cave . . .; the darkness is rather accentuated, yet not complete; perfectly fresh water, depth 20-50 cm., temp. = 24.8 °C. Typhlatya garciai occurs here in enormous numbers; many thousands of individuals are swarming in the lake's waters: they are gracefully swimming (somehow like Troglocaris) 'entre deux eaux', but many of them were seen climbing on the submerged stones.

Chace (1942:100-101) recorded the following observations made by Dr. Howell Rivero who maintained specimens in an aquarium:

The chelipeds are short, ending with a fan-shaped brush with which they scrub the surface of the stones or roots that are in the water, apparently feeding upon this substance. If kept alive, they pick up bread crumbs, apparently feeding upon them . . . These shrimp do not feed upon live food (mosquito larvae, etc.) as happens with the known species so far, and which I have kept alive for some time.

LIFE HISTORY NOTES.—Both the original collection (5 specimens) of the species and that made by Botosaneanu (200 specimens) were made in April. Two males were reported by Chace (1942:99). No mention of the sex of the 200 specimens was made by Botosaneanu and Holthuis (1970). **REMARKS.**—The color of the specimens collected by Botosaneanu was reported by him and Holthuis (1970:123) to vary "between dark pink and perfectly hyaline."



FIGURE 11.—Typhlatya garciai, from type series: a, lateral view of carapace; b, dorsal view of cephalic region; c, mandible; d, e, first and second maxillae; f, g, first and second maxillipeds; h-l, first through fifth pereiopods; m, dorsal view of telson and uropods. (Redrawn from Chace, 1942, pl. 29.)

Typhlatya mitchelli Hobbs and Hobbs

FIGURES 12, 13

Typhlatya mitchelli Hobbs and Hobbs, 1976:2-6, 11, 14-16, 20, 21, figs. 1, 2.

DIAGNOSIS.—Eyes without pigment. Rostrum not extending anteriorly beyond eyes. Flagellar lobule of first maxilliped well developed. Distal podomere of third maxilliped with 11 to 14 transverse rows of spatulate setae on basal portion of flexor surface and 9 to 11 spiniform setae in distal longitudinal row. Exopod of fifth pereiopod reaching at least distal extremity of basis and often as far as proximal fifth of merus; dactyl of fourth pereiopod with 3 denticles on flexor surface; dactyl of fifth pereiopod with about 40 denticulate spines on flexor surface. Male unknown. Body sometimes with spectacular pigmented pattern (unique character in genus).

SIZE.—Postorbital carapace length 4.8 mm (Hobbs and Hobbs, 1976:4).

TYPES.—Holotype (\Diamond) USNM 151904; paratypes, IBM, TTM, USNM.

TYPE-LOCALITY.—Cenote Kabahchen, Maní, Yucatán, Mexico.

RANGE.—Mexico. Known only from the State of Yucatán. The following localities are recorded by Hobbs and Hobbs (1976:4, 6):

Yucatán: (1) type-locality; (2) Cenote de la Paca, 7 km E of Tikuch; (3) Cenote de la Culebra; (4) Cenote de Orizaba, 8 km S of Buenaventura; (5) Cenote de Sodzil, 5 km W of Sucopo; (6) Grutas de Tzab-Nah, 2 km S of Tecoh; (7) Cenote Ch'en Mul, Ruinas de Mayapán; (8) Cenote de Aka Chen, 1 km NE of Tixcancal; (9) Cenote de Xtacabihá, 1 km SW of Xalau.

ECOLOGICAL NOTES.—Known only from pools in cenotes and caves, where it sometimes occurs in association with the more abundant *T. pearsei*.

LIFE HISTORY NOTES.—Of the 25 available specimens all are females which were collected in March, April, and August. The similar absence of males in most collections of *Typhlatya monae*, of which many more specimens have been examined, is noted below.

Typhlatya monae Chace

FIGURE 14

Typhlatya monae Chace, 1954:318-319, 323, fig. 1; 1972:15; 1975:29-30.—Holthuis, 1956a:53.—Husmann, 1966:420.— Chace and Hobbs, 1969:5, 14, 19-21, 30, 31, 34, 38, 57, 80-81, fig. 16.—Straskraba, 1969:25.—Botosaneanu and Holthuis, 1970:122, 123.—Monod and Cals, 1970:69, 73, 75, 78, 82, 84, 85, 93, 94, 101.—Rioja, 1971:524.—Chace and Manning, 1972:17.—Croizat, Nelson, and Rosen, 1974:275, fig. 2.—Peck, 1974a:21, 25, 28; 1974b:34, 36 [by implication].—Cooper and Cooper, 1975:3.—Monod, 1975:99, fig. 1.—Hobbs and Hobbs, 1976:14–16.

Typhlatya nana Vandel, 1964:178; 1965:139 [erroneous spelling].

Typhlatya.—Croizat, Nelson, and Rosen, 1974:276 [in part].— Chace, 1975:29, 30.

DIAGNOSIS.—Eyes with pigment spot. Rostrum not extending anteriorly beyond eyes. Flagellar lobule of first maxilliped well developed. Distal podomere of third maxilliped with 9 or 10 transverse rows of spatulate setae on basal portion of flexor surface and 6 spiniform setae in distal longitudinal row. Exopod of fifth pereiopod much reduced, not nearly reaching ischiomeral articulation; dactyl of fourth pereiopod with 5 or more denticles on flexor surface; dactyl of fifth pereiopod with about 36 denticulate spines on flexor surface. Appendix masculina not extending so far distally as appendix interna.

SIZE.—Postorbital carapace length 4.5 mm (Chace, 1954:319).

TYPES.—Holotype (\mathcal{Q}) USNM 96325; paratypes, USNM.

TYPE-LOCALITY.—Well at "El Molino," about 1 mi (approximately 1.6 km) SE of NYA camp at Sardinera, Isla Mona, Puerto Rico.

RANGE.—West Indies. The range of this species is disjunct.

Puerto Rico. Isla Mona: (1) type-locality; (2) "partially covered concrete water catchment basin . . . in the high central mesa of Mona Island" (Chace, 1954:319); (3-4) "caves in the Guanica Forest on the south coast of Puerto Rico" (Peck, 1974a:21), Shelter Cave, Mar 1974, B. F. Beck and R. Graham, coll. and Cueva Murciélagos, 12-14 June 1974, S. B. and J. Peck, coll.

Leeward Islands. Barbuda: (5) Dark Cave (Chace and Hobbs, 1969:81).

Dominican Republic. Provincia de San Pedro de Macorís: (6) La Furnia de Los Corrales, Villas del Mar (Chace, 1975:29).

ECOLOGICAL NOTES.—The only detailed data are those recorded by Chace (1975:30):

La Furnia de Los Corrales is a subterranean cavity surrounded by abundant vegetation about 400 meters from the sea. The entrance has a maximum height of 1.85 meters, with a cornice one meter thick. The distance to the innermost end of the cavity is 9.20 meters. There is sufficient phreatic water to form a pool about two feet [0.6 m] deep, the bottom of which is covered with a large amount of sedi-



FIGURE 12.—Typhlatya mitchelli, holotypic female: a, lateral view; b, dorsal view of cephalic region; c, antennule; d, base of antenna and scaphocerite; e, mandible; f, g, first and second maxillae; h, i, first and second maxillipeds (fl = flagellar lobule); j, k, first and second pleopods; l, telson and uropods; m, dorsal view of posterior part of telson. (Scales in mm; from Hobbs and Hobbs, 1976, fig. 1.)



FIGURE 13.—Typhlatya mitchelli, all (except i and j) from holotypic female: a, third maxilliped; b, distal part of same; c-g, first through fifth pereiopods; h, distal end of dactyl of fifth pereiopod; i, second pereiopod of female from Cenote Ch'en Mul; j, same of female from Grutas de Tzab-Nah. (Scales in mm; from Hobbs and Hobbs, 1976, fig. 2.)



FIGURE 14.—Typhlatya monae (a, female from Dark Cave, Barbuda; b-n, females from type series; o, p, male from Shelter Cave, Puerto Rico): a, lateral view; b, lateral view of cephalic region; c, dorsal view of same; d, dorsal view of telson and uropods; e, mandible; f, g, first and second maxillae; h-j, first, second, and third maxillipeds; k-n, first, third, fourth, and fifth pereiopods; o, second pleopod; p, appendices interna and masculina. (a, From Chace and Hobbs, 1969, fig. 16; b-n, from Chace, 1954, fig. 1; o, p, original.)

ment of organic origin. Light penetrates into the interior, providing some illumination, but the presence of the shrimps, which were quite numerous, was detected by flashlight.

Continuing with an explanation of the presence of the shrimp in the catchment basin on Isla Mona, mentioned above, Chace noted that Thomas A. Wiewandt had informed him

that, during dry periods on the island, water from the wells in which the shrimp normally occurs is sometimes pumped into the catchment basins, thereby accounting for the presence of *Typhlatya* in such an apparently inimical habitat.

LIFE HISTORY NOTES.—Nothing is known of the life history of this species except that it has been collected in August, October, and January. No specimen with an appendix masculina had been observed until recently, suggesting that "either they [males] are unrecognizable from external characters or they are restricted to a habitat niche that has not yet been investigated" (Chace, 1975:30).

Only in the caves of the Guanica Forest on Puerto Rico have males of this species been found. In March 1974, B. F. Beck and R. Graham obtained 1 male and 2 females. Between 11 and 14 June of the same year, S. B. and J. Peck collected 135 specimens of which only 8 are males. In view of the relatively low frequency of males in the Puerto Rican population, their apparent absence in other areas may reflect inadequate sampling.

REMARKS.—The specimens from the Dominican Republic were reported by Chace (1975:30) to be yellow-orange in life.

Typhlatya pearsei Creaser

FIGURES 15, 16

- Typhlatya pearsei Creaser, 1936:128–131, figs. 31–41; 1938:162– 164.—Pearse, 1936:24; 1945:169, 170, figs. 31–41.—Chace, 1942:100; 1943:30, 32; 1954:319, 323; 1972:15.—Cárdenas, F., 1950:156.—Villalobos F., 1951:215.—Rioja, 1953a:286, 292; 1971:524.—Holthuis, 1955:26; 1956a:52; 1974a:141.—Balss, 1955:1310.—Nicholas, 1962:173.—Chace and Hobbs, 1969:20-21.—Straskraba, 1969:25.—Botosaneanu and Holthuis, 1970:122, 123, 127.—Monod and Cals, 1970:69, 73, 78, 82, 84, 85, 93, 94.—Reddell, 1971a:25; in press.—Chace and Manning, 1972:17.—Croizat, Nelson, and Rosen, 1974:275, fig. 2.—Silva T., 1974:45.—Monod, 1975:99, fig. 1.—Hobbs and Hobbs, 1976:1, 10–16, 20, 21, figs. 5, 6.
- Typhlatya.—Creaser, 1938:159.—Pearse, 1938:13, 15; 1945: 167.—Argano, 1972:33.—Croizat, Nelson, and Rosen, 1974:276 [in part].
- Typhlata.-Cardenas F., 1950:157 [erroneous spelling].
- Typhlatya pearsi.-Rioja, 1953a:293.-Vandel, 1964:178; 1965:139.-Peck, 1974a:21. [Erroneous spelling.]

Typhlatya pearsii.-Cendrero, 1971:1150 [erroneous spelling].

DIAGNOSIS.—Eyes without pigment. Rostrum extending anteriorly to at least midlength of second podomere of antennular peduncle; latter extending no farther than level of lateral spine of antennal scale. Flagellar lobule of first maxilliped well developed. Distal podomere of third maxilliped with 10 or 11 transverse rows of setae on basal portion of flexor surface and 4 to 6 spiniform setae in distal longitudinal row. Exopod of fifth pereiopod, at most, barely surpassing distal extremity of basis; dactyl of fourth pereiopod with 8 denticles on flexor surface; dactyl of fifth pereiopod with more than 40 denticulate spines on flexor surface. Appendix masculina extending much farther distally than appendix interna.

SIZE.—Postorbital carapace length 5.2 mm (Hobbs and Hobbs, 1976:12).

TYPES.—Holotype (Q) USNM 98364; paratypes, USNM.

TYPE-LOCALITY.—"Balam Canche Cave, 4.8 km E, 0.8 km S Chichen Itza," Yucatán, Mexico. More recently the cave has been referred to as "Cueva Balaam Canche" or "Grutas de Balankanche."

RANGE.—Mexico. Known only from subterranean waters of Yucatán:

Yucatán: (1) type-locality; (2) "Santa Elena Cave 4.8 km S of Talcha" [? = Pozo de Santa Elena] (Creaser, 1938:163); (3) Hoctún Cave at Hoctún (Cárdenas F., 1950:156); (4) El Pochote Cave (Cárdenas F., 1950:157); (5) Cueva del Ponte (Nicholas, 1962:173-probably an error in citing the Cárdenas F. record for El Pochote); (6) Cenote de las Abejas; (7) Cenote Kabahchen, Maní; (8) Cenote Calchum, 3 km E San Bernardo; (9) Grutas de Tzab-Nah, 2 km S Tecoh; (10) Cueva de Santa Elena, 5 km S Telchac Puerto; (11) Cenote de Xtacabihá, 1 km SW Xalau; (12) Gruta de Chac, S of Kabah; (13) Cueva de San Isidro, Mérida. (Localities numbered 6-13 are from Hobbs and Hobbs, 1976:13-14. As pointed out by the latter, "the record, 'Caverna Chichén Itzá,' cited by Pearse (1945:169), is almost certainly an error in transcription from Creaser's (1938:162) list of localities in which he included 'Balam Canche,' 4.8 km E, 0.8 km S of Chichén Itzá, Yucatán."

ECOLOGICAL NOTES.—The only information available is that summarized by Holthuis (1956a:52): "In the two caves in which the species was collected the temperature of the water was 23°8 and 25°8C respectively, the pH 7.4 and 6.8, while it contained 4.56 cc and 0.57 cc O_2 per liter and 0.05 g and 0.22 g NaCl per liter respectively." There is no indication as to which of the four caves listed these



FIGURE 15.—Typhlatya pearsei (a, male from Cenote de Hoctún; b-l, o, p, male from Cenote de las Abejas; m, n, female from Cenote de las Abejas): a, lateral view; b, dorsal view of cephalic region; c, antennule; d, base of antenna and scaphocerite; e, mandible; f, g, first and second maxillae; h, i, first and second maxillipeds (fl = flagellar lobule); j, k, first and second pleopods; l, appendices interna and masculina; m, n, first and second pleopods; o, telson and uropods; p, dorsal view of posterior region of telson. (Scales in mm; from Hobbs and Hobbs, 1976, fig. 5.)



FICURE 16.—Typhlatya pearsei, male from Cenote de las Abejas: a, third maxilliped; b, distal part of same; c-g, first through fifth pereiopods; h, distal end of dactyl of fifth pereiopod. (Scales in mm.) (From Hobbs and Hobbs, 1976, fig. 6.)

data apply. Pearse (1938:12) cited the following water temperatures: Balam Canche Cave, 23.5°-25.4° C; Hoctún Cave, 27.2° C; and Cueva de San Isidro, 27.0° C. In a few localities this species is associated with the less common *T. mitchelli*.

LIFE HISTORY NOTES.—Ovigerous females have not been reported for this shrimp. That egg laying does not occur seasonally is indicated by such females having been collected during March, April, August, and November.

Family PALAEMONIDAE

Genus Bithynops

Bythinops Sbordoni, Argano, and Zullini, 1973:24 [nomen nudum].

Bithynops Holthuis, 1974a:135-136 [type-species: Bithynops luscus Holthuis, 1974a:136].

DIAGNOSIS.—Eyes with reduced but pigmented corneal area. Rostrum with dorsal and ventral teeth. Carapace with antennal spine but lacking supraorbital, hepatic, and branchiostegal spines. Telson with 2 pairs of dorsal and 2 pairs of posterior spines, and posterior margin with numerous setae between mesial pair of spines. Mandible with 3-segmented palp. Second maxilliped with podobranch, third with pleurobranch. Second pereiopods very robust and spinulate; third to fifth with simple dactyl. Propodus of fifth pereiopod with fringe of hair on posterodistal margin. Appendix interna absent on first pleopod; appendix masculina distinctly overreaching appendix interna.

RANGE.—Mexico. Known only from the typelocality of *B. luscus*.

NUMBER OF SPECIES.—Monotypic.

Bithynops luscus Holthuis

FIGURE 17

Bythinops luscus Sbordoni, Argano, and Zullini, 1973:24 [nomen nudum].

Bithynops luscus Holthuis, 1974a:135-142, figs. 1, 2.

DIAGNOSIS.—Same as that for genus.

SIZE.—Postorbital carapace length 25 mm (Holthuis, 1974a:136).

TYPES.—Syntypes RNHL.

TYPE-LOCALITY.—"Grutas de l'Arco" [= Grutas del Arco], near San Raphael [= Rafael] del Arco, La Trinitaria (about 16°10'N, 92°01'W), Chiapas, Mexico, altitude 1470 m.

RANGE.—Mexico. Known only from the typelocality.

ECOLOGICAL NOTES.—The type-locality is described in detail by Sbordoni, Argano, and Zullini (1973). The cave encompasses a segment of a small stream with a maximum depth of 20 cm, varying widths, and with alternating pools and rapids. Light reaches the stream through several openings in the cave. Holthuis (1974a:141) noted that "the shrimps occurred throughout the aquatic habitat of the cave, except for a deep pool near the main entrance [They] were observed both walking on the bottom of the stream and swimming. Although they tried to avoid capture by swimming, they were rather easily caught. The individuals occurred in groups and were quite plentiful." A small unidentified bivalve mollusk occurred abundantly in the cave, and in some areas the bottom of the stream was littered with their shells. According to Holthuis, "the suggestion was made that the shrimp possibly fed on these Molluscs."

LIFE HISTORY NOTES.—Ovigerous females were found in February and March, the eggs ranging in diameter between 1.5 and 2.2 mm.

REMARKS.—The color, "when alive [was] observed by dr. Sbordoni to be transparent-whitish. As shown by a colour photograph, and made in the cave, there is a slight reddish shine over the body, while the antennal flagella are also pale reddish or brownish. The cornea is deep black" (Holthuis, 1974a:141).

Genus Creaseria

Palaemon Creaser, 1936:126 [not Weber, 1795:94].

Creaseria Holthuis, 1950:5, 6; 1952:2, 152-153 [type-species, Palaemon morleyi Creaser, 1936:126].

DIAGNOSIS.—Eyes reduced and without pigment. Rostrum with dorsal and ventral teeth. Carapace with antennal and branchiostegal spines, lacking hepatic spine. Mandible with 2-jointed palp. Second pereiopod slightly more robust than first, both chelate. Remaining pereiopods with simple dactyl; propodus of fifth pereiopod with numerous transverse rows of setae on posterodistal surface.

RANGE.—Mexico. Restricted to the Yucatán peninsula in Mexico.

NUMBER OF SPECIES.—Monotypic.

Creaseria morleyi (Creaser)

FIGURES 18, 19

- Palaemon morleyi Creaser, 1936:126–128, 131, figs. 25–30; 1938:163–164.—Pearse, 1936:24; 1945:169, figs. 25–30.— Chace, 1943:31, 33.—Anonymous, 1947:128.—Cárdenas F., 1950:156.—Villalobos F., 1951:215.—Rioja, 1953a:293, 294.— Holthuis, 1955:44.—Balss, 1955:1311.—Hobbs and Hobbs, 1976:1.
- Palaemon.—Pearse, 1938:13, 15; 1945:167.—Cárdenas F., 1950:157.
- Palaemon Morleyi.-Carreño, 1950:24.



FIGURE 17.—Bithynops luscus, from type series: a, lateral view of cephalic region; b, dorsal view of same; c, mandible; d, e, first and second maxillae; j-h, first, second, and third maxillipeds; i-l, first, second, third, and fifth pereiopods; m, n, first and second pleopods of male; o, appendices masculina and interna; p, dorsal view of telson and uropod. (Redrawn from Hol-thuis, 1974a, figs. 1, 2.)

Creaseria morleyi.—Holthuis, 1950:6 [by implication]; 1952: 153-154, 356, pl. 40; 1955:44 [by implication], fig. 22a; 1956a:56-57; 1974a:141.—Chace, 1954:323.—Maccagno and Cucchiari, 1957:207 [by implication].—Nicholas, 1962:174.— Rioja, 1962:38, 40; 1971:522.—Vandel, 1964:179; 1965:140.— Rodríguez de la Cruz, 1965:76, 97-98, pl. 4A.—Andrews, 1970:4.—Reddell, 1971a:25; in press.—Parzefall and Wilkens, 1972:66.—Wilkens, 1973a:327, 328, 330, fig. 3; 1973b:205; 1973c:50-54, 56, 58, 59, figs. 1-3.—Burukovskii, 1974, fig. 96a.—Hobbs and Hobbs, 1976:1, 16-21, figs. 7, 8. Creaseria.—Holthuis, 1952:2, 152-153; 1956a:69.—Balss, 1957: 1549.—Chace, 1972:17.—Argano, 1972:33.

Palaemon morley Rioja, 1953a:286 [lapsus calami]. ?Shrimp.—R. D. Lee, 1966:88.

DIAGNOSIS.—Same as that for genus.

SIZE.—Postorbital carapace length 18.6 mm (Hobbs and Hobbs, 1976:16); total length 42 mm (Holthuis, 1952:154).



FIGURE 18.—Creaseria morleyi from Grutas de Tzab-Nah (a-o, male; p, q, female): a, dorsal view of cephalic region; b, lateral view of carapace; c, lateral view of abdomen; d, antennule; e, base of antenna and scaphocerite; f, mandible; g, h, first and second maxillae; i, j, first and second maxillipeds; k, l, first and second pleopods; m, appendices interna and masculina; n, dorsal view of telson and uropods; o, dorsal view of posterior part of telson; p, q, first and second pleopods. (Scales in mm; from Hobbs and Hobbs, 1976, fig. 7.)

TYPES.—Holotype (J) USNM 98365; paratypes, USNM.

TYPE-LOCALITY.—Cueva de San Isidro, Salar Colony, Mérida, Yucatán, Mexico.

RANGE.-Mexico. Restricted to the Yucatán Pe-

ninsula where it has been found in the following localities:

State of Yucatán: (1) type-locality; (2) Cueva Balaam Canché, 4.8 km E, 0.8 km S of Chichén Itzá; (3) Cenote [= Cueva] Amil on Hacienda Tixcacae, 14 km SE, 2 km E







of Mérida; (4) questionably from Cenote de Sambulha [= San Bulha Cave], Motul (localities 1 through 4, Creaser, 1936:128): (5) Cueva Chac Mol, near Tohil; (6) Cueva Góngora at Oxkutzcab; (7) Cueva Xpukil [= Cueva Spukil] at Calcehtok; (8) Cueva Yunchén at Libre Unión; (9) Cenote [= Cueva] de Hoctún at Hoctún; (10) questionable sight record at Cueva Xconsacab, Tizamin (localities 5 through 10, Creaser, 1938:163); (11) Cueva del Pochote, Muna (Cárdenas F., 1950:156); (12) Grutas de Tzab-Nah, 2 km S of Tecoh; (13) Cenote de la Culebra; (14) Cenote de las Abejas; (15) Cenote de la Paca, 7 km E of Tikuch; (16) Cueva de Sodzil, 5 km W of Sucopo; (17) Pozo [= Cenote] de Santa Elena, 5 km S of Telchac Puerto; (18) Cenote Kabahchen, Maní; (19) Cenote X-ebiz, Hoctún (localities 12-19, Hobbs and Hobbs, 1976:16).

ECOLOGICAL NOTES.—Holthuis (1956a:57) summarized available data on the biology of this species, noting that it "lives in fresh subterranean waters. The temperature of the water of some of the caves varied between 23°8 and 26°8C., the pH between 6.8 and 7.4, the contents of dissolved oxygen between 0.57 and 4.56 cc per liter, the salinity between 0.05 and 0.33 grams NaCl per liter." Creaser (1936:128) pointed out that the shrimp had been seen crawling over the substrate and swimming swiftly; furthermore, they were very sensitive to vibrations in the water. Among the stomach contents of the shrimp examined, he found a "claw of the same species." Reddell (in press) stated that this shrimp "is frequently found in large numbers, especially crawling about the floors of pools over which bats roost."

LIFE HISTORY NOTES.—Specimens have been collected in March, April, June, July, and August; however, no ovigerous females have been reported.

Genus Macrobrachium

Macrobrachium Bate, 1868:363 [type-species: Macrobrachium americanum Bate, 1868:363].

Macrobrachion.--von Martens, 1872:137 [erroneous spelling]. Eupalaemon Ortmann, 1891:696 [type-species: Palaemon acanthurus Wiegmann, 1836:150].

Parapalaemon Ortmann, 1891:696[type-species: Palaemon dolichodactylus Hilgendorf, 1878:840].

Macrobachium .- Bouvier, 1906:492 [erroneous spelling].

- Macroterocheir Stebbing, 1908:39 [type-species: Palaemon lepidactylus Hilgendorf, 1878:838].
- Paralaemon.-Boone, 1935:157 [erroneous spelling].
- Macrobranchium.-Coventry, 1944:535 [erroneous spelling].
- Macrobracium.-Sawaya, 1946:403 [erroneous spelling].
- Marobrachiuu.-Kubo, 1950:105 [erroneous spelling].
- Machrobrachium.—Chace and Hobbs, 1969:88 [erroneous spelling].
- Mecrobrachium.-Peck, 1975:308 [erroneous spelling].

SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY

DIAGNOSIS.—Eyes well developed or reduced and without pigment. Rostrum with dorsal and ventral teeth. Carapace with well-developed antennal and hepatic spines, lacking branchiostegal spine. Mandible with 3-jointed palp. Second pereiopod conspicuously longer and more robust than first, both chelate. Remaining pereiopods with simple dactyl; propodus of fifth with one or more transverse rows of setae on posterodistal surface.

RANGE.—Widespread in tropical and temperate regions of the world.

NUMBER OF SPECIES.—Approximately 30 to 35 American species and subspecies of which only one species is troglobitic. Possibly Macrobrachium faustinum lucifugum Holthuis (1974b:233) will be shown to be restricted to subterranean waters.

Macrobrachium villalobosi Hobbs

FIGURE 20

Macrobrachium villalobosi Hobbs, 1973b:77-80, fig. 3.— Reddell, in press.

Shrimp.-Reddell, 1973b:89.

DIAGNOSIS.—Eyes without pigment and lacking faceted cornea. Chelae of slender second pereiopods subequal in size, lacking teeth, spines (excluding apical ones), and conspicuous mats of setae on fingers or palm. Propodus of fifth pereiopod with single transverse row of setae on posterodistal surface.

SIZE.—Postorbital carapace length 9.2mm (Hobbs, 1973b:79).

TYPES.—Holotype (3) USNM 143633; paratypes, IBM, TTM, USNM.

TYPE-LOCALITY.—Cueva del Nacimiento del Río San Antonio, 10 km SSW of Acatlán, Oaxaca, Mexico.

RANGE.—Mexico. Known only from the typelocality.

ECOLOGICAL NOTES.—A description of the cave from which this shrimp was collected is presented by Reddell (1973b:89).

A small stream exits from below a series of travertine dams which rise above the nacimiento to end at a small opening from which water runs during times of flood. A second entrance is located about 20 m away and slightly higher on the hillside. The lower entrance leads into a small room, down a drop, and then into a fairly low area about 70 m long. At this point it opens into the main passage of the cave. A slope up to the right leads to a wide,



FIGURE 20.—Macrobrachium villalobosi, holotypic male: a, lateral view; b, dorsal view of anterior region; c, ventral view of basal portion of antenna; d, mandible; e, f, first and second maxillae; g-i, first, second, and third maxillipeds; j, chela of second pereiopod; k, l, first and second pleopods; m, appendices masculina and interna; n, dorsal view of telson and uropod; o, posterior extremity of telson. (Scales in mm; from Hobbs, 1973b, fig. 3.)

formation "room" which connects to the right to the upper entrance. The main cave passage extends about 50 m farther before encountering a deep lake in which we found blind catfish and crayfish.

Occurring with Macrobrachium villalobosi were Spelaeomysis olivae Bowman (1973:14), Procambarus (A.) oaxacae reddelli, Alpheopsis stygicola, and the undescribed catfish.

LIFE HISTORY NOTES.—The only specimens available were collected in March and December, and in neither lot was there an ovigerous female (see footnote 3 on p. 23).

Genus Neopalaemon

Neopalaemon Hobbs, 1973a:25 [type-species: Neopalaemon nahuatlus Hobbs, 1973a:26].

DIAGNOSIS.—Eyes reduced, without pigment or faceted cornea. Rostrum with teeth dorsally and ventrally. Carapace with antennal and hepatic spines but lacking supraorbital and branchiostegal spines. Telson with 2 pairs each of dorsal and posterior spines and 5 pairs of plumose setae between mesial pair of posterior spines. Mandible with 2segmented palp. Second maxilliped with epipodite, third with 2 arthrobranchs. Second pereiopod not markedly robust; third through fifth with simple dactyl; propodus of fifth pereiopod lacking transverse rows of setae on posterodistal surface. Appendix interna absent on first pleopod; appendix masculina distinctly overreaching appendix interna.

RANGE.—Mexico. Known only from the typelocality of N. nahuatlus.

NUMBER OF SPECIES.—Monotypic.

Neopalaemon nahuatlus Hobbs

FIGURES 21, 22

Neopalaemon nahuatlus Hobbs, 1973a:25, 26-29, figs. 1, 2.-Holthuis, 1974a:142.—Reddell, in press. ?Large blind shrimp.—Reddell, 1973b:90.

DIAGNOSIS.—Same as that for genus.

SIZE.—Postorbital carapace length 10.8 mm (Hobbs, 1973a:29).

TYPES.—Holotype (σ) USNM 143120; paratypes, IBM, TTM, USNM.

TYPE-LOCALITY.—Cueva del Guano, 10 km NE of Valle Nacional, Oaxaca, Mexico.

RANGE.—Mexico. Known only from the typelocality. ECOLOGICAL NOTES.—Reddell (in press) indicated that "these large shrimps are found in abundance in a deep permanent stream which runs beneath a large bat colony." It shares the stream with *Procambarus* (A.) oaxacae oaxacae (see "Ecological Notes," p. 116).

LIFE HISTORY NOTES.—The only specimens available were collected on 28 December 1972. Among them were males, females, and juveniles; none of the females was ovigerous.

Genus Palaemonetes

Palaemon.-Leach, 1814:401 [not Weber, 1795:94].

- Palaemonopis Stimpson, 1860a:444 [nomen nudum]; 1874:128. Palaemonetes Heller, 1869:157. [type-species: Palaemon Varians Leach, 1814:401].
- Paloemonites .- Gourret, 1892:9 [erroneous spelling].
- Palaeomonetes.—Cary and Spaulding, 1909:11 [erroneous spelling].
- Allocaris Sollaud, 1911:50 [type-species: Allocaris sinensis Sollaud, 1911:50].
- Coutierella Sollaud, 1914:318 [type-species: Coutierella tonkinensis Sollaud, 1914:318.]
- Palaemontes .- Tattersall, 1930:107 [erroneous spelling].
- Paleomonetes .- Dickinson, 1949:23 [erroneous spelling].
- Alaocaris Holthuis, 1949:88 [type-species: Palaemonetes antrorum Benedict, 1896:615].
- Palaemonetus .- Kristensen, 1950:2 [erroneous spelling].
- Palaemonites .- Holthuis, 1955:49 [erroneous spelling].
- Palemonetes.-Reddell and Mitchell, 1969:30 [erroneous spelling].
- Palamidies .- Franz, 1970:74 [erroneous spelling].

DIAGNOSIS.—Eyes well developed or reduced and without pigment. Rostrum with dorsal teeth, rarely without (only in *P. antrorum*) ventral teeth. Carapace with well-developed antennal and branchiostegal spines, lacking hepatic spine. Mandible without palp. First pereiopod moderately slender and chelate, second also chelate and usually more strongly developed than first. Remaining pereiopods nonchelate with simple dactyl; propodus of fifth with transverse rows of setae on posterodistal surface.

RANGE.—Widespread in tropical and temperate regions.

NUMBER OF SPECIES.—Although many species have been described, only 9 have been recorded from the freshwaters of the Americas (a few less than 20 in the world). Of these, two are troglobitic. Strenth (1976) recognizes no subgenera and describes three additional species, one of which is a troglobite from Texas (see footnote 1 on p. 5).



FIGURE 21.—Neopalaemon nahuatlus, holotypic male (except g-k from paratypes): a, antennule; b, antennal scale; c, mandible; d, e, first and second maxillae; f-k, lateral view of cephalic region; l, lateral view of abdomen; m, dorsal view of telson and uropods; n, dorsal view of posterior part of telson. (Scales in mm; from Hobbs, 1973a, fig. 1.)

Palaemonetes antrorum Benedict

FIGURE 23

Hay, 1903:433.—Calman, 1909:93.—Ortmann, 1918:838.— Uhlenhuth, 1921:75, 76, 79, 85, 90, 96, 101.—Kemp, 1925:817.—Spandl, 1926:90, 141.—Chappuis, 1927:87, 150.— Mohr, 1939:196; 1948a:17.—Chace, 1943:34.—Holthuis, 1949:87-89; 1950:11; 1952:202, 203; 1955:51.—Pennak, 1953:458, 466.—Dearolf, 1953:228.—Maccagno and Cucchiari, 1957:212.—Nicholas, 1960:134.—Vandel, 1964:179;

Palaemonetes antrorum Benedict, 1896:615.—Kingsley, 1899: 718.—Eigenmann, 1900:228, 230; 1909:202.—Neher, 1902:96-100, figs. 2-7.—Ulrich, 1902:83, 85, 93-95, 100, pl. 17.—



FIGURE 22.—Neopalaemon nahuatlus, holotypic male: a-c, first, second, and third maxillipeds; d, first pereiopod; e-f, second pereiopod; g-i, third, fourth, and fifth pereiopods; j, first pleopod; k, endopod of same; l, second pleopod; m, appendices masculina and interna. (Scales in mm; from Hobbs, 1973a, fig. 2.)



FIGURE 23.—Palaemonetes antrorum, from San Marcos: a, lateral view of cephalic region; b, antennule; c, scaphocerite; d, mandible; e, f, first and third maxillae; g-i, first, second, and third maxillipeds; j-l, first, second, and third pereiopods; m, dorsal view of telson. (Redrawn from Holthuis, 1952, pl. 49.)

1965:140.—Fleming, 1969:448, 449, 451, fig. 14.—Reddell and Mitchell, 1969:17, 22, 24, 27, 28, 30, 31, 36, 37, 39, 46, 47.— Davis, 1971:82.—Dobkin, 1971:285.—McNatt, 1971:82.— Longley, 1975:119, 120, 305.—Strenth, 1976:1, 2, 5, 9, 10, 12–15, figs. 4, 6.

- Palaemonetes.-Calman, 1909:97 [in part].-Jeannel, 1943:267 [in part].
- Palaemonetes antorum.—Mohr, 1948b:109.—Powell, 1970:280. [Erroneous spelling.]
- Palaemonetes (Alaocaris) antrorum.—Holthuis, 1949:88-91, fig. 1a-e; 1950:11; 1952:200, 202-207, pls. 49, 50, 51a-d; 1955:51 [by implication], fig. 26; 1956a:58.—Chace, 1954: 323; 1959:880, fig. 31.11.—Balss, 1955:1311.—Smalley, 1964a:231 [by implication].—Reddell, 1965:161.—Husmann, 1966:420.—Reddell and Mitchell, 1969:11, 21, 28.—L. E. Fleming, 1969:444, 450.—Burukovskii, 1974, fig. 100.—Longley, 1975:304.

Palaemonetes (Alaocaris) .- Balss, 1957:1548.

Palemonetes antrorum.-Reddell and Mitchell, 1969:30 [erroneous spelling.]

DIAGNOSIS.—Eyes without pigment and faceted cornea. Rostrum without ventral teeth. Second pereiopod differing only slightly from first. Lateral margin of lateral ramus of uropod with only one spine, lacking movable one.

SIZE.—Total length 18 mm (Holthuis, 1952:205). TYPES.—Syntypes, USNM 19326.

TYPE-LOCALITY.—Artesian well at San Marcos, Hays County, Texas, U.S.A.

RANGE.—U.S.A. Restricted to the following localities along the Balcones Escarpment in Texas.

Hays County: (1) type-locality; (2) Beaver Cave, San Marcos

(Uhlenhuth, 1921:90); (3) Ezell's Cave, San Marcos (Uhlenhuth, 1921:85); (4) Frank Johnson's Well, San Marcos (Uhlenhuth, 1921:85); (5) Wonder Cave (Reddell and Mitchell, 1969:11); (6) San Marcos Springs (Powell, 1970:280). Uvalde County: (7) Carson Cave, 4 mi (6 km) SW of Montell, 14 Jul 1974, S. S. Sweet and D. P. Hector, coll.

The last named locality (7), situated some 180 mi (216 km) WSW of San Marcos, represents a noteworthy extension of the range of the species.

ECOLOGICAL NOTES.—Uhlenhuth (1921:81-87) reported that this shrimp was observed in great numbers in the clear bluish water of Ezell's Cave, near the surface of the ponded area of the sluggish stream. There the temperature of the water was 21.5° C. According to the same author (1921:76-81), Frank Johnson's well is a vertical man-made shaft that intersects a subterranean river. He believed that the well, Ezell's Cave, and probably the 188-foot (57-m) deep San Marcos artesian well were all part of the subterranean Purgatory Creek System. Mohr (1948a: 17) reported the species from a shallow subterranean pool in Ezell's Cave.

LIFE HISTORY NOTES.—Holthuis (1952:205) stated, "The fact that no ovigerous females could be found in the very extensive material of this species, which is present in the U.S. National Museum [now the National Museum of Natural History], probably is due to the fact that all this material was collected in the early spring (February, March)." Neher (1902:100) indicated that among his material that was collected during September there were young specimens approximately 5 mm long. As pointed out by Holthuis (1952:205), eggs are probably laid in late spring or early summer.

Palaemonetes cummingi Chace

FIGURE 24

- Palaemonetes (Palaemonetes) cummingi Chace, 1954:319-323, fig. 2; 1959:880.—Holthuis, 1956a:57-58.—Smalley, 1964a: 232.—Reddell and Mitchell, 1969:21.—Villalobos F. and Hobbs, 1974:14-16, fig. 8c.
- Palaemonetes cummingi.—Warren, 1961:9.—Vandel, 1964:179;
 1965:140.—Dobkin, 1971:285-297, figs. 1-5.—Villalobos F. and Hobbs, 1974:14.—Strenth, 1976:2, 9, 10, 12, 14, 15, fig. 6.
 ?Freshwater shrimp.—Mohr and Poulson, 1966:144, 145.
 Palamidies cummingsi.—Franz, 1970:74 [erroneous spelling].

DIAGNOSIS.—Eyes without pigment. Lateral ramus of antennule with mesial free portion distinctly shorter than basal fused portion. Rostrum long and with teeth on ventral margin. Chela of second pereiopod distinctly longer than that of first. Appendix masculina with only 3 spines proximal to distal 5.

SIZE.—Postorbital carapace length 6.9 mm (Chace, 1954:322).

TYPES.—Holotype (Q) USNM 95795.

TYPE-LOCALITY.—Squirrel Chimney, about 11 miles (18 km) northwest of Gainesville, Alachua County (Sec. 21, T. 9S, R. 18E), Florida, U.S.A.

RANGE.—U.S.A. Known only from the typelocality.

ECOLOGICAL NOTES.—The only observations available are those of Robert B. Cumming, the discoverer of the shrimp, as quoted by Chace (1954: 322).

The shrimp was taken [11 July 1953] . . . while I was swimming in open water in the fissure at Squirrel Chimney. [See account of Squirrel Chimney under Troglocambarus maclanei.] It was very near a wall when first seen but swimming freely [On 15 July] I saw a shrimp swimming in open water right down the center of the fissure about 2 inches [5 cm] below the surface . . . but the shrimp seemed sensitive to our lights, and arriving at a spot right below us, dove straight down out of sight. The only animal we saw on the 15th was a shrimp. I returned to Squirrel Chimney on the 17th of July to swim and examine the traps. Swimming, I saw many specimens of P[rocambarus] pallidus but nothing else. The traps contained a few specimens of P. pallidus and that was all. [According to Chace, five more shrimp were seen by Cumming in July and early August but none was captured.]

The shrimp seemed much more at home in an aquarium than cavernicolous crayfish taken on the same day at the same locality. The shrimp swam freely about the aquarium much of the time, but it also rested frequently on the bottom. It sometimes would hang on the air hose near the surface of the water, a habitat it shared with *T*[roglocambarus] maclanei but not *P. pallidus*. The shrimp fed readily on bits of raw liver, having no difficulty in discovering the food and showing no hesitation in feeding as soon as it was discovered. This was not true of the crayfish.

LIFE HISTORY NOTES.—Dobkin (1971:287-288) studied the larval development of this shrimp. A single ovigerous female carrying approximately 30 to 35 eggs was caught in Squirrel Chimney in July 1968. The maximum diameter of the bright green eggs was 1.4 mm. From this clutch, 29 days following capture of the shrimp, 12 larvae were acquired; the female was presumed to have devoured at least some of the hatchlings. Escape from the egg membranes occurred over a period of 4 days, although most of the larvae appeared within 24 hours. Only



FIGURE 24.—Palaemonetes cummingi, holotypic female: a, lateral view of cephalic region; b, dorsal view of same; c, dorsal view of telson and uropods; d, caudal part of telson; e, lateral angle of lateral ramus of uropod; f, mandible; g, h, first and second maxillae; i-k, first, second, and third maxillipeds; l-p, first through fifth pereiopods. (From Chace, 1954, fig. 2.)

2 of them metamorphosed, this occurring on the ninth day after hatching. The first zoea was 4.8 mm in length, and the second and third were about the same size. The first postlarva, appearing 9 days after hatching, measured 5.5 mm. None of the larvae progressed beyond the first postlarval stage.

REMARKS.—Cumming, as quoted by Chace (1954: 322), also made the following observations on the color of the shrimp:

This shrimp was completely colorless and translucent with the exceptions noted below. There was no suggestion of any general body color except white and this was a mere suggestion. There was an organ in the dorsal portion of the cephalothoracic region which was a vivid pea green in color. This looked like an egg mass. It resembled a miniature mass of English peas with each "pea" just under a millimeter in diameter. The gills or something in the gill region was red in color. There was not much red color and it was somewhat diffused coming through the carapace. There was a small black spot just cephalad to the green mass mentioned above when the animal was caught, but when the shrimp fed extensively on liver several days after its capture, the spot became larger and sometime later it became invisible.

Genus Troglocubanus

Palaemonetes Hay, 1903:430, 431 [not Heller, 1869:157]. Troglocubanus Holthuis, 1949:91 [type-species: Palaemonetes eigenmanni Hay, 1903:431].

Trogloocubanus.-Peck, 1975:312 [erroneous spelling].

DIAGNOSIS.—Eyes with degenerated cornea and without pigment. Rostrum with or without dorsal teeth, without ventral teeth. Carapace without hepatic and branchiostegal spines; mandible without palp. First pereiopods slender and chelate, second pereiopods also chelate, larger than first. Remaining pereiopods nonchelate with simple dactyl; propodus of fifth with transverse rows of setae on posterodistal surface.

RANGE.—West Indies and Mexico. Cuba, Jamaica, and San Luis Potosí, Mexico.

NUMBER OF SPECIES.—Six, all of which are troglobitic.

REMARKS.—Silva T. (1974:23) indicated that he had collected a member of the genus ("Especie no descrita") from Cueva del Manatí, Punta Caguanes, Yaguajay, Las Villas, Cuba.

Troglocubanus calcis (Rathbun)

FIGURE 25

Palaemonetes calcis Rathbun, 1912:451-453 [in part], pl. 1,

figs.1-3, 5.—Kemp, 1925:317.—Spandl, 1926:90, 141.—Chappuis, 1927:87.—Wolf, 1934:103.—Chace, 1943:25, 27-29, 31, 34 [in part], pl. 5.—Holthuis, 1949:91.

- Shrimps.-Barbour, 1943:86; 1945:196 [in part].
- ?Camarones ciegos .- Núñez J., 1945:72.
- Troglocubanus calcis.—Holthuis, 1950:11; 1952:144–148, 151, 152, 348, pl. 36; 1956a:59; 1963a:69.—Chace, 1954:323; 1972: 24.—Nicholas, 1962:174.—Vandel, 1964:179; 1965:140.— Chace and Hobbs, 1969:5, 14, 22, 34, 38, 89, 112–113, 115, fig. 28b.—Straskraba, 1969:15.—Botosaneanu and Holthuis, 1970:128, 130.—Botosaneanu, 1973:211.—Villalobos F., 1974: 5, fig. 24.—Silva T., 1974:23, 45.

Troglocubanus (Palaemonetes) calcis.—Balss, 1955:1311. Troglocubanus.—Balss, 1957:1548 [in part].

DIAGNOSIS.—Rostrum with 1 tooth, straight, and overreaching antennular peduncle but not attaining distal extremity of scaphocerite. Carapace with marginal antennal spine. Second maxilla with bifid endite lobe. First maxilliped with unilobulate epipodite.

SIZE.—Total length 36.8 mm (Holthuis, 1952: 146); postorbital carapace length 9 mm (Botosaneanu and Holthuis, 1970:128).

TYPES.—Syntypes, MCZ, USNM.

TYPE-LOCALITY.—Freshwater pool in a limestone cave between Madruga and Aguacate, La Habana, Cuba. According to Silva T. (1974:45), this is probably "Cueva de la Chaveta" to which Núñez J. (1945:72) was referring.

RANGE.—Cuba. In addition to the type-locality, Botosaneanu and Holthuis (1970:128) reported this shrimp from the following localities:

Provincia de Camagüey: (1) Cueva del Agua, Sierra de Cubitas (NE from the city of Camagüey); (2) Cueva de la Lechuza, Sierra de Cubitas.

ECOLOGICAL NOTES.—The only ecological data available are those of Thomas Barbour as quoted by Rathbun (1912:453):

These shrimps were collected from a pool at the bottom of a deep, steeply sloping, limestone cave, situated directly beside the calzada which runs from Madruga to Aguacate, just about a kilometer beyond where this calzada branches off from the one from Madruga to Matanzas. They were found in company with the blind isopod, *Cirolana cubensis* Hay. The shrimps were quite abundant and were usually seen swimming slowly about in the water at some distance from the bottom. I caught several individuals on the first trip, but the bottle got broken and I had to return for more. On the second visit I found them much more abundant and obtained the whole lot by wading or swimming about in the water holding a small electric light and dip net.

Three shrimps, Troglocubanus calcis, T. inermis,

and Typhlatya consobrina, occur within Cueva del Agua.

LIFE HISTORY NOTES.—Specimens have been collected during February or March (Rathbun, 1912: 451) and April (Botosaneanu and Holthuis, 1970: 128). Although no ovigerous females have been recorded, Botosaneanu and Holthuis stated that "several females were seen but could not be caught."



FIGURE 25.—Troglocubanus calcis, holotypic female: a, lateral view of carapace; b, dorsal view of cephalic region; c, telson; d, mandible; e, f, first and second maxillae; g, h, first and second maxillipeds. (Redrawn from Chase, 1943, pl. 5.)

To have been recognized as females, they must have been ovigerous.

Troglocubanus eigenmanni (Hay)

FIGURE 26

- Palaemonetes eigenmanni Hay, 1903:430, 431-433, fig. 2.-Calman, 1909:93.-Eigenmann, 1909:202.-Rathbun, 1912: 453-454.-Kemp, 1924:46; 1925:317.-Spandl, 1926:90, 141.-Wolf, 1934:103.-Chace, 1943:31, 34.-Barbour, 1945:192.-Holthuis, 1949:91; 1950:11; 1952:143; 1955:51.-Reddell and Mitchell, 1969:27.
- Palaemonetes eigenmani.—Pike, 1906:267-275, figs. 1-7.— Straskraba, 1969:15. [Erroneous spelling.]
- Palaemonetes .- Calman, 1909:97 [in part].
- Palaemonetes Eigenmanni.-Chappuis, 1927:87, 150.
- Blind shrimps.-Barbour, 1943:84; 1945:191.
- Shrimp.-Barbour, 1945:198-199.
- Troglocubanus eigenmanni.—Holthuis, 1950:11; 1952:144, 146–148, 350, pl. 37; 1956a:59; 1963a:69; 1974b:233, 241.— Chace, 1954:324; 1972:24.—Maccagno and Cucchiari, 1957:212 [by implication].—Nicholas, 1962:174.—Vandel, 1964:179; 1965:140.—Chace and Hobbs, 1969:5, 14, 22, 34, 38, 89, 113, 115, fig. 28c.—Straskraba, 1969:15.— Botosaneanu and Holthuis, 1970:128–129.—Botosaneanu, 1973:211.—Villalobos F., 1974:5, 6.—Silva T., 1974:23, 46.— Cooper and Cooper, 1975:3.

Troglocubanus (Palaemonetes) eigenmanni.—Balss, 1955:1311. Troglocubanus.—Balss, 1957:1548 [in part].

- Palaemonetes (Palaemonetes) eigenmanni.-L. E. Fleming, 1969:444.
- Troglocubanus eigenmani.—Straskraba, 1969:15 [erroneous spelling].

DIAGNOSIS.—Rostrum with 6 to 8 dorsal teeth, slightly upturned, far overreaching distal end of antennular peduncle, and slightly exceeding distal end of scaphocerite. Carapace with premarginal antennal spine.

SIZE.—Total length 32 mm (Rathbun, 1912: 453); postorbital carapace length 15 mm (Holthuis, 1974b:233).

TYPES.—Syntypes, USNM 26349.

TYPE-LOCALITY.—Cave near Ashton, southwest of Alquízar, Pinar del Río, Cuba.

RANGE.—Cuba. This, the seemingly most common troglobitic freshwater shrimp in Cuba, is known from caves in the provinces of Pinar del Río, La Habana (including Isla de Pinos), and Matanzas.

Provincia de La Habana: (1) cave near Güira de Melena (Rathbun, 1912:453); (2) Cueva Emilio, near Ashton, not far from the towns Alquízar and Artemisa (Botosaneanu and Holthuis, 1970:128); (3) Isla de Pinos, "'Pozzo [= Pozo] Criolla' at the foot of Cerro los Cheo, a few km from Santa Fé" (Holthuis, 1974b:233). Provincia de Matanzas: (4) cave near Alacranes (Chace, 1943:34); cited by Barbour (1943:84) as "Cueva del M" and (1945:198-199) as near Unión de Reyes. *Provincia de Pinar del Rio:* (5) type-locality; (6-8) caves at Modesta, Jaiguán, and San Isidro, near Cañas (Hay: 1903:432); (9) cave near San Cristóbal (Holthuis, 1952:148); (10) Cueva de los Animales, near Ashton, Barrio las Cañas, Artemisa (Botosaneanu and Holthuis, 1970:129); (11) Cueva de Jagüey, Peninsula Guanahacabibes at "El Veral" (Botosaneanu and Holthuis, 1970:129).

ECOLOGICAL NOTES.—The only ecological data that we have encountered include a brief reference to the cave near Alacranes by Barbour (1943:84) who stated that in descending into the cave they found a "great body of water which completely covered the floor of the cave . . . This subterranean lake simply swarmed with life." There he found two species of blind fishes and the shrimp. Botosaneanu and Holthuis (1970:128, 129) referred to subterranean lakes in Cueva Emilio, Cueva de los Animales, and in Cueva del Jagüey. Eigenmann (1909:202) noted that, while it is "essentially" a pelagic species, it often rests "on various objects on the bottom."

LIFE HISTORY NOTES.—To our knowledge, no life history data have been recorded.

Troglocubanus gibarensis (Chace)

FIGURE 27

- Palaemonetes gibarensis Chace, 1943:28-29, pl. 7.-Holthuis, 1949:91.
- Cave shrimps.-Barbour, 1945:198.
- Troglocubanus gibarensis.—Holthuis, 1950:11; 1952:144, 149– 150, pl. 38; 1955:50, fig. 27a; 1956a:60; 1963a:69; 1974b:231.– 234, 241, fig. 1.—Chace, 1954:323; 1972:24.—Nicholas, 1962:174.—Vandel, 1964:179; 1965:140.—Husmann, 1966: 420.—Straskraba, 1969:16.—Chace and Hobbs, 1969:5, 14, 22, 34, 38, 89, 113–114, fig. 27.—Botosaneanu and Holthuis, 1970:129–130.—Botosaneanu, 1973:211.—Villalobos F., 1974: 5, 6, fig. 24.—Silva T., 1974:23, 46.—Burukovskii, 1974, fig. 101a.—Cooper and Cooper, 1975:3.

Troglocubanus (Palaemonetes) gibarensis.—Balss, 1955:1311. Troglocubanus.—Balss, 1957:1548 [in part].

DIAGNOSIS.—Rostrum with 2 or 3 dorsal teeth, straight, tapering to point, and reaching almost to distal end of antennular peduncle. Carapace with marginal antennal spine. Second maxilla with bifid endite lobe. First maxilliped with unilobulate epipodite.

TYPES.—Holotype (3) MCZ 12277; paratypes, MCZ.



FIGURE 26.—Troglocubanus eigenmanni, all (except a) male from cave near Güira de Melena: a, lateral view; b, antenna; c, mandible; d, e, first and second maxillae; f-h, first, second, and third maxillipeds; i-k, first, second, and fourth pereiopods; l, second pleopod; m, appendices interna and masculina; n, dorsal view of telson and uropods; o, dorsal view of posterior region of telson. (a, Redrawn from Hay, 1903, fig. 2, locality not indicated.)

SIZE.—Total length 25 mm; postorbital carapace length 8.6 mm (Chace, 1943:29).

TYPE-LOCALITY .-- Aguada del Montañés, en el

Jobal, Barrio de Cupeycillo, Término de Gibara, Oriente, Cuba.

RANGE.-Cuba. In addition to the type-locality,

this shrimp has been recorded from the following localities in Cuba:

Provincia de Oriente: (1) Cueva de los Panderos, near Gibara (Holthuis, 1974b:231). Provincia de Las Villas: (2) Lago Martí, Cueva Grande de Caguanes, Cayo Caguanes, NE of Yaguajay (Botosaneanu and Holthuis, 1970:129).

ECOLOGICAL NOTES.—In referring to the typelocality, Chace (1948:28) indicated that the specimens were taken "from a well, 29 yards deep, entering an underground stream" Holthuis (1974b: 232-233) described Cueva de los Panderos as follows:

This cave lies about 2 km from Gibara at an altitude of 20 m above sea level. Its opening is the so-called Loma de Cupeycillo, situated on the second or third main terrace, in a region with abundant vegetation. The distance between the entrance of the cave and the sea is less than 1 km, but the distance between the sea and the phreatic lakes in the



FIGURE 27.—Troglocubanus gibarensis, holotypic male: a, lateral view; b, dorsal view of cephalic region; c, telson; d, caudal part of telson; e, mandible; f, g, first and second maxillae; h, i, first and second maxillaeds. (From Chace, 1943, pl. 7.)

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caves is not known. The cave is rather large, about 500 m long; at the end it descends abruptly to a body of water consisting of a row of two or three "lakes," separated by mounds of clastic material fallen down from the ceiling of the cave. The length of these lakes in the explored part of the cave is about 30 m, their depth usually lies between 0.5 and 1.5 m, (sometimes the depth is greater), and their width lies between 2 and 3 m, sometimes more. The water at the day of collecting was slightly brackish, but the salinity evidently is variable. On the bottom there is a heavy layer of silt (30 to 40 cm thick). The water temperature was $24^{\circ}C$.

LIFE HISTORY NOTES.—The collector (Dr. Howell Rivero) of the type specimens "kept the present specimens alive for a time and found they were live feeders, taking mosquito larvae quite voraciously but discarding bread crumbs after sampling them" (Chace, 1943:29). No other data are available for this species.

Troglocubanus inermis (Chace)

FIGURE 28

- Palaemonetes calcis Rathbun, 1912:451 [in part], pl. 1:fig. 4.-Chace, 1943:25 [in part].
- Palaemonetes inermis Chace, 1943:27-28, 31, pl. 6.-Holthuis, 1949:91.

Shrimps.-Barbour, 1943:86; 1945:196 [in part].

Troglocubanus inermis.—Holthuis, 1950:11; 1952:150–152, 354, pl. 39; 1956a:60; 1963a:69.—Chace, 1954:323; 1972:24.— Nicholas, 1962:174.—Vandel, 1964:179; 1965:140.—Straskraba, 1969:15.—Chace and Hobbs, 1969:5, 14, 22, 34, 38, 89, 114–115, fig. 28d.—Botosaneanu and Holthuis, 1970: 130.—Botosaneanu, 1973:211.—Villalobos F., 1974:5, 6, fig. 24.—Silva T., 1974:23, 46–47.

Troglocubanus (Palaemonetes) inermis.—Balss, 1955:1311. Troglocubanus.—Balss, 1957:1548 [in part].

DIAGNOSIS.—Rostrum usually without teeth (rarely with one), straight, tapering rapidly to point, and reaching distal article of antennular peduncle. Carapace without antennal spine but sometimes with subacute angle immediately ventral to orbit. Second maxilla with bifid endite lobe. First maxilliped with unilobulate epipodite.

SIZE.—Total length 22 to 30 mm (Holthuis, 1952:152; and Silva T., 1974:47); postorbital carapace length 6.0 to 12.0 mm (Chace, 1943:27; Botosaneanu and Holthuis, 1970:130).

TYPES.—Holotype (Q) MCZ 12275; paratypes, MCZ.

TYPE-LOCALITY.-Cave between Madruga and

Aguacate, La Habana, Cuba. (See "Type-Locality" under Troglocubanus calcis.)

RANGE.—Cuba. Known only from one locality each in the provinces of Camagüey and La Habana.

Provincia de Camagüey: (1) Cueva del Agua, Sierra de Cubitas, near Finca La Entrada, NE of Camagüey (Botosaneanu and Holthuis, 1970:130). Provincia de La Habana: (2) type-locality.

ECOLOGICAL NOTES.—In the type-locality, this shrimp was taken from "a pool," and, in Cueva del Agua, it was found in a subterranean "lake," one of several in which the water temperature ranges from 22.4° to 25° C. In both localities, it was found with *Troglocubanus calcis*, and in the latter instance the two species "were found swimming together" with *Typhlatya consobrina* (Botosaneanu and Holthuis, 1970:130).

LIFE HISTORY NOTES.—One male and four females were obtained in the type-locality in February or March, 1912; four males and five females were taken from Cueva del Agua on 25 April 1969. No ovigerous females have been observed.

Troglocubanus jamaicensis Holthuis

FIGURE 29

Troglocubanus jamaicensis Holthuis, 1963a:66-69, fig. 3.-Hartnoll, 1964b:78.-Chace and Hobbs, 1969:5, 14, 22, 34, 38, 89, 115-116, fig. 28e.-Straskraba, 1969:24.-Botosaneanu and Holthuis, 1970:128.-Chace, 1972:24.-Villalobos F., 1974:5, 6.-Peck, 1975:308.

Troglocubanus.-Peck, 1974b:34, 36 [by implication].

DIAGNOSIS.—Rostrum usually without teeth (rarely with one), convex dorsally, tapering to point, and reaching almost to or to distal end of second segment of antennular peduncle. Carapace with marginal antennal spine. Second maxilla with bifid endite lobe. First maxilliped with unilobulate epipodite.

SIZE.—Total length 22 mm; postorbital carapace length 9 mm (Holthuis, 1963a:67).

TYPES.—Holotype (3) RNHL D.17446; paratypes, RNHL.

TYPE-LOCALITY.—Cave near Lucky Hill Cooperative Farm near Goshen, Saint Mary Parish, Jamaica.

RANGE.—Jamaica. Known only from the typelocality.

Trogloocubanus jamaicensis.—Peck, 1975:312 [erroneous spelling].



FIGURE 28.—Troglocubanus inermis, holotypic female: a, lateral view; b, dorsal view of cephalic region; c, telson; d, caudal part of telson; e, mandible; f, g, first and second maxillae; h, i, first and second maxillipeds. (From Chace, 1943, pl. 6.)

ECOLOGICAL NOTES.—No data are available except that the shrimp was found in a stream in a limestone cave. "A number of the shrimps were active in mid-water, and several were swimming upside down along the surface apparently feeding on floating material" (Hartnoll, 1964b:78).

LIFE HISTORY NOTES.—A single male and two females, neither ovigerous, were collected on 11 March 1962; two males and two females were obtained on 31 March 1973 by R. Norton and R. Zimmerman.

Troglocubanus perezfarfanteae Villalobos F.

FIGURE 30

Troglocubanus sp.—Reddell, 1967:82; 1971a:26.—Reddell and Mitchell, 1971b:143-144.—Reddell and Elliott, 1973:171.— Holthuis, 1974a:142.


FIGURE 29.—Troglocubanus jamaicensis, from type series: a, lateral view of cephalic region; b, antenna; c, third maxilliped; d-h, first through fifth pereiopods; i, j, first and second pleopods of male; k, dorsal view of posterior part of telson. (Redrawn from Holthuis, 1963a, fig. 3.)

Troglocubanus.-Reddell, 1973a:32.

Troglocubanus perezjarjanteae Villalobos F., 1974:1-5, figs. 1-23.—Reddell, in press.

DIAGNOSIS.—Rostrum without spines, slightly upturned, tip not reaching distal end of first article of antennular peduncle. Carapace lacking antennal spine. Second maxilla with endite lobe entire. First maxilliped with bilobed epipodite.

SIZE.—Postorbital carapace length 8.5 mm (Villalobos F., 1974:1).

TYPES.—Holotype (Q) USNM 139136.

TYPE-LOCALITY.—Sótano de la Tinaja, 11.7 km ENE of Valles, San Luis Potosí, Mexico.

RANGE.—Mexico. Known only from a single specimen collected in the type-locality.

ECOLOGICAL NOTES.—The single "specimen was obtained from near the surface of a deep lake in the deepest part of Sótano de la Tinaja. Its extreme transparency has probably aided it in escaping notice during the extensive explorations of caves in the Sierra de El Abra" (Reddell, in press).

LIFE HISTORY NOTES.—The only specimen available is a female collected on 9 April 1965.



FIGURE 30.—Troglocubanus perezfarfanteae, holotypic female: a, lateral view; b, dorsal view of cephalic region; c, mandible; d, e, first and second maxillae; f, first maxilliped; g, dorsal view of telson. (All redrawn from Villalobos F., 1974.)

Family ALPHEIDAE

Genus Alpheopsis

Betaeus.-Stimpson, 1860b:32 [not Dana, 1852b:16].

Alpheopsis Coutière, 1896:382 [type-species: Betaeus trispinosus Stimpson, 1860b:32].

Jousseaumea.-Rathbun, 1901:111 [not Coutière, 1896:381].

DIAGNOSIS.—Rostrum acute, overreaching and partially obscuring eyes dorsally. Carapace with or without supraorbital spines or tubercles. Posterolateral angle of sixth abdominal segment with articulated plate. Telson with 2 pairs of dorsal and 2 pairs of posterior spines. Mandible with incisor

process and with 2-jointed palp. First pereiopods with chelae usually subequal in size and slightly larger than those of second. Second pereiopods with chelae subequal in size and carpus multiarticulate; merus and ischium undivided.

RANGE.—While marine representatives are widespread in tropical regions, freshwater members are known to occur only in Africa (Gabon and Cameroon) and Middle America (Oaxaca, Mexico). (For a summary of the ranges of the known species, see Hobbs, 1973b:77.)

NUMBER OF SPECIES.—Approximately 20, only one of which is troglobitic.

Alpheopsis stygicola Hobbs

FIGURES 31, 32

Alpheopsis stygicola Hobbs, 1973b:73-77, figs. 1, 2.-Reddell, in press.

DIAGNOSIS.—Eyes with small pigment spot but lacking faceted cornea. Carapace with acute supraorbital spines. Antennule with 9 or 10 articles in dorsolateral flagellum proximal to bifurcation; shorter ramus consisting of 3 articles. Blade of scaphocerite distinctly exceeding distolateral spine. Chelae symmetrical. Carpus of second pereiopod consisting of 5 articles. Dactyl of third through fifth pereiopods simple, lacking spines on flexor margin. First through fourth pereiopods with compound epipodites.

SIZE.—Postorbital carapace length 6.2 mm (Hobbs, 1973b:76).

TYPES.—Holotype (3) USNM 143629; paratypes, IBM, TTM, USNM.

TYPE-LOCALITY.—Cueva del Nacimiento del Río San Antonio, 10 km SSW of Acatlán, Oaxaca, Mexico.

RANGE.—Mexico. Known only from the typelocality.

ECOLOGICAL NOTES.—This shrimp was collected from the same cave as were Spelaeomysis olivae, Macrobrachium villalobosi, and Procambarus (A.) oaxacae reddelli. See "Ecological Notes" for Macrobrachium villalobosi. One specimen was regurgitated by an albinistic catfish.

LIFE HISTORY NOTES.—The only specimens known (19) were collected in March and December. Among them were no ovigerous females.

Family HIPPOLYTIDAE

Genus Barbouria

Hippolyte.—von Martens, 1872:136 [not Leach, 1814:431].
Hippolysmata.—Kingsley, 1878a:56 [not Stimpson, 1860b:26].
Barbouria Rathbun, 1912:455 [type-species: Hippolyte Cubensis von Martens, 1872:136].

DIAGNOSIS.—Eyes pigmented and with faceted cornea. Rostrum armed with 4 to 5 dorsal and 2 or 3 ventral teeth and reaching anteriorly much beyond antennal spine. Carapace with antennal and branchiostegal spines. Posterolateral angle of sixth abdominal segment without articulated plate. Telson with 2 pairs of dorsal spines and 3 pairs of posterior spines. Mandible without incisor process but with 3-jointed palp. First pereiopods with welldeveloped chelae. Second pereiopods with chelae of subequal size, carpus and merus multiarticulate. Dactyli of third through fifth pereiopods simple with 2 spines on flexor margin.

RANGE.—West Indies. Antigua Island, Bahama Islands, Cayman Islands, and Cuba.

NUMBER OF SPECIES.—Two, one of which is an inhabitant of brackish or saltwater pools near the coast.

Barbouria cubensis (von Martens)

FIGURES 33, 34

Hippolyte Cubensis von Martens, 1872:136, 258, pl. 5: fig. 14. Hippolyte cubensis.—Kingsley, 1878a:56; 1878b:89.

- Hippolysmata cubensis .- Kingsley, 1878a:56; 1878b:89, 90.
- Barbouria poeyi Rathbun, 1912:455-457, pls. 2-5 [typelocality: cave near seashore, between Morro Castle and Cojimar].—Kemp, 1924:45.—Wolf, 1934:102.—Chace, 1943: 30, 33.—Barbour, 1943:82; 1945:194.—Rioja, 1953a:294.— Jaume, 1954:1500.—Balss, 1955:1312.—de la Torre y Callejas, 1960:97.
- Barbouria poegi.-Spandl, 1926:89 [erroneous spelling].

Barbouria poey.-Spandl, 1926:140, 229 [lapsus calami].

- Barbouria Poeyi.-Chappuis, 1927:90.-Jeannel, 1943:267.
- Fairy shrimp.-Barbour, 1943:81.

Shrimps.—Barbour, 1945:193.

- red Hippolitid.-Barbour, 1945:199.
- Barbouria cubensis.—Holthuis, 1947:7, 33; 1955:99, fig. 67; 1956a:63-64; 1963b:272-277, fig. 2; 1974b:234, 239-242.—Chace, 1954:323; 1972:107, 110.—Nicholas, 1962:173-174.—Vandel, 1964:180; 1965:140.—Riedl, 1966:217, 218, 223, 237, fig. 142.—Chace and Hobbs, 1969:5, 14, 17, 29, 34, 39, 116-117, figs. 28f, 29.—Straskraba, 1969:12-13.—Botosaneanu and Holthuis, 1970:121, 131-132.—Rioja, 1971:524.—Botosaneanu, 1973:213.—Burukovskii, 1974, fig. 140.—Silva T., 1974:23.—Cooper and Cooper, 1975:3.



FIGURE 31.—Alpheopsis stygicola, holotypic male: a, lateral view; b, dorsal view of anterior region; c, dorsal view of basal part of antennule; d, dorsal view of portion of lateral ramus of same; e, ventral view of basal portion of antenna; f, preaxial view of mandible; g, postaxial view of same; h, first pleopod; i, second pleopod; j, appendices interna and masculina; k, dorsal view of telson and uropods. (Scales in mm; from Hobbs, 1973b, fig. 1.)



FIGURE 32.—Alpheopsis stygicola, holotypic male: a, lateral view of pleurobranchs and coxal epipodites of pereiopods 1-5 and associated pleural region (α = alpha element of epipodite, β = beta element of epipodite, cx = coxa, pl = pleurobranch); b, c, first and second maxillae; d-f, first, second, and third maxillipeds; g-k, first through fifth pereiopods. (Scale in mm; from Hobbs, 1973b, fig. 2.)



FIGURE 33.—Barbouria cubensis, male from Cojimar, Provincia de La Habana, Cuba. (From Chace and Hobbs, 1969, fig. 29.)

Barbouria.—Balss, 1957:1542.—Straskraba, 1969:6.—Riedl and Ozretić, 1969:667, fig. 5.—Botosaneanu and Holthuis, 1970:122.—Botosaneanu, 1973:213.

DIAGNOSIS.—Eyes reduced, cornea narrower than stalk. Carapace and rostrum forming continuous arch dorsally; 3 dorsal teeth on carapace posterior to caudal margin of orbit. Carpus and propodus of third through fifth pereiopods multiarticulate. Endopod of first pleopod without retinacular hooks.

SIZE.—Postorbital carapace length about 12 mm (Chace and Hobbs, 1969:117).

TYPES.—Syntypes, ZBM 3739 (cotypes of Barbouria poeyi, USNM 44351, USNM 44355).

TYPE-LOCALITY.-Cuba.

RANGE.—West Indies. Coastal region of the provinces of La Habana, Matanzas, and Oriente, Cuba, the Island of Abaco, Bahama Islands, and Cayman Brac Island, Cayman Islands. The following localities have been reported:

Cuba. Provincia de La Habana: (1) type-locality; (2) small

hole 0.5 km E of Río Cojímar and 80 to 100 m from the sea (Jaume, 1954:1500). *Provincia de Matanzas:* (3) Punta de Guana, a "grieta" about 2 km from Matanzas (Botosaneanu and Holthuis, 1970:131). *Provincia de Oriente:* (4) Pozo de la Yana, a "casimba" near Guarda la Vaca (= Guardalabarca) (Botosaneanu and Holthuis, 1970:131); (5) "Casimba" near Velazques [= Velazco], 9 to 10 km W of Gibara and 80 m from the sea (Holthuis, 1974b:239).

Bahama Islands. Islands of Abaco: (6) Pond (no other data) (Holthuis, 1974b:240). Caicos Islands, Providenciales: (7) cave pool less than 0.5 mi (about 0.8 km) N Blue Hills airstrip, 25 Mar 1975, Donald W. Buden, coll. (This record was taken from a manuscript by Donald W. Buden and Darryl L. Felder. They have kindly permitted us to include it here.)

Cayman Islands. Cayman Brac Island: (8) South coast (Botosaneanu and Holthuis, 1970:131).

ECOLOGICAL NOTES.—In mentioning the typelocality of *Barbouria poeyi*, Barbour (1945:194) stated that this "cave," actually a sinkhole, was enlarged to provide a swimming hole, and no shrimp was seen thereafter. According to Botosaneanu and Holthuis (1970:132), *Barbouria cubensis*



FIGURE 34.—Barbouria cubensis, male from small pool 0.5 km E of Cojimar: a, dorsal view of cephalic region; b, base of antenna and scaphocerite; c, mandible; d, e, first and second maxillae; f-h, first, second, and third maxillipeds; i-m, first through fifth pereiopods; n, dactyl of fifth pereiopod; o, second pleopod; p, appendices interna and maculina: q, dorsal view of telson and uropods; r, dorsal view of posterior part of telson.

frequents the "giant network of cracks, completely or partly filled with brackish water (or even with almost salty water), which pierces in all directions the limestones along the sea shores." Access to these cracks occurs in the form of sinkholes, casimbas (small natural wells), or grietas (fissures). Inasmuch as in all of the known localities the water is salt or brackish, and in at least some the level fluctuates with the tides, underground connection with the sea is almost certain. In the casimba near Playa Velazques (Holthuis, 1974b:240) there occurs

a small pool . . . 5 m long, 1.5 m wide, situated in an area with a rich vegetation. Its bottom consists of sand, mud with an H₂S odour, and a number of blocks of madreporarian coral. The water surface occupies an area of 2 m^2 . The maximum depth of the water at the time of collecting was 25 cm, but the level is strongly influenced by the tides. The temperature of the water is 28 °C. The water was distinctly brackish. No large clefts or cracks were visible in the walls of this pool, but it is almost certain that subterranean passages leading away from it do exist. The "casimba" is well exposed to the sunshine, but is shady in a few places.

Barbouria was very plentiful in this small pool: more than 300 specimens of various sizes were observed in it. The animals were resting on the surface of the rocks, but when disturbed hid themselves quite rapidly among the stones and about 10 minutes after the first disturbance not a single shrimp could be observed anymore.

LIFE HISTORY NOTES.—Nothing is known of the life history of this shrimp. Chace and Hobbs (1969: 117) reported that "all of the more than 100 specimens examined of *Barbouria cubensis* have an appendix masculina on the second pleopod. It is possible that the female of this shrimp is still unknown." No mention of the sex of specimens collected has been made since that time.

REMARKS.—The color of this shrimp is apparently variable. Barbour (1945:193) described them as red, appearing as though they had been boiled, with white-tipped walking legs. Earlier he (1943:81) referred to them poetically as fairy shrimps possessing the most heavenly crimson hue, and in the description furnished to Rathbun (1912:457) he stated that "in life they were a beautiful, translucent, crimson color, while the long antennae and the first pair of chelate appendages were pure white, contrasting strongly with the color of the body of the animal and the other legs." According to Vandel (1965:140), the shrimp is purple in color. Holthuis (1974b:240) indicated that "they may be red, pink, or whitish. This color evidently depends on the state of contraction or expansion of the red chromatophores, as is seen in so many shrimps inhabiting anchialine habitats."

Genus Calliasmata

Calliasmata Holthuis, 1973:37 [type-species: Calliasmata pholidota Holthuis, 1973:37].

DIAGNOSIS.—Eyes reduced, with small pigment spot. Rostrum unarmed and not reaching so far anteriorly as antennal spine. Carapace devoid of spines other than antennal. Posterolateral angle of sixth abdominal segment without articulated plate. Telson with 2 pairs of dorsal and 3 pairs of posterior spines. Dorsolateral flagellum of antennule with shorter ramus consisting of one reduced article. Mandible without incisor process or palp. First pereiopods with well-developed chelae. Second pereiopods with chelae of subequal size and carpus multiarticulate. Dactyli of third through fifth pereiopods simple but bearing 3 to 5 spines each. (Modified from Holthuis, 1973:37, and Chace, 1975:37-43.)

RANGE.—Sinai Peninsula. Ellice Islands, Hawaiian Islands, and Dominican Republic.

NUMBER OF SPECIES.—Two, both of which occur in anchialine pools.

Calliasmata rimolii Chace

FIGURES 35, 36

Calliasmata rimolii Chace, 1975:37-43, figs. 5-7. Calliasmata.-Cooper and Cooper, 1975:3.

DIAGNOSIS.—Integument devoid of scales and associated pits. Rostrum directed anteroventrally. Posteroventral angle of pleuron of first abdominal segment rounded; pleura of third, fourth, and fifth abdominal segments without ventral spine; posteroventral extremity of fifth segment in form of acute angle. Endopod of first pleopod of female bilobed distally with retinacular hooks limited to mesial lobe. Color pale red.

Size.—Postorbital carapace length 12 mm (Chace, 1975:41).

TYPES.—Holotype (φ) USNM 151205; paratypes, USNM.

TYPE-LOCALITY.—"Cave 4 km from town of Estero Hondo (19°51'N, 71°11'W), Provincia de Puerto Plata, northern Dominican Republic" (Chace, 1975:41).



FIGURE 35.—Calliasmata rimolii, holotypic female (except i from paratypic female): a, lateral view; b, dorsal view of cephalic region; c, mandibles; d, e, first and second maxillae; f, g, first and second maxillipeds; h, dorsal view of telson and uropods; i, posterior part of telson. (From Chace, 1975, fig. 6.)



FIGURE 36.—Calliasmata rimolii, holotypic female: a, third maxilliped; b, first pereiopod; c, chela of same; d, right second pereiopod; e, chela of same; f, left second pereiopod; g, third pereiopod; h, dactyl of same; i, fourth pereiopod; j, dactyl of same; k, fifth pereiopod; l, dactyl of same; m, first pleopod; n, endopod of same. (From Chace, 1975, fig. 7.)

RANGE.—Dominican Republic. Known only from the type-locality.

ECOLOGICAL NOTES.—According to Chace (1975: 42),

the cave in which C. rimolii was found is situated in a

Pleistocene escarpment about one kilometer long and about 500 meters from the sea. The cave, the entrance to which was shaded by dense vegetation, was completely full of water, forming an underground pool with a maximum depth of two meters. Light penetrated to the bottom of the pool and there was little organic sediment. The water was clear and barely brackish with a temperature of 25°C, compared with an outside air temperature of 26°C at the time of collection. *Calliasmata rimolii* was numerous and was the only animal found in the cave.

Probably this cave qualifies as an anchialine habitat, as defined by Holthuis (1973:3), even though the water in the lakes was "barely brackish" and no tidal influence was apparent.

LIFE HISTORY NOTES.—The only data available are that five females were collected on 20 April 1973.

Suborder REPTANTIA

Section ASTACURA

Family CAMBARIDAE

Subfamily CAMBARINAE

Genus Cambarus

Astacus .- Fabricius, 1798:407 [not Fabricius, 1775:413]. Cambarus Erichson, 1846:95 [type-species: Astacus bartonii Fabricius, 1798:407].-Fowler, 1912:341. Gambarus.-Huxley, 1880:81 [erroneous spelling]. Orconectes .-- Cope, 1881:881 [not Cope, 1872a:419]. Camburus.-Faxon, 1885b:358 [erroneous spelling]. Camberus .-- W. S. Miller, 1895:336 [erroneous spelling]. Camparus.-Williamson, 1899:47 [erroneous spelling]. S[ambarus].-Steele, 1902:11 [erroneous spelling]. Bartonius Ortmann, 1905a:97 [type-species: "Cambarus bartoni" Fabricius, 1798:407.] Oronectes .- Stiles and Hassall, 1927:219 [erroneous spelling]. Orconetes .- Wolf, 1934:104 [erroneous spelling]. Bartontius .- Rioja, 1941:193 [erroneous spelling]. Canbarus.-Thompson, 1967:47 [erroneous spelling]. cambarus .- Padgett, 1970:19 [lapsus calami]. Cambaras.-Bouchard, 1973:106 [erroneous spelling]. Cambraus .-- Peters, 1975:iii [erroneous spelling]. Subgenus Aviticambarus Hobbs, 1969b:96, 99 [type-species: Orconectes hamulatus Cope, 1881:881]. Subgenus Depressicambarus Hobbs, 1969b:96, 102 [typespecies: Astacus latimanus LeConte, 1856:402]. Subgenus Erebicambarus Hobbs, 1969b:95, 99 [type-species: Cambarus bartoni tenebrosus Hay, 1902a:232]. Subgenus Hiaticambarus Hobbs, 1969b:95, 105 [type-species: Cambarus longulus Girard, 1852:90]. Subgenus Jugicambarus Hobbs, 1969b:95, 106 [type-species: Cambarus bartonii asperimanus Faxon, 1914:391]. Subgenus Lacunicambarus Hobbs, 1969b:96, 110 [type-species: Cambarus diogenes Girard, 1852:88]. Subgenus Puncticambarus Hobbs, 1969b:101 [type-species: Cambarus extraneus Hagen, 1870:73]. Subgenus Veticambarus Hobbs, 1969b:95, 96 [type-species: Cambarus pristinus Hobbs, 1965:268]. Subgenus Jugocambarus .- D. G. Hart and C. W. Hart, 1974:74 [erroneous spelling].

Subgenus Erebicambaruss.—Hobbs III, 1975:291 [lapsus calami].

DIAGNOSIS.—Third maxilliped not enlarged, reaching little, if at all, beyond apex of rostrum, and bearing teeth on mesial margin of ischium. Branchial count 17 + ep. Male with boss on caudomesial angle of coxa of fourth pereiopod; hooks on ischia of third pereiopods only; first pleopods symmetrical and terminating in 2 parts bent at least 90 degrees to shaft of appendage, cephalic surface without shoulder. Female with annulus ventralis slightly movable; first pleopods always reduced, sometimes vestigial or absent.

RANGE.—North America. From "Wisconsin to New Brunswick and southward to Texas and the panhandle of Florida" (Hobbs, 1969b:126).

NUMBER OF SPECIES AND SUBSPECIES.—Sixty-two, seven of which are troglobitic.

Subgenus Aviticambarus

Subgenus Bartonius Ortmann, 1905a:97 [in part].

- Subgenus Cambarus.-Fowler, 1912:341 [in part] [not Erichson, 1846:97].
- Subgenus Aviticambarus Hobbs, 1969b:99 [type-species: Orconectes hamulatus Cope, 1881:881].

DIAGNOSIS.—Eyes without pigment. Areola 5 to 8 times as long as wide, constituting 40 to 45 percent of entire length of carapace and bearing many moderately deep punctations. Chela slender and elongate; mesial surface of palm with scattered or with several rows of tubercles; palm and fingers sometimes bearing moderately conspicuous setal tufts; fingers rather slender, never widely gaping, with low median longitudinal ridges; proximal opposable margin of dactyl not deeply concave; conspicuous tufts of setae never present at mesial base of fixed finger, its lateral base not deeply impressed.

RANGE.—U. S. A. Along the Sequatchie Uplift, from the upper part of the Sequatchie Valley in Bledsoe County, Tennessee, southward to Blount County, Alabama, and in the Tennessee River basin between Florence and Guntersville.

NUMBER OF SPECIES.—Two; both members of the subgenus are troglobitic.

REMARKS.—John E. and Martha R. Cooper (pers. comm.) indicate that two undescribed troglobites, also from the Tennessee River basin in northern Alabama, are members of this subgenus, and that descriptions of them are in preparation.

Cambarus (Aviticambarus) hamulatus (Cope)

FIGURE 37

- Orconectes hamulatus Cope, 1881:881-882, pl. 7: fig. 1, 1a,b.-Cope and Packard, 1881:879-882.—Packard, 1888:19, 122, 126, 128, 155, pl. 21: figs. 3, 3a,b, 6; 1894:742.—Hobbs, 1969b:99; 1974a:11.—Hobbs and Barr, 1972:61.
- Cambarus hamulatus.-Faxon, 1884:145; 1885a:43, 45, 59, 81-84, 161, 174, pl. 4: fig. 6; pl. 9: fig. 1a, 1a'; 1890:628; 1914:422 .- Underwood, 1886:369 .- Packard, 1888:40-42, 82, 86, 110-112, 122, 127, fig. 10; 1890:393.-Parker, 1890:154, 155.-Lönnberg, 1894:126; 1895:4, 5.-Hay, 1899:959, 966; 1902b:435-437, fig. 8.-Ortmann, 1902:277; 1905a:118, 120, 121, 127 .- Steele, 1902:16, 18 .- Harris, 1903a:606; 1903b:59, 67, 101, 116, 151, 154, 162 .- Banta, 1907:72, 103 .- Graeter, 1909:470.-Spurgeon, 1915:388.-Garman, 1924:91.-Spandl, 1926:95 .- Stiles and Hassall, 1927:219 .- Chappuis, 1927:91, 120.-Wolf, 1934:104.-R. S. Fleming, 1938:299, 300, 302.-Mohr. 1939:202 [in part].-Hobbs, 1942b:158, 163; 1952:689, 693; 1959:895; 1967b:12.-Jeannel, 1943:272.-Dearolf, 1953:229.-Pennak, 1953:458.-Williams, 1954:900, 914.-Balss, 1955:1312 .- Eberly, 1958:6; 1960:31 .- Barr, 1960:6 .--Nicholas, 1960:133 .- Hobbs and Barr, 1960:13, 14, 16-19, 23, figs. 1-10; 1972:37, 62, 63.-Hobbs and Bedinger, 1964:9.-Vandel, 1964:461, 501; 1965:391, 423.-Poulson, 1964:762, 764.-Cooper, 1967:14; 1968b:183.-Cooper and Cooper, 1969:28 .- M. R. Cooper, 1969:205 .- Peck, 1974c:56.
- Cambarus (Bartonius) hamulatus.—Ortmann, 1905a:120; 1918:838, 849.—Creaser, 1931:6, 7.—Balss, 1955:1311.
- Cambarus (Cambarus) hamulatus.—Fowler, 1912:341 [by implication].—Ortmann, 1931:95, 96.—R. S. Fleming, 1938:300; 1939:310, 311.—R. Rhoades, 1941:146, 148 [in part].— Hobbs, 1941b:114.
- Oronectes hamulatus.-Stiles and Hassall, 1927:219 [by implication; erroneous spelling].
- Orconetes hamulatus .- Wolf, 1934:104 [erroneous spelling].
- Cambarus (Faxonius) hamulatus.-R. S. Fleming, 1938:301.
- Cambarus (Cambarus) hamueatus.—R. S. Fleming, 1958:303 [erroneous spelling].
- Cambarus (Aviitcambarus) hamulatus.—Hobbs, 1969b:99, 102, 127, 129, 130, 161, figs. 2e, 5, 13f, 14f, 17j; 1972b:109, 146, figs. 10a, 87a, 89h, 93b, d.—Holt, 1973a:231, 246, 248.— Hobbs III, 1975:276.
- Cambarus (cf. hamulatus) .- Cooper and Cooper, 1970:23.

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

SIZE.—Carapace length 35.2 mm; postorbital carapace length 28.5 mm. TYPES.—Syntypes (JII, Q) MCZ 3678.

TYPE-LOCALITY.—Nickajack Cave, 0.5 mi (0.8 km) S of Shellmound, lat. 34°59′23″N, long. 85°36′38″W, Marion County, Tennessee, U.S.A. (The cave is now partially flooded by an impoundment of the Tennessee River.)

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

Alabama. Blount County: (1) Randolph Cave, 1 mi (1.6 km) SW of Blount Springs, NW 1/4, NE 1/4, SW 1/4, Sec. 12, T. 13S, R. 3W, 31 Nov 1965, J. E. and M. R. Cooper, coll.; (2) Rickwood Caverns, 6 mi (9.7 km) NW of Warrior, NW 1/4, SW 1/4, SW 1/4, Sec. 28, T. 13S, R. 3W, ? Mar 1966, R. Franz, coll. Jackson County: (3) Talley Ditch Cave, 5 mi (8.1 km) NW of Stevenson, SE 1/4, SW 1/4, NE 1/4, Sec. 27, T. 1S, R. 7E, 1 Aug 1967, S. B. Peck, coll.; (4) Salt River Cave, 1.3 mi (2.1 km) W of Gonce, NW 1/4, NE 1/4, NW 1/4, Sec. 2, T. 1S, R. 6E, 27 Nov 1964, R. Brandon and R. Altig, coll.; (5) Jess Elliott Cave, 0.3 mi (0.5 km) NE of Haddon Spring, NE 1/4, NE 1/4, NE 1/4, Sec. 31, T. 1S, R. 6E, 23 Sep 1967, J. E. C. and M. R. C., coll.; (6) Geiger Cave, about 9 mi (14.5 km) WNW of Fackler, NE 1/4, NW 1/4, SW 1/4, Sec. 36, T. 2S, R. 5E, 29 Oct 1967, R. Graham, coll.; (7) Tumbling Rock Cave, SW 1/4, SW 1/4, NE 1/4, Sec. 35, T. 2S, R. 5E, 11 Jun 1961, L. B. Conrad, coll.; (8) Horseskull Cave, 1 mi (1.6 km) S of Harris Chapel, NW 1/4, NW 1/4, SE 1/4, Sec. 15, T. 1S, R. 9E, ? Feb 1971, R. G., coll.; (9) Crow Creek Cave, about 2 mi (3.22 km) NW of Stevenson, NE 1/4, SW 1/4, NW 1/4, Sec. 10, T. 2S, R. 7E, ? Dec 1969, R. G., coll.; (10) Russell's Cave, 4 mi (6.4 km) NW of Bridgeport, NW 1/4, SW 1/4, SE 1/4, Sec. 5, T. 1S, R. 8E, 28 Feb 1960, Joe Still, coll. Marshall County: (11) King School Cave, about 2 mi (3.2 km) WNW of Martling, NW 1/4, SW 1/4, NW 1/4, Sec. 34, T. 7S, R. 4E, 16 Dec 1967, J. French and W. Torode, coll.; (12) Buds Cave, SW 1/4, SW 1/4, NE 1/4, Sec. 30, T. 6S, R. 5E, 11 Jul 1973, S. B. Peck, coll.

Tennessee. Bledsoe County: (13) Aaron Tollett's Cave, 1 mi (1.6 km) N of Litton, lat. 35°44'24"N, long. 85°01'24"W, 2 Apr 1960, T. C. Barr, Jr., coll. Franklin County: (14) Salt River Cave (same as (4) above), lat. 34°59'18"N, long. 85°58'32"W (Hobbs and Barr, 1960:17). Marion County: (15) type-locality; (16) Winehouse Cave, exact location unknown (Hay, 1902b:437); (17) Ship Cave, Coppinger Cove, lat. 35°11'46"N, long. 85°36'02"W (Hobbs and Barr, 1960:17); (18) Honeycutt Cave, Sweden's Cove, lat. 35°03'55"N, long. 85°47'54"W (Hobbs and Barr, 1960:17); (19) Speegle Saltpeter Cave, Speegle Cove, lat. 35°08'19"N, long. 85°43'53"W (Hobbs and Barr, 1960:17); (20) Lost Pig Cave, Sweden's Cove, lat. 35°03'18"N, long. 85°45'24"W (Hobbs and Barr, 1960:17); (21) Whiteside Cave, 0.4 mi (0.6 km) NW of Whiteside, lat. 34°59'29"N, long. 85°30'27"W, 29 Jul 1968, S. B. P., coll.; (22) Blowing Cave, in roadside park in Sequatchie, lat. 35°07'14"N, long. 85°35'39"W, 29 Aug 1968, S. B. P., coll.

ECOLOGICAL NOTES.—The only available pertinent ecological information related to this species is that



FIGURE 37.—Cambarus (Aviticambarus) hamulatus, topotypes (a, d-g, first form male; b, c, from second form male; h, female): a, b, mesial view of first pleopods; c, d, lateral view of first pleopods; e, dorsal view of carapace; f, dorsal view of distal podomeres of cheliped; g, basis of ischium of third pereiopod; h, annulus ventralis; i, epistome; j, antennal scale. (After Hobbs and Barr, 1960, figs. 1–10.)

reviewed by Hobbs and Barr (1960:17) and a brief note by Cooper (1968b:183). Inasmuch as Nickajack Cave has been flooded, the conditions existing there at the time the following observations were made no longer obtain. The stream in the cave was a permanent one approximately five to seven meters wide, ranging in depth from about one to five meters and had neither sand nor gravel bars. Among the notes recorded by Hay (1902b:435-436) on this crayfish in the cave is the following:

It was not until I began to look for them under rocks in the cave stream that I found how common they were. They appeared habitually to live under such, where they scooped out a cavity in which to lie and from which they seemed seldom to travel. When disturbed, if they sought to escape, it was by crawling away rather than by swimming, and they would seldom move more than a few feet. Most often, however, they would lie perfectly still, and after the cloud of mud caused by raising the stone had cleared away, they could be seen lying quietly in their cavity or treading the mud to avoid being covered up. They were easily caught in the hands, as even after they had been touched they made no great effort to get out of danger. Indeed, in one case, I let a large specimen drop back into the water and a minute or so later found it lying at my feet; it had sunk like a stone and had not tried even to crawl away. They seemed to be totally devoid of the senses of sight and hearing, and the sense of touch did not seem to be nearly as well developed as in C. pellucidus [= Orconectes pellucidus].

Cooper (1968b:183) noted that "three specimens of the troglobitic crayfish, *Cambarus hamulatus*, for which Nickajack is the type locality, were taken on 29 July in the trap with the *G*[yrinophilus] palleucus. This is the only aquatic organism which has been found in intimate association with the salamander in this cave. It occurs in the main stream in the cave as well as in the smaller stream, and is a common inhabitant of other caves in Marion County [Tennessee]."

LIFE HISTORY NOTES.—First form males have been collected in February, April, July, August, September, and November. Females carrying eggs or young have not been reported.

Cambarus (Aviticambarus) jonesi Hobbs and Barr

FIGURE 38

?Cambarus (Cambarus) hamulatus.-R. Rhoades, 1941:148 [in part].

1961:175.—Hobbs and Bedinger, 1964:9.—Jegla, Poulson, and Cooper, 1965:639.—Cooper, 1966:97; 1967:14.—Cooper and Cooper, 1969:28; 1970:23.—Hobbs, 1967b:7, 8; 1969b:95. —Peck, 1974c:56.—D. G. Hart and C. W. Hart, 1974:115.— Cooper and Kuehne, 1974:492.—Anonymous, 1975a:9.

Cave crayfishes .- Cooper, 1968a:34 [in part].

- Cambarus (cf. jonesi).-Cooper, 1968b:185.-Cooper and Cooper, 1970:23.
- Cambarus (Aviticambarus) jonesi.—Hobbs, 1969b:99, 129, 130, figs. 5, 17k; 1972b:109, 146, figs. 10b, 93a,c; 1974b:10, 85, fig. 22.—Hobbs and Barr, 1972:3.—Holt, 1973a:231, 246, 248.— Hobbs III, 1975:276.
- Crayfish .- Powell, 1970:238 [in part].

Troglobitic crayfishes.—Cooper and Cooper, 1971:30 [in part]. Blind crayfish.—Anonymous, 1972b:2 [in part].

DIAGNOSIS.—Body and eyes without pigment, latter lacking facets. Rostrum emarginate or with marginal spines or tubercles. Areola comparatively wide, 5.4 to 6.8 times as long as wide. One cervical spine or tubercle usually present on each side of carapace. Central projection of first pleopod of male long, somewhat tapering, bearing weak subapical notch, and strongly arched with apex directed proximally; mesial process disposed caudally subparallel to central projection, reaching about as far caudally as latter.

SIZE.—Carapace length 27.2 mm; postorbital carapace length 22.9 mm.

TYPES.—Holotype, allotype, and morphotype, USNM 104407, 104408, 104799(GI, Q, GI); paratypes, TU, USNM.

TYPE-LOCALITY.—Cave Spring Cave, 12.1 mi (19.5 km) NW of Valhermosa, Morgan County (SE 1/4, NE 1/4, SW 1/4, Sec. 4, T. 6S, R. 3W), Alabama, U.S.A.

RANGE.—U.S.A. This crayfish is restricted to the Tennessee River basin between approximately 8 mi (12.9 km) W of Florence and the environs of Guntersville, Alabama.

The following localities unless accompanied by references were provided by John E. and Martha R. Cooper for populations tentatively identified as C. (A.) jonesi. According to them, there is considerable variation from one population to another, and analyses of the variations, now in progress, may require descriptions of additional taxa.

Alabama. Colbert County: (1) McKinney Pit Cave, Sec. 10, T. 4S, R. 1W (Cooper and Cooper, 1970:23). Lauderdale County: (2) Key Cave, Sec. 35, T. 3S, R. 12W (Cooper and Kuehne, 1974:492). Limestone County: (3) Rockhouse Cave, Sec. 34, T. 5S, R. 3W (Cooper, 1968b:185); (4) White Spring Cave, Sec. 11, T. 5S, R. 4W, 24 Sep 1967, John E. Cooper,

Cambarus jonesi Hobbs and Barr, 1960:13, 14, 16, 17, 19-23, figs. 11-20.-Nicholas, 1960:133; 1969:14.-Hart and Hobbs,

Martha R. Cooper, and John D. Veitch, coll. *Madison County:* (5) Shelta Cave, Huntsville, SW 1/4, SE 1/4, NE 1/4, Sec. 27, T. 3S, R. 1W (Hobbs and Barr, 1960:23); (6) Matthews Cave,

Sec. 23, T. 45, R. 2W, 26 Aug 1967, Stewart B. Peck, coll.; (7) Byrd Spring Cave, Sec. 25, T. 4S, R. 1W, 18 Aug 1967, J.E.C. and Alan Fiske, coll.; (8) Bobcat Cave, Sec. 26, T.



FIGURE 38.—Cambarus (Aviticambarus) jonesi (a, e-j, holotypic first form male; b, d, morphotypic second form male; c, allotypic female): a, b, mesial view of first pleopods; c, annulus ventralis; d, e, lateral view of first pleopods; f, dorsal view of carapace; g, basis and ischium of third perciopod; h, dorsal view of distal podomeres of cheliped; i, epistome; j, antennal scale. (After Hobbs and Barr, 1960, figs. 11-20.)

4S, R. 2W, 23 Nov 1973, J.E.C., M.R.C., and William W. Torode, coll. Marshall County: (9) Beech Spring Cave, Sec. 7, T. 7S, R. 2E, ? Jul 1969, Richard C. Graham and James Wilson, coll.; (10) Kellers Cave, Sec. 24, T. 6S, R. 2E, 26 Jun 1967, S.B.P. and A.F., coll. Morgan County: (11) typelocality; (12) Talucah Cave, Sec. 35, T. 5S, R. 2W, 10 Apr 1966, J.E.C., M.R.C., and J.D.V., coll.

ECOLOGICAL NOTES.—Martha R. Cooper (pers. comm.) pointed out to us that the description of Cave Spring Cave quoted from R. Rhoades (1941) by Hobbs and Barr (1960:22) applies to a cave in Madison County having the same name rather than to the type-locality of *Cambarus (A.) jonesi*.

Although there are no published ecological data on this crayfish, Cooper (1968a:33-34) presented a rather concise description of Shelta Cave emphasizing the fluctuations in the water level.

The main room and much of the East Room is typically floored with shallow lakes broken by small islands of projecting rock. At some times of the year, normally in the autumn and winter, the water in these rooms disappears completely, leaving only tacky mud with occasional drip puddles and tiny trickles of streams. At other times, however, the entire enormous volume of the cave may be filled with water nearly to the foot of the entrance drops. The East Room connects with the Big room by means of a low-level, tunnel-like passage about two feet [0.6 m] high, through which a stream is often flowing the West Room contain[s] another extensive lake which appears to be the only relatively permanent body of water in the cave. A clear, rapid stream flows from this lake in the direction of the main room, but dives beneath the floor and apparently follows channels beneath the main cave during periods of low water. West Lake is floored with soft, deep silt containing fairly numerous small pieces of breakdown.

John E. Cooper (1966:97), who has conducted an intensive ecological study of the crayfish inhabitants of Shelta Cave, reported that C. (A.) jonesi occurs in the pools with two other troglobitic crayfishes; it is present in far fewer numbers than Orconectes a. australis, yet is more common than the third, an undescribed species.

LIFE HISTORY NOTES.—First form males have been collected in every month except February, April, and October. There are no reported observations of females carrying eggs or young.

REMARKS.—The Coopers, mentioned above, are preparing an account of their study of the ecology of the three troglobitic species frequenting Shelta Cave. No doubt, as a result of their work, considerable information relating to the life history and ecology of *Cambarus* (A.) jonesi will become available.

Subgenus Erebicambarus

Subgenus Bartonius Ortmann, 1905a:97 [in part].

- Subgenus Cambarus.—Fowler, 1912:341 [in part] [not Erichson, 1846:97].
- Subgenus Erebicambarus Hobbs, 1969b:99 [type-species: Cambarus bartoni tenebrosus Hay, 1902a:232].
- Subgenus Erebicambaruss.—Hobbs III, 1975:291 [lapsus calami].

DIAGNOSIS.—Eyes with pigment. Areola 4 to 16 times as long as wide (about 6 times as wide in the only troglobitic species) and constituting 37.8 to 44.4 percent of entire length of carapace (41.0 to 44.0 percent in troglobitic species). Chela stocky except in troglobite, not depressed, with comparatively long palm, mesial surface of latter usually with single row of low tubercles (additional row of small ones flanking it in troglobite); neither palm nor fingers with conspicuous setal tufts; except in troglobite, fingers robust, never widely gaping, with well-defined dorsomedian longitudinal ridges; lateral base of fixed finger never deeply impressed; proximal opposable surface of dactyl never deeply concave. Third pereiopod of male without tubercle on basis opposing hook on ischium.

RANGE.-U.S.A. According to Hobbs (1969b:132),

the range of the subgenus extends southward from a belt across the southern part of Indiana and Ohio, with small pockets in southeastern Illinois and western West Virginia, through the karst lands of Kentucky, between the Great Valley and northward-flowing segment of the Tennessee River in Tennessee, into northern Alabama. A disjunct segment occurs along the eastern portion of the Ozark Plateau in southern Missouri.

NUMBER OF SPECIES.—Seven have been recognized; however, it is highly probable that C. (E.) cahni R. Rhoades (1944:146), once tentatively considered to be a troglobite (Hobbs and Barr, 1960:25), is a synonym of Cambarus (E.) tenebrosus Hay (1902a: 232), a common troglophile. Cambarus (E.) hubrichti is the only troglobitic member of the subgenus.

Cambarus (Erebicambarus) hubrichti Hobbs

FIGURE 39

"A third undescribed variety" of Missouri white crayfish.-Mohr, 1950:6.

Cambarus sp.-Hubricht, 1950:17.

- Cambarus hubrichti Hobbs, 1952:689-693, figs. 1-8; 1959:895. -Wells, 1957a:639; 1957b:640; 1959:3, 5, 7-9, 12, 13, figs.
 - 9, 10.-Conant, 1960:32.-Nicholas, 1960:133.-Hobbs and



FIGURE 39.—Cambarus (Erebicambarus) hubrichti (b, c, e, g-j, holotypic second form male; a, d, h, first form male; f, allotypic female): a, b, mesial view of first pleopods; c, d, lateral view of first pleopods; e, dorsal view of carapace; f, annulus ventralis; g, dorsal view of distal podomeres of cheliped; h, basis and ischium of third perciopod; i, epistome; j, antennal scale. (After Hobbs and Barr, 1960, figs. 21-30.)

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Barr, 1960:13-16, 23-25, figs. 21-30.—Hart and Hobbs, 1961:182.—Vandel, 1964:470; 1965:398.—Hobbs and Bedinger, 1964:9, 14, 15.—Bedinger and Hobbs, 1965:93-94, fig. 1h.—D. G. Hart and C. W. Hart, 1974:133.—Peck, 1974c:56.

Cambarus hubricht.-Hobbs, 1952:693 [lapsus calami].

Cambarus Hubrichti.-Cooper and Poulson, 1968, fig. 8.

Cambarus (Erebicambarus) hubrichti.—Hobbs, 1969b:99-101, 130-132, 143, 155, 166, fig. 17e; 1972b:118, 146, figs. 10d, 103a; 1974b:14, fig. 42.—Hobbs and Barr, 1972:3.—Hobbs III, 1975:276.

DIAGNOSIS.—Body without pigment; eyes with small pigment spot but lacking facets. Rostrum with or without small corneous marginal tubercles. Areola broad, about 6 times as long as wide. One to 3 cervical spines present on each side of carapace. Central projection of first pleopod of first form male short, not tapering, bearing subapical notch, and strongly arched with tip directed almost proximally; mesial process not so strongly recurved and extending caudally slightly beyond tip of central projection.

SIZE.—Carapace length 47.8 mm; postorbital carapace length 40.1 mm.

TYPES.—Holotype and allotype, USNM 92295, 92296 ($_{\mathcal{O}}$ II, $_{\mathcal{Q}}$); paratypes, USNM.

TYPE-LOCALITY.—Lewis Cave, 15 mi (24.2 km) NW of Doniphan, SW 1/4, NE 1/4, Sec. 30, T. 25N, R. 1E, Ripley County, Missouri, U.S.A.

RANGE.—U.S.A. This crayfish occurs in the subterranean waters of the White River basin in the Ozark region of southeastern Missouri.

Missouri. Carter County: (1) Midco Cave, NE 1/4, SW 1/4, Sec. 27, T. 27N, R. 2W (Wells, 1957b:640); (2) Cave in Big Spring State Park, 30 Jul 1967, George A. Kastler, coll. Oregon County: (3) Dewey Minick Cave, NE 1/4, SW 1/4, Sec. 22, T. 25N, R. 4W (Wells, 1957b:640); (4) Cave at Eleven Point River near Hogan's Club House, above Greer Spring, 4 Mar 1956, coll.? Phelps County: (5) Meramac Spring, date and collector unknown. Pulaski County: (6) Slaughter Sink, 1 mi (1.6 km) SSE of Boiling Spring, Sec. 34, T. 37N, R. 10W, Nov 1967, R. Irwin, coll. Ripley County: (7) type-locality. Shannon County: (8) Medlock Cave, NE 1/4, NW 1/4, SW 1/4, Sec. 10, T. 31N, R. 6W, 29 Jun 1941, C. B. Obrecht et al., coll.; (9) Welch Cave, 1 mi (1.6 km) N of Akers, SW 1/4, SW 1/4, Sec. 11, T. 31N, R. 6W, date?, O. L. Cartwright, coll.

ECOLOGICAL NOTES.—There are no ecological data available for this crayfish except for an unpublished note accompanying a specimen collected by Daniel M. Stout in Welch Cave: "This cave must be entered by boat over an extremely deep underground river. I estimate the river's depth to be 30 to 50 feet [9.1 to 15.2 m]. There are many crayfish in the deep waters adjoining the main river"

In experiments to determine the response of certain troglobitic crayfishes to light, Wells (1959:12) called attention to "the failure of mature animals [C. hubrichti] to respond to light under conditions of these experiments. None of the seven adult animals tested responded to illumination of the cephalic region, tail, or any other part of the body.... The one juvenile specimen of this species available for study, however, showed marked photosensitivity."

LIFE HISTORY NOTES.—First form males have been collected in March, June, and November. Females with eggs or young have not been observed.

Subgenus Jugicambarus

- Subgenus Cambarus Erichson, 1846:97 [in part].-Fowler, 1912:341 [in part].
- Subgenus Bartonius Ortmann, 1905a:97 [in part].
- Subgenus Jugicambarus Hobbs, 1969b:95, 106 [type-species: Cambarus bartonii asperimanus Faxon, 1914:391].—Bouchard, 1973:105 [emendation].
- Subgenus Jugocambarus.—D. G. Hart and C. W. Hart, 1974:74 [erroneous spelling].

DIAGNOSIS .- Eyes with or without pigment, lacking in all troglobites. Areola 3.8 to 46.0 times as long as broad (among troglobitic species, 15.5 to 40 times as long as broad except in C. (J.) cryptodytes which has acuminate rostrum) and constituting 33.0 to 47.0 percent of entire length of carapace (among troglobitic species, except for C. (J.) cryptodytes, constituting 40 to 47 percent), and bearing few to many punctations. Chela subrectangular, depressed only in burrowing species; mesial surface of palm with single serrate or cristiform row of tubercles and as many as 3 rows in troglobites; both palm and fingers often bearing conspicuous setal tufts (in all troglobites except some specimens of C. (J.) cryptodytes); fingers comparatively robust except in troglobitic species, never widely gaping, with well-defined dorsomedian longitudinal ridges; proximal opposable margin of dactyl never deeply concave; conspicuous tuft of setae never present at mesial base of fixed finger, its lateral base never deeply impressed.

RANGE.-U.S.A. According to Hobbs (1969b:142),

the discontinuous range of the group extends from northeastern Oklahoma through the Ozarks into eastern Missouri and from the western Highland Rim [in Tennessee] to the Blue

Ridge in North Carolina and Georgia; in the Alleghanies, it reaches northward to southwestern Pennsylvania. The disjunct C. [(J.)] cryptodytes, which occurs in the Florida panhandle and southwestern Georgia, is tentatively included in this subgenus.

NUMBER OF SPECIES.—Eighteen species of which four are troglobitic.

Cambarus (Jugicambarus) cryptodytes Hobbs

FIGURE 40

- Cambarus (Cambarus) cryptodytes Hobbs, 1941b:110, 112-114, figs. 2, 3, 7, 11, 13, 15, 18, 21, 24, 28, 29.
- Cambarus cryptodytes.—Hobbs, 1942a:854; 1942b:9, 12, 21, 32, 156-158, 162-163, figs. 196-200; 1952:689, 693; 1959:895; 1971b:122, fig. 18.—Pennak, 1953:458.—Pylka and Warren, 1958:334.—Hobbs and Hart, 1959:149.—Hobbs and Barr, 1960:13-16, 31, figs. 48-57.—Nicholas, 1960:132.—Warren, 1961:2, 6, 7, 10.—Hobbs and Bedinger, 1964:9.—Hobbs and Walton, 1968:251.—Sutton and Relyea, 1971:58.—Holsinger and Peck, 1971:30.—Hobbs and Means, 1972:393.—D. G. Hart and C. W. Hart, 1974:139.
- Cambarus (Jugicambarus) cryptodytes.—Hobbs, 1969b:107, 142-144, 161, figs. 9, 19d; 1972b:122, 146, figs. 10e, 107b; 1974b:18, fig. 64; 1975a:14.—Hobbs and Barr, 1972:3.— Hobbs and Cooper, 1972:49, 55.—Holt, 1973a:246, 248.— Hobbs III, 1975:276.

cambarus cryptodytes .- Padgett, 1970:19.

Crayfish.-Peck, 1974b:31 [in part].

DIAGNOSIS.—Body and eyes without pigment, latter lacking facets. Rostrum tapering gently from base, lacking marginal spines or tubercles. Areola broad, less than 5 times as long as wide. Cervical spine absent or represented by small tubercle. Central projection of first pleopod of first form male short, not tapering, bearing subapical notch, and directed caudally at angle of about 90 degrees; mesial process directed at angle slightly greater than 90 degrees and extending caudally much beyond tip of central projection.

SIZE.—Carapace length 26.4 mm; postorbital carapace length 20.8 mm.

TYPES.—Holotype, allotype, and "morphotype," USNM 79339, 79340, 79343 (σ I, ϕ , σ II); paratypes, MCZ, USNM.

TYPE-LOCALITY.—Well on farm of R. W. Williams, 2 miles (3.2 km) south of Graceville, Jackson County, Florida, U.S.A.

RANGE.—U.S.A. This crayfish is known from several caves in Jackson County, Florida, and from a single cave in Decatur County, Georgia.

The following localities, unless accompanied by

references or collectors and/or dates, were taken from Franz and Sutton (in press).

Florida. Jackson County: (1) type-locality; (2) Gerard's Cave [= Sam Smith's Cave], 3.8 mi (6.1 km) NW of Marianna, SW 1/4, NE 1/4, Sec. 23, T. 5N, R. 11W (Pylka and Warren, 1958:334); (3) Judge Cave, NW 1/4, SW 1/4, Sec. 35, T. 5N, R. 10W (Warren, 1961:7); (4) Pottery Cave, NW 1/4, NW 1/4, Sec. 27, T. 5N, R. 10W (Warren, 1961:7); (5) Soda Straw Cave, Sec. 2, T. 4N, R. 10W (Warren, 1961:7); (5) Soda Straw Cave, Sec. 23, T. 5N, R. 11W (Warren, 1961:7); (6) Washed-out Cave, Sec. 23, T. 5N, R. 11W (Warren, 1961:7); (7) Cave approximately 300 yards (273 m) from N end of Waddell's Mill Pond, 11 mi (17.6 km) NNW of Marianna, 31 May 1965, F. J. Moore, C. Potter, and F. Hurt, coll.; (8) Honey-Comb Hill Cave, SE 1/4, SE 1/4, Sec. 28, T. 5N, R. 10W; (9) Gerome's Cave; (10) Milton's Well Cave; (11) Rockwell Cave; (12) Vetter Cave; (13) Pool Cave.

Georgia. Decatur County: (14) Climax Cave, 3 mi (4.8 km) N of Climax (Warren, 1961:7).

ECOLOGICAL NOTES.—Although the type series of the species was collected in a bucket from an open well, all subsequent specimens have been taken from caves. The only available information on the cave habitats is that of Pylka and Warren (1958: 334), who indicated that in Gerard's Cave, three pools were present, two of which were about four feet (1.2 m) in diameter, and a third, the extent of which could not be determined, "extends under the wall of the cave and appears to be rather deep." A small swiftly flowing stream coursed between the latter and the opposite wall under which it disappeared. The clear water had a pH of 6 and a temperature of 67.5° F (19.7°C), and the bottom of the pools was covered with a layer of fine silt.

LIFE HISTORY NOTES.—First form males have been collected in September and October. Females with eggs or young have not been observed.

Cambarus (Jugicambarus) setosus Faxon

FIGURE 41

Cambarus setosus Faxon, 1889:237, pl. 1: figs. 1-3, 7, pl. 2: fig. 1; 1890:621, 625-628, 630; 1914:422.—Garman, 1889:235.
—Parker, 1890:155-157, 161.—Packard, 1894:736.—Lönnberg, 1895:4, 5.—Hay, 1899:959, 966; 1902b:436.—Ortmann, 1902:277; 1905a:118, 121, 127.—Steele, 1902:3, 7, 16-20.—Harris, 1903a:606; 1903b:59, 123-126, 134, 145, 153, 162.—Banta, 1907:72.—Graeter, 1909:470.—Spurgeon, 1915: 385-394, figs. 1, 2, 5-8.—Spandl, 1926:95, 96.—Chappuis, 1927:92.—Creaser and Ortenberger, 1933:15, 16, 41, figs. 6, 30.—Wolf, 1934:105.—Hobbs, 1942b:163; 1952:689, 693; 1953:20; 1959:895; 1967b:12; 1976:550.—Jeannel, 1943: 272.—Burbanck, Edwards, and Burbanck, 1948:360, 361, 367.—Hubricht, 1950:17.—Mohr, 1950:6.—Bovbjerg, 1952:52.



FIGURE 40.—Cambarus (Jugicambarus) cryptodytes (a, e-j, holotypic first form male; b, d, morphotypic second form male; c, allotypic female): a, b, mesial view of first pleopods; c, annulus ventralis; d, e, lateral view of first pleopods; f, antennal scale; g, dorsal view of carapace; h, epistome; i, basis and ischium of third pereiopod; j, dorsal view of distal podomeres of cheliped. (After Hobbs and Barr, 1960, figs. 48-57.)

--Derouet, 1953:103.--Pennak, 1953:458.--Williams, 1954: 804, 808, 809, 820, 901-904, 914, figs. 225-232, 234.--Wells, 1957a:639; 1959:3, 5-12, figs. 2, 4, 7, 8.--Lübke, 1958:155.-- Nicholas, 1960:133.—Hobbs and Barr, 1960:13-16, 25-29, 31; 1972:37, 39, 61, 62.—Conant, 1960:32.—Wiens and Armitage, 1961:40.—Hart and Hobbs, 196i:181.—Finger-



FIGURE 41.—Cambarus (Jugicambarus) setosus, from Smallins Cave (a, e-j, first form male; b, d, second form male; c, female): a, b, mesial view of first pleopods; c, annulus ventralis; d, e, lateral view of first pleopods; f, dorsal view of carapace; g, antennal scale; h, epistome; i, basis and ischium of third pereiopod; j, dorsal view of distal podomeres of cheliped. (After Hobbs and Barr, 1960, figs. 37-47.)

- man, et al., 1964:415-421, figs. 1-4.—Vandel, 1964:403, 470, 501, figs. 32, 76; 1965:342, 398, 423, figs. 32, 76.—Poulson, 1964:759.—Hobbs and Bedinger, 1964:9, 14, 15, fig. 3.— Bedinger and Hobbs, 1965:93, 94, fig. 1s.—Larimer, 1966: 204, 205.—Larimer, Trevino, and Ashby, 1966:410, 413.— Reimer, 1966:11; 1969:51, 53, 61, 62, figs. 3, 19, 33.—Barr, 1968:90.—Delamare Deboutteville, 1970, fig. 7c.—Black, 1971:8.—G. Moore, 1972:310.—Bouchard, 1973:105.—D. G. Hart and C. W. Hart, 1974:140.—Peck, 1974c:56.
- Cambarus ayersii Steele, 1902:3, 7, 18-20, 50, 53, pl. 6: fig. 14 [type-locality: Fishers Cave (=Sequiota Cave), Green County, Missouri].—Faxon, 1914:422.—Creaser and Ortenburger, 1933:41.—Hobbs, 1942b:163; 1952:689, 693; 1953: 20.—Burbanck, Edwards, and Burbanck, 1948:361.—Hubricht, 1950:17.—Mohr, 1950:6.—Wells, 1952:613; 1957a:639; 1959:3, 5-12, figs. 1, 3, 5, 6.—Williams, 1954:809, 903, 911.— Duke-Elder, 1958:104, 114 [by implication], 115, 724, 787.— Hobbs and Barr, 1960:27, 31.—Larimer, Trevino, and Ashby, 1966:413.
- Cambarus (Bartonius) setosus.—Ortmann, 1905a:120; 1918:838, 849 [by implication].—Creaser, 1931:6, 7.—Balss, 1955:1311.
- Cambarus (Cambarus) setosus.—Fowler, 1912:341 [by implication].—Ortmann, 1931:95.—Creaser and Ortenburger, 1933: 17.—Hobbs, 1941b:114.—Reimer, 1969:50.
- Cambarus (Bartonius) ayersi.—Ortmann, 1918:838, 849 [by implication].—Balss, 1955:1311.
- Cambarus (Cambarus) ayersi.-Ortmann, 1931:95.
- Cambarus (Bartonius) ayersii.-Creaser, 1931:6, 7.
- Cave crayfish.-Mohr, 1939:202.
- Cambarus (Cambarus) ayersii .- Hobbs, 1941b:114.
- Cambarus ayersi.-Pennak, 1953:458.-Mohr, 1956:38.-Fingerman and Lowe, 1957:165.-Vandel, 1964:470; 1965:398.
- Cambarus (Jugicambarus) setosus.-Hobbs, 1969b:106-108, 139, 142, 143, 161, 162, 166, fig. 19j; 1972b:122, 147, figs. 10c, 87b, 107a; 1974b:19, fig. 66.-Hobbs and Cooper, 1972: 49, 55.-Hobbs III, 1975:276.

DIAGNOSIS.—Body and eyes without pigment, latter lacking facets. Rostrum usually with marginal spines. Areola narrow, greater than 15 times as long as broad and often obliterated at or near midlength. One to several cervical spines present. Central projection of first pleopod of first form male long, somewhat tapering, with shallow subapical notch, and recurved at angle of approximately 120 to 130 degrees; mesial process disposed caudally subparallel to central projection and reaching no farther caudally than latter.

SIZE.—Carapace length 40.5 mm; postorbital carapace length 36.2 mm.

TYPES.—Syntypes, MCZ 4200 (4 d II, φ), MCZ 4201 (3 d I, d II, 4 φ, 4 d juv., 2 φ juv.), MCZ 4202 (2 d II, 3 φ, 3 d juv., 4 φ juv.), USNM 25828 (d II, φ).

TYPE-LOCALITY.—Wilson's Cave [= Whisner Cave], 2 mi (3.2 km) NW of Sarcoxie, near Springfield (Sec. 6, T. 27N, R. 29W), Jasper County, Missouri, U.S.A.

RANGE.—U.S.A. This crayfish occurs in southwestern Missouri and probably in northeastern Oklahoma. Because of a lack of first form males from several of the localities in the area, only tentative determinations of populations in them are possible.

Missouri. Christian County: (1) Smallins Cave, 7.4 mi (11.9 km) SE of Galloway, NW 1/4, SW 1/4, Sec. 12, T. 27N, R. 21W (Creaser and Ortenburger, 1933:41). Dade County: (2) Carrico Cave, SW 1/4, NE 1/4, NW 1/4, Sec. 26, T. 30N, R. 27W, Feb 1964, Jerry D. Vineyard, coll. Green County: (3) Jones Springs, approximately 3.5 mi (5.6 km) E of Springfield, SW 1/4, NE 1/4, Sec. 27, T. 29N, R. 21W, 12 Jun 1951, C. G. Goodchild, coll.; (4) Moore's Cave, 3 mi (4.8 km) SW of Springfield, date ?, Charles E. Mohr, coll.; (5) Sequiota Cave [= Fishers Cave] in the Sequiota State Fish Hatchery, in Galloway (Steele, 1902:18; Williams, 1954:911); (6) Wood Cave, about 2 mi (3.2 km) from Smallins Cave (Burbanck, Edwards, and Burbanck, 1948:363). Jasper County: (7) typelocality; (8) "Wells in central part of Jasper County" (Steele, 1902:16); (9) Downers Cave, Sarcoxie, date?, Byron Marshall, coll.; (10) Cave on Cool Brook, 7 mi (11.2 km) E and 0.5 mi (0.8 km) N of Carthage (Williams, 1954:904); (11) Cave on Cool Brook, 8 mi (12.9 km) E of Carthage (Williams, 1954:904).

Oklahoma. Delaware County: (12) "Cave between Spavinaw and Jay" [= Twin Cave] (Hobbs and Barr, 1960:27). Mayes County: (13) Spring Creek, 5 mi (8.0 km) S of Locust Grove (Hobbs and Barr, 1960:27).

The published record (Williams, 1954:904) from Imboden, Lawrence County, Arkansas, based on material in the Smithsonian Institution collected by Byron C. Marshall, should be considered in error unless confirmed. Mr. Marshall was located at Imboden, and it is probable that the specimens sent to the museum by him were collected in Missouri. The Oklahoma records cited above by Hobbs and Barr, and later by Black (1971:8), are also based on tentative identifications and should be confirmed by securing first form males from these two localities (see Hobbs and Cooper, 1972: 49).

ECOLOGICAL NOTES.—Most of the specimens of this species in collections were taken in Smallins Cave. "This is a large stream cave in which the stream is perennially subject to 'torrential floods.' It is spacious for 600 feet [182 m] beyond which it is necessary to wade in deep rimstone pools frequently floored with gravel" (Bretz, 1956:298).

Few new data have been recorded since the summary of Hobbs and Barr (1960), and most of the following quotations are taken from that publica-

Cambarus sp.-Black, 1971:8 [in part].

tion. William (1954:903) indicated that his specimens were collected in caves in which

the water was clear and cold. Only one of these specimens has been taken in the twilight zone of a cave in the daytime and it was found under a rock. The rest of the collections have been made from pools in the region of total darkness in the daytime, or have been made near the entrance of a cave . . . at night. This is in opposition to the observations recorded by Faxon (1889:237) who stated that *C. setosus* was active in wells and at the mouth of a cave in broad daylight.

Crayfishes in the dark regions of the caves did not seem to be affected by the light of lanterns. Individuals were found resting in open water on the solid rock or mud bottom, and rarely were taken from under cover. All of the specimens were easily picked up by hand, but they swam feebly when disturbed. This again is in opposition to observations recorded by Faxon (1889:237) who reported *C. setosus* as extremely difficult to capture even if the water was only slightly agitated.

Additional notes made by Mr. Robert T. Bray (pers. comm.) on specimens collected in Smallins Cave include the following observations. On 24 April 1949, he collected two specimens; one was taken from a pool about 235 yards (215 m) from the entrance of the cave where "a faint glimmer of light can be seen from the entrance . . ." and this specimen was

neither white nor brown but a sort of mixture of the two. The second specimen was taken from a pool 20 inches [50.8 cm] deep, a few feet farther back than the first. No light from the entrance can be seen at this point The temperature of the water in these pools is 54°F. [12.2°C]. All the crayfish I observed were affected by the light and moved slowly for cover whenever my light was on them." In October, Mr. Bray sent two additional specimens with the following accompanying notes. "Both these specimens were taken in the same pool, just eight feet farther back in the cave from that of last April. The temperature of the water here as well as at the entrance of the cave is 57°F. [13.9°C], in contrast to the 54°F. [12.2°C] recorded last April. So much surface water probably accounts for the three degree rise. Another noteworthy fact is that both these creatures were noticeably more sluggish than those of last spring; they presented no difficulty in capture while those before were quite active and temporarily eluded capture. These two specimens have considerably more pigment than those of before although the cave, at this point, is in perpetual darkness.

The apparent discrepancies in the observations made by Williams and those made by Miss Ruth Hoppin (reported by Faxon) are supported by Bray. It would be interesting to know whether or not these differing responses may be correlated with seasonal, diurnal, or flooding conditions in the cave. The latter is suggested because of the probable lowered mineral content of the water during flooding, and it is at least possible that this might affect the crayfishes. It seems unlikely that the temperature differences observed by Bray are to be correlated with the response of the animals to being disturbed, for if any effect were produced one would expect the animals to be more active at the higher temperature.

Experimental data on response to light obtained by Wells (1959:11-12) permitted the following conclusions.

C. setosus and C. ayersii [= C. setosus] were similar in their responses to light. All specimens examined were photosensitive. No differences in the response patterns were noted with crayfish of different sizes. No sex difference was observed. . . . A response could be measured only when the head of the animal was illuminated [but experiments indicated that the eyes, eyestalks, antennae and antennules do not act as receptors. Wells suggests that] possibly the cerebral ganglion is functioning directly as a photoreceptor in these cave crayfishes. . . . It is suggested that the long wave-length limit of sensitivity for C. setosus and C. ayersii is between $\lambda 6600A$ and $\lambda 7300A$ in the red. The short wave-length limit of sensitivity has not been determined.

Burbanck, Edwards, and Burbanck (1948:367), in testing the tolerance of this species and Cambarus rusticus [probably Orconectes neglectus neglectus (Faxon, 1885c:142)] to lowered oxygen concentrations, found that "the cave and stream crayfish reduced the water to approximately the same oxygen tension—no significant difference between .1978 and .2452 respectively" although C. setosus lived longer, 829.9 \pm 35.0 minutes as opposed to the stream form which lived only 272.3 \pm 21.5 minutes. They concluded that the cave crayfish "seem to have a lower rate of metabolism than the stream crayfish."

Fingerman, et al. (1964:419-421) found that in the eye of C. setosus the lamina ganglionaris and the retinal structures are lacking or exceedingly degenerate; of the three recognized medullae, the medulla interna and externa are much reduced as compared with the medulla terminalis, the only one of the three containing neurosecretory cells. In comparing the neurosecretory cells on the ventral side of the supraesophageal ganglia between the bases of the circumesophageal connectives in three crayfishes, they found a greater similarity between Cambarus (J.) setosus and Orconectes virilis (Cambarinae) than between either and Cambarellus shufeldtii (Cambarellinae). Contrasts were also drawn in their observations with those of Parker (1890).

Larimer (1966:204-205), extending the observations of Wells and Fingerman et al. on the photoreceptors in C. (J.) setosus, made a study of the caudal photoreceptor in vitro along with those of *Procambarus* (S.) clarkii (Girard) and P. (G.) simulans (Faxon). He found that every individual of the three "showed active photoreceptors in its caudal ganglion. Latencies in response to the standard stimulus were approximately equal for the receptors of all three species."

In view of Kennedy's (1963) conclusion concerning the multiple function of the neurons in P. (S.) clarkii serving as photoreceptors as well as interneurons receiving impulses from tactile setae of the caudal region, Larimer (1966:205) stated that "the cephalically-blind cavernicolous crayfish rely on tactile and proprioceptive information for locomotion, orientation and position sense. They may, therefore, have retained the important interneurone functions of the caudal receptors for their positive adaptive value, without loss of the photosensitive properties."

LIFE HISTORY NOTES.—First form males have been collected in February, May, June, August, and October. Females carrying eggs have been photographed (e.g., Mohr, 1939:202), but the photographers, to our knowledge, failed to report the dates.

Cambarus (Jugicambarus) tartarus Hobbs and Cooper

FIGURE 42

Cambarus sp.-Looney and Puckett, 1970:11.-Black, 1971:8, 10 [in part], fig. 7.

Cambarus (Jugicambarus) tartarus Hobbs and Cooper, 1972: 49-55, figs. 1-12.—Hobbs, 1974b:19, fig. 68.—Hobbs III, 1975:276.

DIAGNOSIS.—Body and eyes without pigment, latter lacking facets. Rostrum with or without small marginal tubercles, sometimes tapering to apex without distinct angle at base of acumen. Cervical spine absent. Areola narrow, 15.5 to 17.5 times as long as wide. Central projection of first pleopod, short, not tapering, bearing subapical notch and strongly recurved with tip directed proximally; mesial process directed at angle of approximately 120 degrees and extending caudally beyond tip of central projection. SIZE.—Carapace length 30.4 mm; postorbital carapace length 26.5 mm.

TYPES.—Holotype, allotype, and morphotype, USNM 131951, 131411, 132754 (GI, Q, GI).

TYPE-LOCALITY.—Stansberry-January Cave System, 4 mi (6.4 km) N of Colcord (Sec. 11, T. 21N, R. 22E), Delaware County, Oklahoma, U.S.A.

RANGE.—U.S.A. Known only from the typelocality. The records of *Cambarus* sp. from Jail, Rodman, and Star caves (all in Delaware County, Oklahoma) cited by Black (1971:8) are tentatively assumed to be for this species; however, we have seen no specimen from any of them.

ECOLOGICAL NOTES.—The St. Joe Limestone in which this cave developed belongs to the lower Mississippian System. One of us (Hobbs III) visited the cave and observed that the stream flows with a sluggish to moderate current through pooled areas as much as two meters in depth and over shallow gravel beds. The crayfish were noted to be most abundant on the gravel substrate, either moving about among the rocks or resting beneath slabs of breakdown overlying the gravel. No burrows were noted along the stream and further observations may show that during spates, the crayfish penetrate the hyporheic zone.

LIFE HISTORY NOTES.—First form males have been collected in April and May. Females carrying eggs or young have not been observed.

REMARKS.—An interesting account of the history of the Stansberry-January Cave together with a description and geological and biological notes are presented by Looney and Puckett (1970). They reported the presence of blind crayfish (*Cambarus*) [= C. (J.) tartarus] and the salamander Typhlotriton spelaeus.

Cambarus (Jugicambarus) zophonastes Hobbs and Bedinger

FIGURE 43

- Cambarus zophonastes Hobbs and Bedinger, 1964:9-15, figs. 1, 2, 4-11.—Bedinger and Hobbs, 1965:93-94, fig. 1.— Reimer, 1966:11.—Hobbs and Barr, 1972:1.
- Cambarus (Jugicambarus) zophonastes.—Hobbs, 1969b:107, 108, 139, 142, 143, 161, 166, fig. 19k; 1972b:124, 147, fig. 106d; 1974b:20, fig. 67.—Hobbs and Barr, 1972:3.—Hobbs and Cooper, 1972:49, 55.—Hobbs III, 1975:276.

DIAGNOSIS.—Body and eyes without pigment, latter lacking facets. Rostrum with strongly con-



FIGURE 42.—Cambarus (Jugicambarus) tartarus (a, c, e-l, holotypic first form male; b, e, morphotypic second form male; d, allotypic female): a, b, mesial view of first pleopods; c, lateral view of carapace; d, annulus ventralis; e, f, lateral view of first pleopods; g, dorsal view of carapace; h, epistome; i, basal podomeres of third, fourth, and fifth pereiopods; j, antennal scale; k, caudal view of first pleopods; l, dorsal view of distal podomeres of cheliped.

vergent margins bearing spines. Areola narrow, at least 29 times as long as wide. Cervical spine, if

present, represented by acute tubercle little if any larger than adjacent ones. Central projection of

SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY



FIGURE 43.—Cambarus (Jugicambarus) zophonastes, holotypic first form male (except d from allotypic female): a, mesial view of first pleopod; b, caudal view of first pleopods in situ; c, lateral view of first pleopod; d, annulus ventralis; e, dorsal view of carapace; f, epistome; g, dorsal view of cephalic region; h, dorsal view of distal podomeres of cheliped; i, antennal scale; j, basis and ischium of third pereiopod. (After Hobbs and Bedinger, 1964, pl. 1.)

first pleopod short, strongly tapering to acute apex, lacking subapical notch, and directed caudoproximally at approximately 125 degrees; mesial process extending subparallel to central projection and reaching caudally about same distance.

SIZE.—Carapace length 31.5 mm; postorbital carapace length 28.5 mm.

TYPES.—Holotype and allotype, USNM 108356, 108357 (\Im I, \Im); paratypes, USNM.

TYPE-LOCALITY.—Hell Creek Cave, Stone County, NE 1/4, NE 1/4, Sec. 30, T. 15N, R. 10W, Arkansas, U.S.A.

RANGE.—U.S.A. Known only from the typelocality.

ECOLOGICAL NOTES.—Hell Creek Cave, situated in the Plattin Limestone of Ordovician age, is some 1500 feet (450 m) long as measured along the stream flowing through it. The crayfish were found approximately 150 feet (45 m) from the entrance, an area of perpetual darkness.

Here the stream fills the lower portion of a vertical, jointcontrolled solution channel. The stream is 1 to 1.2 m wide and ranges in depth from 0.3 to 4.3 m, being deepest where the stream enters the water-filled channel.

The temperature of the water, measured on 3 October 1961, was 58°F [14.4°C] and, on 7 November 1961, was 56°F [13.3°C]. Normal flow of the stream is estimated to be about 200 gallons [757 1] per minute. Flow of the stream increases within a short time after rainfall in the vicinity [Hobbs and Bedinger, 1964:13].

The crayfish showed no response to light of lanterns . . . When the water was roiled and became turbid, some specimens crawled up the sides of the stream to clear water near the surface [Bedinger and Hobbs, 1965:94].

LIFE HISTORY NOTES.—First form males have been collected in May, October, and November. An ovigerous female was observed on 25 May 1975 by William W. Deane (pers. comm. from J. F. Payne, Jr., of Memphis State University).

Subgenus Puncticambarus

Subgenus Bartonius Ortmann, 1905a:97 [in part].

Subgenus Cambarus.-Fowler, 1912:341 [in part] [not Erichson, 1846:97].

Subgenus Puncticambarus Hobbs, 1969b:101 [type-species: Cambarus extraneus Hagen, 1870:73].

DIAGNOSIS.—Eyes with pigment. Areola 2.1 to 6.2 times as long as wide, constituting 30.3 to 40.0 percent of entire length of carapace and bearing many moderately deep punctations. Chela elongate, somewhat depressed, and with mesial margin of palm bearing 2 rows of tubercles; neither palm nor fingers with conspicuous setal tufts; fingers with well-defined dorsal longitudinal ridges; fixed finger costate and usually impressed at base, never with conspicuous tuft of setae at mesial base; proximal opposable margin of dactyl never deeply concave. Third pereiopod of male with tubercle on basis opposing hook on ischium.

RANGE.—North America. "From Michigan, Ontario and New York southward, west of the Appalachians, onto the Cumberland Plateau, around the southern flank of the Smokies, and onto the Piedmont and lower slopes of the Blue Ridge to Maryland" (Hobbs, 1969b:133).

NUMBER OF SPECIES.—Ten, only one of which is restricted to subterranean waters.

Cambarus (Puncticambarus) nerterius Hobbs

FIGURE 44

?Cambarus.-Vachon, 1952:111.

Cambarus nerterius Hobbs, 1964:189-194, figs. 1-10.-Hobbs and Hart, 1966:49.-Culver, 1968:18.-D. G. Hart and C. W. Hart, 1974:110.

Cambarus spp.-Culver, 1967:35.

Cambarus (Puncticambarus) nerterius.—Hobbs, 1969b:101, 102, 135, 160, figs. 7, 17n; 1972b:106, 128, 147, figs. 90c, 111b; 1974b:21, fig. 73.—Holt, 1973a:238, 240, 246, 247, 250.— Hobbs and Bouchard, 1973:49, 50.

DIAGNOSIS.—Body pigmented but pale; eyes reduced but with pigment and faceted cornea. Rostrum angular at base of acumen but lacking marginal spines or tubercles. Areola 3.5 to 6.2 times as long as wide. Single cervical spine present on each side of carapace. Central projection of first pleopod of first form male gently recurved, moderately long, tapering and bearing subapical notch; mesial process inflated basally, tapering distally, and reaching only slightly beyond apex of central projection.

SIZE.—Carapace length 52.2 mm; postorbital carapace length 43.7 mm.

TYPES.—Holotype, allotype, and morphotype, USNM 111295, 111296, 111297 (JI, Q, JI); paratypes, USNM.

TYPE-LOCALITY.—Matt's Black Cave, 2 mi (3.2 km) S of Renick, Greenbrier County, West Virginia, U.S.A.

RANGE.—U.S.A. Greenbrier and Elk river basins in Greenbrier and Pocahontas counties, West Virginia. West Virginia. Greenbrier County: (1) type-locality; (2) McClung Cave, 5 mi (8.1 km) N of Lewisburg, lat. 37°52'52"N, long. 80°23'24"W (Hobbs, 1964:194); (3) Luddington Cave, 5 mi (8.1 km) N of Lewisburg, 0.5 mi (0.8 km) from entrance to Matt's Black Cave, lat. 37°53'28"N, long. 80°23'22"W (Hobbs, 1964:194); (4) General Davis Cave, lat. 37°45'20"N, long. 80°33'15"W (Hobbs, 1964:194); (5) McFerrin's Water Cave, lat. 37°56'04"N, long. 80°28'38"W (Hobbs, 1964:194); (6)



FIGURE 44.—Cambarus (Puncticambarus) nerterius (a, b, f-l, holotypic first form male; c, e, morphotypic second form male; d, allotypic female): a, lateral view of carapace; b, c, mesial view of first pleopods; d, annulus ventralis; e, f, lateral view of first pleopods; g, dorsal view of carapace; h, epistome; i, basal podomeres of third, fourth, and fifth pereiopods; j, antennal scale; k, caudal view of first pleopods; l, dorsal view of distal podomeres of cheliped.

Culverson Creek Cave, lat. 37°56'28"N, long. 80°27'10"W, 9 May 1964, S. Sprague, coll.; (7) Fuller's Cave [= Thorny Hollow Cave], about 1 mi (1.6 km) SE of Unus, lat. 37°56'00"N, long. 80°25'38"W, 14 Sep 1968, T. Vigour and D. Newson, coll.; (8) Piercys Mill Cave, lat. 37°50'44"N, long. 80°34'21"W, 13 Aug 1966, J. R. Holsinger, coll.; (9) McLaughlin-Unus Cave, 14 Aug 1966, W. Biggers and J. R. H., coll.; (10) Clyde Cochrane Sink Cave, 12 Aug 1966, W. B. and J. R. H., coll. *Pocahontas County*: (11) My Cave, about 3 mi (4.8 km) N of Slaty Fork, 2 Jun 1966, T. Williams, coll.

ECOLOGICAL NOTES.—All of the specimens were collected from streams (one from a dry stream bed) in the caves listed. In only one locality was a specimen found in an epigean habitat; it was immediately adjacent to the mouth of a cave in a stream issuing from it.

LIFE HISTORY NOTES.—First form males have been collected in June, July, August, and September. A single ovigerous female was found in May. No other data are available.

Genus Orconectes

Astacus.-Rafinesque, 1817:42 [not Fabricius, 1775:413]. Cambarus Erichson, 1846:95 [in part].

Orconectes Cope, 1872a:419 [type-species: Orconectes inermis

- Cope, 1872a:419].
- Camtarus .- Packard, 1888:156 [erroneous spelling].
- Oreonectes .- Lönnberg, 1894:126 [erroneous spelling].
- Camborus.-Williamson, 1899:47 [erroneous spelling].

Cambrus.-Price, 1900:155 [erroneous spelling].

- Orconectis.-Harris, 1903b:113 [erroneous spelling].
- Faxonius Ortmann, 1905a:97 [type-species: Astacus limosus Rafinesque, 1817:42].

G[ambarus].-Ortmann, 1905a:112 [erroneous spelling].

Orconetes .- Wolf, 1934:104 [erroneous spelling].

Faxonicus.---R. S. Fleming, 1938:302 [erroneous spelling].

Cambarrus.-R. S. Fleming, 1939:305 [erroneous spelling].

Fexonius.-Rioja, 1914:193 [erroneous spelling].

Orconecctes .- Williams, 1952:330 [erroneous spelling].

Orconectas .- Villalobos F., 1953:351 [erroneous spelling].

Gambarus.-Croizat, 1958:908 [erroneous spelling].

Orconnectes .- Threinen, 1958:1 [erroneous spelling].

Oronectes .- Bacescu, 1967:218 [erroneous spelling].

Orchonectes.-Dimond, Kadunce, Getchell, and Blease, 1968: 760 [erroneous spelling].

Orconectus .- Ray and Stevens, 1970:58 [erroneous spelling].

Orconeotes .-- Unestam, 1973:4 [erroneous spelling].

Orcenectes .- D. G. Hart and C. W. Hart, 1974:45 [erroneous spelling].

Oroconectes .- Hobbs III, 1975:273 [erroneous spelling].

DIAGNOSIS.—Third maxilliped not enlarged, reaching little, if at all, beyond apex of rostrum, and bearing teeth on mesial margin of ischium. Branchial count 17 + ep. Male with boss on caudomesial angle of coxa of fourth pereiopod; hooks on ischia of third or of third and fourth pereiopods; first pleopods symmetrical and terminating in 2 or rarely 3 parts, none of which bent at right angle to shaft of appendage; shoulder on cephalic surface, if present, situated immediately proximal to base of central projection. Female with annulus ventralis slightly to freely movable and with moderately welldeveloped first pleopods.

RANCE.—North America. From Saskatchewan to Ontario, Canada, and, in the United States, from southwestern Maine southward to Virginia (east of the Appalachians) and from Montana to New Mexico eastward to New York and to the Mobile and Tennessee river basins in Alabama and northwestern Georgia. Also known from the Rogue River Basin in Oregon (probably an introduction). Introduced into Western Europe.

NUMBER OF SPECIES.—Seventy-four species and subspecies of which seven are troglobitic.

Orconectes australis australis (Rhoades)

FIGURE 45

- Cambarus hamulatus.—Mohr, 1939:202 [in part, Wonder Cave].
- Cambarus (Faxonius) pellucidus australis R. Rhoades, 1941: 142-145, 148, fig. 35.
- Orconectes pellucidus australis.—Hobbs, 1942a:353; 1948a:16, 19, 20, figs. 6, 13; 1948b:85; 1967b:8, 9, 12, 15; 1969b:120, 130.—R. Rhoades, 1944:117, 121; 1962:65, 69, 79, 92.— Eberly, 1958:3; 1960:30.—Barr, 1960:6; 1961:32, fig. 10.— Fingerman and Mobberly, 1960:44-45.—Nicholas, 1960:133; 1969:14.—Hart and Hobbs, 1961:175, 176, 178 [in part].— Jegla, Poulson, and Cooper, 1965:639.—C. W. Hart and D. G. Hart, 1966:8.—Larimer, Trevino, and Ashby, 1966: 410-413.—Cooper, 1967:14.—Jones and Varnedoe, 1968:2.— M. R. Cooper, 1969:203, 206, fig. 1.—Cooper and Cooper, 1969:28; 1970:22-23.—Hobbs and Barr, 1972:12, 13, 22, 32, 41, 63.—D. G. Hart and C. W. Hart, 1974:115.
- Orconectes (Orconectes) pellucidus australis.—Hobbs, 1942b: 154 [by implication].
- Cambarus.-Jeannel and Henrot, 1949:24.-Hobbs and Barr, 1972:12.
- Cambarus pellucidus australis.—Jeannel and Henrot, 1949: 84.—R. Rhoades, 1959:399.—Hobbs and Barr, 1972:2, 12, 51, 63.
- Orconectes pellucidus.—Pennak, 1953:458 [in part].—Eberly, 1958:1, 2 [in part]: 1960:29, 30 [in part].—Barr, 1960:5 [in part].—Smalley, 1961:129.—Poulson, 1964:757.—Moore and Nicholas, 1964:71 [in part].—Cooper, 1966:97.—Hobbs, 1967b:12 [in part].—Hobbs and Barr, 1972:12, 22, 40-41 [in part].
- Orconectes (Orconectes) pellucidus.-Hobbs, 1959:890 [in part].-Hobbs and Barr, 1972:12, 51.



FIGURE 45.—Orconectes australis australis, from Blind Fish Cave (a, c, f-m, first form male; b, e, second form male; d, female): a, b, mesial view of first pleopods; c, lateral view of carapace; d, annulus ventralis; e, f, lateral view of first pleopods; g, antennal scale; h, epistome; i, lateral view of carapace; j, dorsal view of carapace; k, caudal view of first pleopods; l, ventral view of thoracic region; m, dorsal view of distal podomeres of cheliped. (After Hobbs and Barr, 1972, fig. 3.)

- Orconectes pellucidus pellucidus.—Hart and Hobbs, 1961:176, 178, 180, 184 [in part].—C. W. Hart and D. G. Hart, 1966: 9.—Hobbs and Barr, 1972:12.
- Orconectes pellucidus subspecies.—R. Rhoades, 1962:69 [in part].—Hobbs and Barr, 1972:14 [in part].
- Colorless crayfish.—Tarkington, Varnedoe, and Veitch, 1965, map 6.

Troglobitic crayfish.—Conrad, 1966, photograph on cover.

Orconectes australis australis.—Barr, 1967a:161 [by implication].—Hobbs, 1969b, fig. 4; 1972b:78, 148, figs. 11a, 60c, 61b; 1974b:26-27, fig. 97.—Hobbs and Barr, 1972:2, 3, 4, 8-11, 22, 23, 27, 29, 31, 34, 35, 81, 83, figs. 2, 3, 50-v, 6, 7, 8i-cc.—Holt, 1973a:229, 231, 246, 248.—D. G. Hart and C. W. Hart, 1974:71, 74, 82, 115.—Mathews, Bosnak, Tennant, and Morgan, 1975:67-68.—Hobbs III, 1975:276, 296 [by implication], fig. 2.

Orconectes .- Barr, 1968:85 [in part].

- Blind crayfish.—Jones and Varnedoe, 1968:11, 18, 31.— Nicholas, 1970:22, illustrated.
- White crayfish.—Jones and Varnedoe, 1968:45, 79.—Graham, 1969:4.—Hobbs and Barr, 1972:13.
- Cave crayfishes.—Cooper, 1968a:34 [in part].
- Orconectes Pellucidus.—Cooper and Poulson, 1968:130, fig. 8. Crayfish.—Torode, 1968:152; 1969:16.—Powell, 1970:238 [in
- part].-Hobbs and Barr, 1972:13.
- Orconectes australis.—Barr and Holsinger, 1971:115 [in part].—Hobbs and Barr, 1972:4, 8-10, 13, 14, 29, 35, 65 [in part].

Troglobitic crayfishes.—Cooper and Cooper, 1971:30.—Hobbs and Barr, 1972:10 [in part].

Cambarus pellucidus .-- Hobbs and Barr, 1972:51 [in part].

DIAGNOSIS.—Hobbs and Barr (1972:14):

Albinistic; eyes reduced and without pigment; rostrum with marginal spines or tubercles; . . . 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; . . . hooks on ischiopodites of third, and sometimes fourth pereiopods [of males]. First pleopod of firstform 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; noncorneous 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.

SIZE.—Carapace length 48.0 mm; postorbital carapace length 39.0 mm.

TYPES.—Holotype, allotype, and "morphotype," USNM 79363, 79364, 79365 (3I, 9, 3II); paratypes, RR, ANSP, MNHA, L. Hubricht.

TYPE-LOCALITY.-Shelta Cave, Madison County

(SE 1/4, NE 1/4, Sec. 27, T. 3S, R. 1W), Alabama, U.S.A.

RANGE.—U.S.A. Orconectes a. australis ranges through the limestones of Mississippian Age from the northern tributaries of the Tennessee River in Jackson and Madison counties, Alabama, northnortheastward on the western edge of the Cumberland Plateau to Fentress County, Tennessee, and Wayne County, Kentucky, where it intergrades with O. a. packardi.

The following localities, unless accompanied by references or names of collectors and/or dates, were taken from Hobbs and Barr (1972:17–18).

Alabama. Jackson County: (1) Limrock Blowing Cave, SW 1/4, SE 1/4, NW 1/4, Sec. 11, T. 4S, R. 4E; (2) Doodle Bug Hole [= Blowing Cave], SE 1/4, NW 1/4, NE 1/4, Sec. 30, T. 1S, R. 4E (C. W. Hart and D. G. Hart, 1966:8); (3) Saltpeter Cave, NW 1/4, SE 1/4, SW 1/4, Sec. 16, T. 3S, R. 3E (R. Rhoades, 1941:145); (4) Kennamer Cave, SW 1/4, NW 1/4, SE 1/4, Sec. 27, T. 4S, R. 3E; (5) Salt River Cave, NW 1/4, NE 1/4, NW 1/4, Sec. 2, T. 1S, R. 6E; (6) McFarland Cave, NW 1/4, NW 1/4, NW 1/4, Sec. 22, T. 3S, R. 3E (R. Rhoades, 1941:145); (7) Paint Rock Cave, NE 1/4, SE 1/4, SW 1/4, Sec. 29, T. 4S, R. 3E; (8) Guess Creek Cave, SE 1/4, SW 1/4, SE 1/4, Sec. 22, T. 3S, R. 4E; (9) Jess Elliott Cave, NE 1/4, NE 1/4, NE 1/4, Sec. 31, T. 1S, R. 6E; (10) Doug Green Cave, NW 1/4, SW 1/4, SW 1/4, Sec. 9, T. 2S, R. 4E; (11) Bell Spring Cave, SE 1/4, SE 1/4, NE 1/4, Sec. 9, T. 2S, R. 6E; (12) Fern Cave, SE 1/4, SE 1/4, SE 1/4, Sec. 21, T. 4S, R. 3E (C. W. Hart and D. G. Hart, 1966:8); (13) Borderline Cave, SE 1/4, NE 1/4, NW 1/4, Sec. 17, T. 2S, R. 3E; (14) Larkins Cave, SE 1/4, NW 1/4, NE 1/4, Sec. 27, T. 4S, R. 4E; (15) Sauta Cave [= Blowing Cave], SW 1/4, NE 1/4, SE 1/4, Sec. 7, T. 5S, R. 5E; (16) Canyon Cave, NW 1/4, NE 1/4, SE 1/4, Sec. 36, T. 4S, R. 3E; (17) Donna's Pit Cave, NE 1/4, SE 1/4, NE 1/4, Sec. 9, T. 3S, R. 3E, Nov 69, J. Wilson, coll.; (18) Cedar Trough Cave, SE 1/4, SE 1/4, NW 1/4, Sec. 7, T. 2S, R. 7E, May 1970, R. C. Graham, coll.; (19) Beanfield Cave, NW 1/4, SE 1/4, SE 1/4, Sec. 22, T. 2S, R. 4E, Oct 69, R. C. G., coll.; (20) House of Happiness Cave, 4 mi (6.4 km) WSW of Scottsboro, NE 1/4, SW 1/4, NW 1/4, Sec. 4, T. 5S, R. 5E, 1 Sep 1968, S. B. Peck, coll.; (21) Crowson Cave, SE 1/4, SW 1/4, NE 1/4, Sec. 28, T. 2S, R. 3E, 4 Jul 1969, W. W. Torode, coll.; (22) Engle Double Pit, SE 1/4, NE 1/4, SW 1/4, Sec. 15, T. 3S, R. 3E, 3 Jan 1968, R. C. G., coll.; (23) Pack Rat Cave, Hambrich Sinks, SE 1/4, NE 1/4, NE 1/4, Sec. 9, T. 2S, R. 3E, 2 Jan 1942, W. B. Jones, coll.; (24) Pig Pen Cave, 2 mi N of Woodville, NW 1/4, SE 1/4, NE 1/4, Sec. 36, T. 4S, R. 3E, Oct 68, W. W. T., coll. Madison County: (25) type-locality; (26) Sadler Spring Cave, NE 1/4, SW 1/4, NE 1/4, Sec. 3, T. 4S, R. 1E (R. Rhoades, 1941: 145); (27) Hering Cave [= Cave Spring Cave], NW 1/4, NW 1/4, NE 1/4, Sec. 10, T. 5S, R. 2E (R. Rhoades, 1941:144); (28) Aladdin Cave, NW 1/4, NE 1/4, SW 1/4, Sec. 30, T. 2S, R. 3E; (29) Burwell Cave, SE 1/4, SW 1/4, NW 1/4, Sec. 36, T. 2S, R. 2W; (30) Huntsville Cave [= Big Spring Cave], NW 1/4, SW 1/4, SW 1/4, Sec. 36, T. 3S, R. 1W (R. Rhoades, 1941:144); (31) Fuqua Spring Cave, SW 1/4, NE 1/4, NW 1/4, Sec. 15, T. 1S, R. 2E; (32) Byrd Spring Cave, SE 1/4, NW 1/4, NE 1/4, Sec. 25, T. 4S, R. 1W; (33) Matthews Cave, SE 1/4, NW 1/4, SW 1/4, Sec. 12, T. 4S, R. 2W; (34) Cold Spring Cave, SE 1/4, SW 1/4, NE 1/4, Sec. 28, T. 3S, R. 1E; (35) Huskey Cave, SW 1/4, SE 1/4, NE 1/4, Sec. 17, T. 3S, R. 1W, 12 Aug 1970, W. W. T., coll.

Tennessee. Coffee County: (36) Blowing Cave, 4-5 mi (6.5-8 km) N of Tullahoma, lat. 35°25'34"N, long. 86°11'53"W, 20 Jan 72, W. W. Barnes, coll. Fentress County: (37) Buffalo Cave, lat. 36°22'35"N, long. 84°57'36"W; (38) Sells Cave, lat. 36°33'25"N, long. 85°00'24"W; (39) Wolf River Cave, lat. 36°31'58"N, long. 84°56'38"W. Franklin County: (40) Wet Cave, Rowark Cove, lat. 35°13'47"N, long. 85°55'13"W; (41) Walker Spring Cave, lat. 35°13'36"N, long. 85°54'57"W; (42) Caroline Cove Cave, lat. 35°03'54"N, long. 86°07'41"W; (43) Partin Spring Cave, lat. 35°15'56"N, long. 85°52'50"W. Grundy County: (44) Big Mouth Cave, lat. 35°19'58"N, long. 85°49'36"W (Hart and Hobbs, 1961:178); (45) Wonder Cave, lat. 35°16'24"N, long. 85°50'59"W; (46) Bear Cave [= Bear Hole], lat. 35°27'07"N, long. 85°34'48"W; (47) Crystal Cave, lat. 35°16'25"N, long. 85°51'15"W. Overton County: (48) Raven Bluff Cave, lat. 36°29'33"N, long. 85°21'36"W; (49) Sheep Cave, lat. 36°12'41"N, long. 85°11'38"W. Putnam County: (50) Bridge Creek Cave, lat. 36°02'12"N, long. 85°16'25"W; (51) Blind Fish Cave, lat. 36°03'19"N, long. 85°20'31"W (Hart and Hobbs, 1961:175); (52) Johnson Saltpeter Cave, lat. 36°04'19"N, long. 85°19'54"W. Warren County: (53) Cumberland Caverns, lat. 35°40'09"N, long. 85°40'51"W; (54) Turkeyscratch Cave, lat. 35°44'23"N, long. 85°36'00"W; (55) Hubbards Cave, lat. 35°32'55"N, long. 85°40'10"W, Dec 1975, M. D. Tuttle, coll. White County: (56) Indian Cave, lat. 35°49'01"N, long. 85°31'14"W; (57) Wildcat Cove Cave, lat. 35°56'38"N, long. 85°25'25"W; (58) Ward Cave [= Dairy House Cave], lat. 35°56'32"N, long. 85°27'03"W; (59) Ross Cave, exact location unknown.

ECOLOGICAL NOTES.—Orconectes a. australis is most frequently found in pooled areas of moderately fast flowing subterranean streams, but it is often observed moving about on gravel and rocky substrates of more rapidly flowing sections of stream passages. Hobbs and Barr (1972:21) indicated that in Blind Fish Cave this species occurs "in a wide, deep, and slowly moving stream, rather than a small underground brook of the type found in the other caves." Also, Cooper (1966:97) reported that this crayfish is the largest "and by far the most numerous macroscopic organism in the aquatic community" of Shelta Cave, where water is pooled considerably and lacks any definable flow. R. Rhoades (1941:144) stated that according to Dr. Walter B. Jones, "the presence of crayfishes in caves seems to be correlated with the presence of blind fishes and aquatic insects. In caves without connections with the surface, food chains develop among the animals present." In 1962 (p. 92), Rhoades pointed out that "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."

LIFE HISTORY NOTES.—From Hobbs and Barr (1972:21–22):

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.

REMARKS.—Further details of the biology of this species are available in J. E. Cooper's dissertation (1975). Parts of this study are being prepared for publication.

Orconectes australis packardi Rhoades

FIGURE 46

- Orconectes pellucidus packardi R. Rhoades, 1944:113, 115, 117, 121-122, fig. 3a-f; 1962:65, 68-69, 79, 90-92, fig. 8.—Hobbs, 1948a:19, 21, figs. 8, 11.—Eberly, 1958:3; 1960:30.—Cole, 1959:81.—Hart and Hobbs, 1961:180.—Cooper and Beiter, 1972:880.—Hobbs and Barr, 1972:2, 12, 22, 63.
- Cambarus pellucidus.—Jillson, 1954:23.—Hobbs and Barr, 1972:51 [in part].
- Orconectes pellucidus.—Eberly, 1958:1, 2 [in part]; 1960:29, 30 [in part].—Barr, 1960:5 [in part].—Moore and Nicholas, 1964:71 [in part].—Hobbs and Barr, 1972:22, 40-41 [in part].
- Orconectes (Orconectes) pellucidus.-Hobbs, 1959:890 [in part].-Hobbs and Barr, 1972:12, 51.
- Orconectes pellucidus packardii.—Nicholas, 1960:133.—C. W. Hart and D. G. Hart, 1966:8, 9.—D. G. Hart and C. W. Hart, 1974:115.
- Orconectes australis packardi.—Barr, 1967a:161, 190, 191.— Hobbs III, 1971a:140, 144; 1975:276, 296 [by implication], fig. 2.—Hobbs and Barr, 1972:2, 4, 8–11, 13, 14, 18, 21–32, 35, 41, 81–83, figs. 2, 4, 5a–n, 8a–h.—Hobbs, 1972b:78, 148, figs. 60d, 61c; 1974b:27, fig. 98.—D. G. Hart and C. W. Hart, 1974:67, 71, 72, 74, 82, 134.
- Orconectes .- Barr, 1968:85 [in part].



FIGURE 46.—Orconectes australis packardi (a, c, j-k, l, holotypic first form male; b, e, "morphotypic" second form male; d, allotypic female): a, b, mesial view of first pleopods; c, lateralview of carapace; d, annulus ventralis; e, f, lateral view of first pleopods; g, antennal scale;h, epistome; i, dorsal view of carapace; j, basal podomeres of third and fourth pereiopods; k,caudal view of first pleopods; l, dorsal view of distal podomeres of cheliped. (After Hobbs andBarr, 1972, fig. 4.)

Orconectes australis.—Barr and Holsinger, 1971:115 [in part].—Hobbs and Barr, 1972:4, 8-10, 35, 65 [in part]. Orconectes pellucidus ssp.—D. G. Hart and C. W. Hart, 1974:115.

DIAGNOSIS.—Hobbs and Barr (1972:23):

Albinistic; eyes reduced and without pigment; rostrum with marginal spines or tubercles; . . . 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; ... hooks on ischiopodites of third pereiopods [of males] 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.

SIZE.—Carapace length 32.0 mm; postorbital carapace length 25.6 mm.

TYPES.—Holotype, allotype, and "morphotype," USNM 81310, 81312, 81311 ($_{\mathcal{O}}$ I, φ , $_{\mathcal{O}}$ II); paratypes, MCZ, USNM, RR.

TYPE-LOCALITY.—Cumberland Crystal Cave [= Sloans Valley Cave] at Sloans Valley, Pulaski County, Kentucky, U.S.A.

RANGE.—U.S.A. This crayfish 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 gene exchange occurs between it and the nominate subspecies.

The following localities, unless accompanied by references or collectors and/or dates, were taken from Hobbs and Barr (1972:27, 29).

Kentucky. McCreary County: (1) Eureka Cave, 0.6 mi (1 km) NNW of Nevelsville (R. Rhoades, 1944:121); (2) Steele Hollow Cave, 1.7 mi (2.7 km) WNW of Bell Farm. Pulaski County: (3) type-locality; (4) Hydens Cave, 1.3 mi (2.1 km) NE of Blue John, about 6 mi (9.7 km) from Sloans Valley (C. W. Hart and D. G. Hart, 1966:8); (5) Old Kentucky Cave, 6 mi (9.7 km) S of Somerset; (6) Pourover Cave, 0.8 mi (1.3 km) ENE of Colo in Happy Hollow; (7) Wind Cave, 5.0 mi (8 km) SE of Somerset (Hart and Hobbs, 1961:180); (8) Baker Cave, near Plato. Rockcastle County: (9) Duvalt Cave, 3 mi (4.8 km) SE of Mt. Vernon; (10) Fletchers Spring Cave, 1.0 mi (1.6 km) N of Sand Springs on Dry Fork; (11) Pine Hill Cave, at Pine Hill on U.S. Hwy. 25 (Hobbs III, 1971a:142); (12) Teamers Cave, 1.2 mi (1.9 km) NE of Mullins (Hart and Hart, 1966:9). *Wayne County:* (13) Blowing Cave, 0.75 mi (1.2 km) SE of Sunnybrook at head of Carpenters Fork; (14) Horse Hollow Cave, 0.75 mi (1.2 km) NW of Parmleysville in Horse Hollow (C. W. Hart and D. G. Hart, 1966:9); (15) Kogers Cave, 2.0 mi (3.2 km) N of Hidalgo on west side of Shearer Valley; (16) Johnson Fork Cave, 0.4 mi (0.6 km) E of Burfield on N side of Johnson Fork.

ECOLOGICAL NOTES.—The only published information is that of R. Rhoades (1944:121) who reported this crayfish to be "abundant in the edges of quiet pools which make up the stream in the upper part of Cumberland Crystal Cave."

LIFE HISTORY NOTES.—First form males have been found in January, February, March, June, August, September, and October. Although no ovigerous females have been observed, a single female carrying young was collected in Old Kentucky Cave on 29 January 1967 (Hobbs and Barr, 1972:32).

Orconectes incomptus Hobbs and Barr

FIGURE 47

- Orconectes pellucidus pellucidus.—Hart and Hobbs, 1961:176 [in part].—C. W. Hart and D. G. Hart, 1966:9.—D. G. Hart and C. W. Hart, 1974:115.
- Orconectes incomptus Hobbs and Barr, 1972:2, 4, 8-11, 32-36, figs. 2, 9.—Hobbs, 1972b:78, 148, figs. 60b, 61a; 1974b:30-31, fig. 99.—Bouchard, 1974:41.—Hobbs III, 1975:276, 296 [by implication], fig. 2.

DIAGNOSIS.—Hobbs and Barr (1972:32):

Albinistic; eyes reduced and without pigment; rostrum devoid of marginal spines or tubercles; . . . 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; . . . well-developed hooks on ischiopodites of third pereiopods only. First pleopod of firstform 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.

SIZE.—Carapace length 24.3 mm; postorbital carapace length 20.0 mm.

TYPES.—Holotype, allotype, and morphotype,



FIGURE 47.—Orconectes incomptus (a, c, f-l, holotypic first form male; b, e, morphotypic second form male; d, allotypic female): a, b, mesial view of first pleopods; c, lateral view of carapace; d, annulus ventralis; e, f, lateral view of first pleopods; g, dorsal view of carapace; h, antennal scale; i, epistome; j, basal podomeres of third and fourth pereiopods; k, caudal view of first pleopods; l, dorsal view of distal podomeres of cheliped. (After Hobbs and Barr, 1972, fig. 9.)

USNM 130299, 130300, 130301 (JI, Q, JII); paratypes, USNM, H. H. H.

TYPE-LOCALITY.—Cherry Cave, lat. 36°28'09"N, long. 85°36'28"W, Jackson County, Tennessee, U.S.A.

RANGE.—U.S.A. This crayfish is known to occur in only four caves on the Eastern Highland Rim in Tennessee.

Tennessee. Jackson County: (1) type-locality; (2) Carter Cave, lat. 36°16'53"N, long. 85°44'10"W (Hart and Hobbs, 1961:176); (3) Haile Cave, lat. 36°20'00"N, long. 85°43'08"W (Hobbs and Barr, 1972:35). Putnam County: (4) Bartlett Cave, lat. 36°13'41"N, long. 85°44'36"W, 31 Jul 1975, sight record by J. R. Holsinger.

ECOLOGICAL NOTES.—Orconectes incomptus has been observed only in relatively shallow pool areas of moderately flowing streams. Substrates varied from calcite crystals covering bottoms of rimstone pools to small gravel. A female was observed apparently feeding on leaf detritus accumulated in a pool in Cherry Cave on 31 March 1970. Haile Cave supports large bat populations (predominantly *Myotis* grisescens) during the summer months, and extensive guano deposits cover the floor of the cave in places (Barr, 1961:275). Undoubtedly this serves as food (directly or indirectly) for numerous cavernicoles including O. incomptus.

LIFE HISTORY NOTES.—A single first form male was collected from the type-locality on 9 August 1959; no ovigerous females or ones with young have been seen.

Orconectes inermis inermis Cope

FIGURE 48

Crawfish.-Stelle, 1864:37.

- Astacus pellucidus.—Cope, 1871a:4; 1871b:368; 1872c:297.— Hobbs and Barr, 1972:36.
- Orconectes inermis Cope, 1872a:409, 410, 419, fig. 116; 1872b:161, 162, 173, 174, fig. 116.—Hagen, 1872:495.— Packard, 1873:94; 1888:39.—Faxon, 1885a:42-43.—Lönnberg, 1894:126; 1895:4, 5.—Hay, 1896:484, 485.—Blatchley, 1897:171.—Hobbs, 1942a:335, 350, 352, pl. 3:figs. 3, 12; 1948a:19, 20, figs. 10, 14; 1974a:14.—Eberly, 1955:281, 282; 1958:3; 1960:30.—Holthuis, 1956b:113, 116.—Crocker, 1957: 13.—R. Rhoades, 1959:399-401 [by implication]; 1962:65.— Creaser, 1962:2, 3.—Fitzpatrick, 1963:60; 1967:141, 142.— Krekeler and Williams, 1966:394.—Barr, 1967a:186; 1967b:481.—Crocker and Barr, 1968:56.—Poulson and White, 1969:974, 975.—Hobbs and Barr, 1972:1, 3, 4, 8-10, 12, 22, 35, 37-43, 47, 48, 51, 52, 58, 60-65 [in part].—Relyea and Sutton, 1975a:173-175.

- Cambarus pellucidus .- Packard, 1872a:30; 1873:94 [in part]; 1888:15, 16, 19, 39-42, 82, 86, 118, 119, 122, 123 [in part]; 1890:393 .- Smith, 1874:639 [in part]; 1875:477 [in part] .-Collett, 1874:305 .- Elrod and McIntire, 1876:226 .- Faxon, 1884:139 [in part]; 1885a:42, 158, 168 [in part]; 1890:621, 626[?], 628[?] [in part]; 1898:647 [in part]; 1914:392.-Sloan, 1888:15.-Hay, 1891:147, 148; 1893:283-286, pl. 14:figs. 1, 3, 4, 7-9, 13, 14; 1896:478, 482-485, 489, fig. 3; 1897:208-210; 1899:959, 966 [in part]; 1902a:230, 235 [in part] .--Ortmann, 1892:11 [in part]; 1902:277-279 [in part]; 1905a:92, 107, 108 [in part]; 1918:838, 848 [in part]; 1931:64 part].-Lönnberg, 1894:126 [in part].-Blatchley, [in 1897:138, 142, 144, 170, 171, 174, 209 [in part] .--? Price, 1900:155 .- Steele, 1902:16 [in part] .- Eigenmann, 1903:169 [in part].-Harris, 1903b:77, 112, 117, 118, 152 [in part].-Banta, 1907:70.-Graeter, 1909:470 [in part].-Osborn, 1912:923 .- Spurgeon, 1915:385-394 [in part] .- Pratt, 1916: 392 [in part]; 1935:455 [in part]; 1948:455 [in part].-Pope, 1926:170.-Spandl, 1926:95, 141 [in part].-Chappuis, 1927: 91, 120 [in part] .- Bolivar and Jeannel, 1931:302 .- Creaser, 1932:336 [in part].-Wolf, 1934:105.-Jeannel, 1943:32, 272 [in part] .- Hobbs and Barr, 1972:37-39, 51, 58, 62 [in part] .--- D. G. Hart and C. W. Hart, 1974:79.
- Eyeless Crawfish .-- Cox, 1872:149 .-- Sloan, 1888:16.
- Blind Crawfish.—Cox, 1872:152, 153.—Smith, 1873:244.— Hovey, 1912:117.—Pope, 1926, fig. 157.—Gurnsey, 1931:22.— Malott, 1949:67.
- Crayfishes .-- Collett, 1879:293.
- Blind crayfishes.-Collett, 1879:362.-Pope, 1926:163, 169.-Hartman, 1973:24.
- Sightless crayfishes.-Collett, 1879:365.
- Orconectes pellucidus .- Cope, 1879:492, 494, 495 [in part], fig. 116 .- Cope and Packard, 1881:879, 881, 882 [in part] .-Packard, 1888:128, 155 [in part], pl. 21: figs. 2[?], 5; pl. 22: figs. 5, 6, 7[?].-Anonymous, 1903:21, 22.-Pennak, 1953:458 [in part].-Eberly, 1955:281, 282 [in part]; 1958:1-6 [in part]; 1960:29-32 [in part] .- Barr, 1960:5 [in part] .-Huheey, 1961:43-45 .- Penn and Fitzpatrick, 1963:793 [in part].-Minckley, 1963:51.-Poulson, 1964:759.-Vandel, 1964:509, 570, 575 [in part]; 1965:429, 483, 486 [in part] .--Jegla, 1964a:81; 1969:135-137.-[?]Mohr and Poulson, 1966:119, 121-123 .- Poulson and Jegla, 1966:98; 1969:195 .-M. C. Moore, 1967a:8; 1971:53.-[?]D. H. Thompson, 1967:46 .- Jegla and Poulson, 1968:273-282, figs. 1-5 .--Poulson and Smith, 1969, fig. 3 .- Powell, 1970:234, fig. 106.—Pengelley and Asmundson, 1971:77.—Hobbs and Barr, 1972:22, 37, 39-41 [in part] .- Hobbs III and Burdsall, 1972:4, 6 [in part], fig. 3.-Hobbs III, 1972b:10 [in part].
- Eyeless creatures .- Hovey, 1880:886.
- Orconectes.-Hovey, 1882:223 [in part].-Hobbs and Barr, 1960:12 [in part].-[?] Mohr and Poulson, 1966:123.-Barr, 1968:85, 90, 95 [in part].
- Cambarus (Orconectes) pellucidus.—Hovey, 1882:222 [in part].—Hobbs and Barr, 1972:37.
- Cambarus pellucidus inermis.—Packard, 1888:41.—Hobbs and Barr, 1972:38.
- Blind crayfish.—Packard, 1888:14, 24.—Sloan, 1888:16.— Garman, 1889:234, 236.—Jordan and Evermann, 1896:706 [in part].—[7] Zeleny, 1906:160.—Pope, 1926:170.—Jackson,


FIGURE 48.—Orconectes inermis inermis, topotypes (a, c, f-l, first form male; b, e, second form male; d, female): a, b, mesial view of first pleopods; c, lateral view of carapace; d, annulus ventralis; e, f, lateral view of first pleopods; g, epistome; h, dorsal view of carapace; i, caudal view of first pleopods; j, ventral view of thoracic region; k, antennal scale; l, dorsal view of distal podomeres of cheliped. (After Hobbs and Barr, 1972, fig. 10.)

- 1948:16; 1953:31; 1955:57.—Berg, 1958:6.—Langhammer, 1958:22 [in part].—Henrisey, 1962:48.—Moore and Reupke, 1963:34, 36.—Anonymous, 1964:114; 1968:48; 1971:2; 1972a:3 [in part].—Gietkowski, 1969:53.—Powell, 1970:126.—Hultman, 1970:62.—Gardner, 1973:82.—D. Miller, 1973:14.
- Eyeless crayfishes .- Sloan, 1888:16.
- Cambarus pellucidus variety inermis.-Hay, 1893:284.
- Cambarus inermis.—Faxon, 1898:647.—Hobbs and Barr, 1972: 38.
- Cambarus pelucidus.--[?] Eigenmann, 1900:228 [erroneous spelling].
- Orconectis inermis.-Harris, 1903b:113 [erroneous spelling].
- Cambarus (Faxonius) pellucidus.—Ortmann, 1905a:107, 108 [by implication]; 1905b:435 [in part]; 1931:64 [in part].— Fage, 1931:373 [in part].
- White crawfish .- A. J. Rhoades, 1905:6.

Cambarus .- Bolivar and Jeannel, 1931:299 [in part], fig. 1.

- Cambarus pellucidus var. testii.—Wolf, 1934:105 [in part].— Hobbs and Barr, 1972:39.
- Cambarus (Fexonius) pellucidus.-Rioja, 1941:193 [erroneous spelling].

Cambarus Pellucidus .-- [?] Jackson, 1942:4.

- Orconectes (Orconectes) inermis.-Hobbs, 1942b:154 [by implication]; 1959:890.-Hobbs and Barr, 1972:40 [in part].
- Cave crayfish.—Mohr, 1949:1.—Berg, 1958:15.—Mohr and Poulson, 1966:91, 92, 120, 123.—Love, Bundy, Nutter and Dishman, 1973:15.—Anonymous, 1974:2.
- Cambarus (Cambarus) pellucidus testii.—Balss, 1955:1311.— Hobbs and Barr, 1972:39.
- Cave crayfishes.-Mumford, 1957:286 [in part].-Hobbs and Barr, 1972:64 [in part].
- Orconectes pellucidus inermis.—R. Rhoades, 1959:401; 1962:68, 81 [in part].—Nicholas, 1960:133.—Hart and Hobbs, 1961:176 [in part].—Hart, 1962:121.—Jegla, Poulson, and Cooper, 1965:639.—Jegla, 1965:647; 1966:345-357.—C. W. Hart and D. G. Hart, 1966:8.—M. R. Cooper, 1969:203, 206, 207, fig. 1.—Jegla and Poulson, 1970:347-354, figs. 1-4.— Hobbs and Barr, 1972:37, 40, 41, 51, 52, 64.—D. G. Hart and C. W. Hart, 1974:14, 115.
- Orconectes (Orconectes) pellucidus.—Hobbs, 1959:890 [in part].
- Orconectes pellucidus pellucidus.—Eberly, 1960:30 [in part].— Rhoades, 1962:90, fig. 8.—Minckley, 1963:47, 74.—Frey, 1965:624 [in part].—C. W. Hart and D. G. Hart, 1966:8 [in part].—Krekeler and Williams, 1966:394.—Hobbs and Barr, 1972:39-41, 51 [in part].
- White crayfish.—Flanders, 1962:18.—Moss, 1963:86.—Rea, 1963:10, 11.—Knight, 1964:13.—Anonymous, 1965c:65.— Carl, 1966:144.—Hosley, 1966:207.—Peterson, 1967:32.— Langenfeld, 1968:120.—Bassett, 1969:11.—Frushour, 1971: 10.—Horton, 1971:100.—Ritter, 1971:63.
- Crayfish.-Fogel, 1964:39.
- Orconectes pellacious.—Anonymous, 1965b:91537 [erroneous spelling].—Hobbs and Barr, 1972:41.
- Orconectes inermis testii.-Barr, 1966:17.-Hobbs and Barr, 1972:41.
- Orconectes sp.--C. W. Hart and D. G. Hart, 1966:8.--D. G. Hart and C. W. Hart, 1974:115.
- Orconectes inermis inermis.—Barr, 1967a:161.—Prins, 1968: 672.—Hobbs III, 1971a:140; 1971b:20, 21; 1972a:37, 39, 40;

1973a:11; 1973b:16, 17; 1973c:58, 59; 1973d:182; 1975:273, 276, 278, 282-292, 296-299, figs. 2, 3; 1976:405-411.-Hobbs, 1972b:79, 148, figs. 11c, 60e, 61d; 1974b:31, fig. 100.-Hobbs and Barr, 1972:2, 4, 9-11, 35-49, 51, 52, 55, 63, 65, 81-83, figs. 1, 10, 12c-z, 13.-Hobbs III and Wells, 1972:126.-Schulze, Whitaker, and Love, 1973:6.-D. G. Hart and C. W. Hart, 1974:72, 79, 141.

- Orconectes "probably O. inermis" .- Barr, 1968:90.
- Troglobitic crayfish .- Mixon, 1971:70.
- Oreonectes inermis inermis.—Hobbs III and Welch, 1972:66 [erroneous spelling].
- Oronectes inermis inermis.—Hobbs III and Wells, 1972:125 [erroneous spelling].
- Orconectes i. inernis.—Hobbs III and Wells, 1972:125 [erroneous spelling].
- Orconectes pellucidus subspecies.—Hobbs and Barr, 1972:14 [in part].

inermis x testii.—Hobbs and Barr, 1972:39, 41, 42, 50, 52, 65. Albinistic crayfishes.—Hobbs and Barr, 1972:60 [in part].

- Troglobitic crayfishes .- Hobbs III, 1973c:59.
- Oroconectes inermis inermis.—Hobbs III, 1975:273 [erroneous spelling].

DIAGNOSIS.—Hobbs and Barr (1972:43):

Albinistic; eye reduced and without pigment; rostrum with marginal spines, tubercles, or at least angular emarginations at base of acumen; 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; 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; noncorneous 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.

SIZE.—Carapace length 36.4 mm; postorbital carapace length 29.2 mm.

TYPES.—Not extant. Topotypes, USNM 131405 (J. Q. J. I.).

TYPE-LOCALITY.—Sibert's Well Cave [not Wyandotte Cave as stated by Cope (1871a:4); see Hobbs, 1942a:355], NE 1/4, SE 1/4, Sec. 28, T. 3S, R. 2E, Crawford County, Indiana, U.S.A.

RANGE.—U.S.A. This crayfish ranges from Green and Hart counties, Kentucky, north-northwestward into Crawford County, Indiana, intergrading with O. *i. testii* northward to Monroe County, Indiana.

The following localities, unless accompanied by

references or collectors and/or dates, were taken from Hobbs and Barr (1972:46-47).

Indiana. Crawford County: (1) Archibald Cave, SE 1/4, NE 1/4, SE 1/4, Sec. 12, T. 3S, R. 1E; (2) Wyandotte Cave (including Crawfish Spring), NW 1/4, SW 1/4, NW 1/4, Sec. 27, T. 3S, R. 2E (Cope, 1871a:4); (3) Sibert's Well Cave [typelocality]; (4) Marengo Cave, SW 1/4, NE 1/4, NW 1/4, Sec. 31, T. 3S, R. 1E (Hay, 1893:284); (5) Wildcat Cave, SW 1/4, SW 1/4, SE 1/4, Sec. 21, T. 3S, R. 2E (Hay, 1893:286); (6) Carter Byrnes Cave, exact location unknown; (7) Everton Cave [= Evaston Cave], NW 1/4, SW 1/4, NE 1/4, Sec. 22, T. 3S, R. 2E (Blatchley, 1897:175); (8) B-B Hole Cave [= Jackson's Secret Cave], NW 1/4, SE 1/4, SW 1/4, Sec. 21, T. 3S, R. 2E (Henrisey, 1962:48). Harrison County: (9) Boone's Mill Cave, SE 1/4, SE 1/4, NE 1/4, Sec. 24, T. 5S, R. 3E (Peterson, 1967:32); (10) Binkley's Cave, W 1/2, NE 1/4, SW 1/4, Sec. 6, T. 4S, R. 3E [not in Crawford County as reported by Hobbs and Barr, 1972:81]; (11) Bradford Cave [= Bedford Cave, Hobbs and Barr, 1972:82], SE 1/4, SE 1/4, SE 1/4, Sec. 3, T. 2S, R. 4E (Packard, 1888:16); (12) Small Cave, 4 mi (6.4 km) NE of Mauckport (Eberly, 1955:281); (13) King's Cave, NE 1/4, SE 1/4, SW 1/4, Sec. 34, T. 3S, R. 4E (Banta, 1907:70); (14) Rhodes Cave [= Bussabarger's Cave], SW 1/4, NE 1/4, NW 1/4, Sec. 29, T. 3S, R. 3E (Collett, 1879:362); (15) Baker Hollow Cave, NW 1/4, SW 1/4, SE 1/4, Sec. 6, T. 3S, R. 3E (Hobbs III, 1975:285); (16) Wallier Cave, SE 1/4, NW 1/4, SW 1/4, Sec. 14, T. 6S, R. 4E (Horton, 1971:100); (17) Widewater Cave, SW 1/4, SW 1/4, SW 1/4, Sec. 25, T. 1S, R. 2E (Hosley, 1966:207). Lawrence County: (18) Blue Spring Cave, SW 1/4, SE 1/4, SW 1/4, Sec. 6, T. 4N, R. 1W; (19) Christmas Pit, SW 1/4, NE 1/4, SW 1/4, Sec. 20, T. 4N, R. 1E (Hobbs III, 1975:286); (20) Shiloh Cave, NW 1/4, SE 1/4, NW 1/4, Sec. 18, T. 5N, R. 1W (Hay, 1893:283); (21) Sullivan Cave, NW 1/4, SW 1/4, SE 1/4, Sec. 20, T. 6N, R. 2W; (22) Donaldson's Cave [including Donaldson's-Bronson's Cave, Mitchell Caves, Shawnee Cave, Twin Cave, and effluent stream from Donaldson's Cave], NW 1/4, NE 1/4, NW 1/4, Sec. 4, T. 3N, R. 1E (Hay, 1893:286); (23) Wagoner Cave, SW 1/4, NE 1/4, NE 1/4, Sec. 19, T. 5N, R. 2W; (24) Harrison Cave, NW 1/4, NE 1/4, SW 1/4, Sec. 16, T. 3N, R. 1W (Hobbs III, 1975:286); (25) Pless Cave, SE 1/4, NE 1/4, SE 1/4, Sec. 5, T. 4N, R. 1W; (26) Connerly's Cave [= Connely's Cave], NE 1/4, SW 1/4, SE 1/4, Sec. 4, T. 3N, R. 2W (Collett, 1874:304); (27) Donnehue's Cave [= Dunnihue's, Donnihue's Cave], SW 1/4, NE 1/4, SE 1/4, Sec. 28, T. 5N, R. 1W (Hay, 1893:286); (28) Down's Cave, exact location unknown (Hay, 1893:286); (29) Hamer's Cave, SE 1/4, SW 1/4, SE 1/4, Sec. 32, T. 4N, R. 1E (Collett, 1874:303); (30) Avoca Spring Cave, NW 1/4, NW 1/4, SW 1/4, Sec. 32, T. 6N, R. 1W (Frushour, 1971:10); (31) Crying Pit Cave, NE 1/4, NE 1/4, NW 1/4, Sec. 34, T. 5N, R. 2W (Bassett, 1969:11); (32) Gyger Bend I Cave, SW 1/4, NE 1/4, SW 1/4, Sec. 21, T. 5N, R. 1W (M. C. Moore, 1967a:8); (33) Hugh's Christian Annex Cave, exact location unknown (Anonymous, 1965c:65); (34) Ilco Cave, SW 1/4, NW 1/4, SE 1/4, Sec. 33, T. 6N, R. 1W (Hobbs III, 1975:286); (35) Kern's Pit, SE 1/4, NE 1/4, SW 1/4, Sec. 11, T. 4N, R. 2W (Hobbs III, 1975:286); (36) Popcorn Spring Cave, NW 1/4, SW 1/4, SE 1/4, Sec. 5, T. 6N, R. 2W (Hobbs

III, 1975:287). Martin County: (37) Chapman Rizer Cave, SE 1/4, NE 1/4, SE 1/4, Sec. 2, T. 3N, R. 3W (Hobbs III, 1975:287). Orange County: (38) Well [= Cave] in Orleans, exact location unknown (Packard, 1888:24); (39) Wesley Chapel Gulf Cave [= Lost River Cave], NE 1/4, NW 1/4, SE 1/4, Sec. 9, T. 2N, R. 1W (Sloan, 1888:15); (40) Cave near Paoli, exact location unknown (Hay, 1893:286); (41) Murray Spring Cave, SE 1/4, NW 1/4, NW 1/4, Sec. 6, T. 1N, R. 1E; (42) Wells Cave, SW 1/4, NW 1/4, SE 1/4, Sec. 15, T. 1S, R. 1E (Hobbs III, 1975:289); (43) Wildcat Cave, NE 1/4, NE 1/4, NE 1/4, Sec. 15, T. 15, R. 1E (Rea, 1963:10-11); (44) Hudelson Cavern [= Brown Cavern], SE 1/4, SW 1/4, NE 1/4, Sec. 14, T. 2N, R. 1W (Malott, 1949:67). Washington County: (45) River Cave [= Wet Clifty Cave], NE 1/4, SE 1/4, SE 1/4, Sec. 14, T. 3N, R. 2E; (46) Endless Cavern [= Dry Clifty Cave], NE 1/4, SE 1/4, SE 1/4, Sec. 14, T. 3N, R. 2E; (47) Fredericksburg Cave, SE 1/4, NW 1/4, SE 1/4, Sec. 4, T. 1S, R. 3E; (48) Trapper's Cave, NE 1/4, SW 1/4, NE 1/4, Sec. 2, T. 1S, R. 3E (Hobbs III, 1975:290); (49) Beck's Mill Cave, SE 1/4, SW 1/4, NW 1/4, Sec. 11, T. 1N, R. 3E (Fogel, 1964:39); (50) Lamplighter Cave, SE 1/4, NW 1/4, NE 1/4, Sec. 14, T. 3N, R. 2E (Hobbs III, 1975:290); (51) Sinking Creek Cave, NW 1/4, SW 1/4, SW 1/4, Sec. 2, T. 1S, R. 2E (Gietkowski, 1969:53); (52) Stillhouse Cave, SE 1/4, Sec. 11, T. 3N, R. 2E (Love, Bundy, Nutter, and Dishman, 1973:15); (53) What's Its Name Cave, near Cave River Valley (D. Miller, 1973:13). [Note: Records of the occurrence of this cravfish in Bartholomew. Brown, and Jefferson counties, Indiana, are based on erroneous citations by Hay, 1893, and/or R. Rhoades, 1959].

Kentucky. Breckenridge County: (54) Cave and stream, 5 mi (8.1 km) W of Big Springs; (55) Bandy Cave, 3.0 mi (4.8 km) S of Irvington; (56) Thornhill Cave, 3 mi (4.8 km) W of Big Springs; (57) Lockard Cave, 3 mi (4.8 km) SE of Bewleyville; (58) Bat Cave, exact location unknown; (59) McCubbins Cave, exact location unknown (Jegla and Poulson, 1968:273). Green County: (60) Brush Creek Cave, 0.8 mi (1.3 km) E of Lobb; (61) Scott Cave, 1.9 mi (3.1 km) ESE of Eve. Hardin County: (62) Bland Cave, 7 mi (11.2 km) W of Sonora; (63) Nelson Cave, 1.5 mi (2.4 km) W of Star Mills. Hart County: (64) Turner Cave, 3.7 mi (6.0 km) SE of Magnolia; (65) Cooch Webb Cave, 0.4 mi (0.6 km) N of Bear Wallow; (66) Rider Mill Cave, 2.5 mi (4 km) N of Priceville; (67) Cub Run Cave, 1.8 mi (2.9 km) W of Cub Run. Meade County: (68) Joe Jones Cave, near lower reaches of Doe Run; (69) Rockhaven Cave in Otter Creek State Park; (70) Shacklett's Cave, SW of Garrett; (71) Lime Kiln Cave, 1.4 mi (2.3 km) NW of Battletown.

ECOLOGICAL NOTES.—Orconectes inermis inermis is a frequent inhabitant of caves in north-central Kentucky and south-central Indiana where, according to Blatchley (1897:209), it "inhabits shallow pools with muddy bottom rather than rapid flowing water." Hobbs III (1973b:17) also noted that it "occurred in greatest numbers where the stream gradient was minimal, where there was a sufficient supply of food (organic detritus), and where the substrate was mud and silt. In areas of low stream gradient the water is commonly pooled and relatively deep, the substrate is mud with a silt cover and quantities of allochthonous detritus." He (1976:411) also indicated that whereas this crayfish was shown to demonstrate a substrate preference for gravel-rocky areas, individuals move from such substrates in search of food. Thus, the need for food in the cave ecosystem overcomes the preference for a substrate on which cover is available.

Packard (1888:24) reported an observation made by Moses N. Elrod on a crayfish procured from a well in Orleans, Orange County, Indiana. This crayfish had been offered and had devoured a troglobitic isopod belonging to the genus Caecidotea, a species that occurs within the same subterranean waters as the crayfish. Apparently this observation, together with those of Putnam (1877:16) on the feeding of Orconectes pellucidus, led Packard to state that the blind crayfish "appears to prefer living small crustacea, and is not omnivorous in its appetite." On the contrary, Hobbs III (1976:408) found, on the basis of analyses of the gut content, that in caves in southern Indiana this crayfish feeds predominantly on plant material washed into the caves following periods of substantial precipitation. In a few caves where populations of isopods and amphipods were comparatively large, analyses of the consumed food indicated that these crustaceans were indeed utilized as food items. Consequently, one must conclude that O. i. inermis is not a strict carnivore, nor is its diet limited to plant material; rather, it is an opportunist that feeds upon virtually any available organic matter, living or dead, including individuals of its own species.

Hay (1891:148) presented the following observations on this crayfish: "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." In 1893 (pages 283-284), he recorded more detailed observations of the population in Shiloh Cave, stating that

when first observed, the crayfish were generally . . . 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. [This has also been observed by one of us (Hobbs III) in members of the population in Pless Cave and Blue Springs Cave, Lawrence County, Indiana.] 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.

Blatchley (1897:209) noted that the crayfish "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." Hay (1893:284) also indicated that they "did not appear to be at all sensitive to the light." Hobbs III (1976:408-409) found that most individuals respond in no noticeable way to light; however, occasional ones are stimulated to greater activity by light and move until they are no longer in a direct beam. These observations are in agreement with Welsh's (1934: 387) report that the caudal light receptor in certain epigean crayfishes "does not function in the perception of direction of illumination."

Using mark-recapture data, Hobbs III (1973b:17) estimated the population of O. *i. inermis* in Pless Cave to be 1623 \pm 216 in the 540 m study area. "Individuals remained in one major area of the streams, with moderate movement both up and downstream. These home ranges of individuals overlap the ranges of other individuals, thus generating competition for food, space, and mating partners."

LIFE HISTORY NOTES.—More data are available concerning the molting, activity, and reproductive cycles of this crayfish than for any of its troglobitic congeners. Most of these data were gathered by Jegla (1964b, 1969) while studying an intergrade population, Orconectes inermis x testii, in Shiloh Cave. He noted that molting within the population is intermittent, not restricted to definite seasons; however, two periods of approximately two-month duration (February-March and August-September) constitute the periods of maximum number of molting individuals. He also reported that the adult male population consists of 60 to 70 percent form II during the summer months and 77 to 97 percent form I during the fall and winter months. Hobbs

and Barr (1972:49) noted that first form males were present in collections made throughout the year except in March and April and indicated their apparent absence during those months was almost certainly due to small sample size of collections made at that time. Jegla (1969) reported an ovarian cycle in females of the Shiloh Cave population, beginning during the early fall, with oviposition occurring during the summer. Mohr and Poulson (1966:91-92) also discussed the reproductive cycle of the same population affixing its basic timing to biological clocks. According to them, however, spring floods trigger ovulation.

A single ovigerous female was found in Donaldson's Cave in June 1924. When it was examined by Hobbs and Barr (1972:49) almost a half-century later, they found 27 eggs either attached to her pleopods or in the container with her. Jegla (1969: 137) reported seeing only four females carrying eggs during the period of his study in Shiloh Cave: one on 30 June, two on 16 August, and one on 20 August, carrying an average of 45 eggs that were 2.0 to 2.5 mm in diameter.

REMARKS.—Further details on the biology of this crayfish are available in Hobbs III (1973e). Parts of this study are in press, and much of the remainder is in preparation for publication.

Orconectes inermis testii (Hay)

FIGURE 49

Cambarus pellucidus inermis. —Faxon, 1885a:83.—Packard, 1888:41.

- Cambarus pellucidus.—Packard, 1888:16 [in part].—Faxon, 1890:621 [in part].—Blatchley, 1897:127, 138, 142, 144, 170, 171, 174.—Ortmann, 1902:277-279 [in part]; 1905a:92, 107, 108 [in part].—Graeter, 1909:470 [in part].—Spurgeon, 1915: 387-394 [in part].—Pratt, 1916:392 [in part]; 1935:455 [in part]; 1948:455 [in part].—Spandl, 1926:95.—Hobbs, 1942a: 352 [in part].—Hobbs and Barr, 1972:38, 39, 50, 51 [in part].
- Blind crayfish.—Garman, 1889:234–236 [in part].—Jordan and Evermann, 1896:706 [in part].—Banta, 1905:853.—?Zeleny, 1906:160.—Anonymous, 1958:11; 1965a:95.—Langhammer, 1958:22 [in part].—Powell, 1961:82, 89.—Backer, 1968:12.— Love, 1972:14.—Hobbs and Barr, 1972:51.—Anonymous, 1972a:3 [in part].—?M. Cox, 1973:3.
- Cambarus pellucidus var. testii Hay, 1891:148.—Spandl, 1926: 95.—Wolf, 1934:105 [in part].—Hobbs and Barr, 1972:39, 50, 51.
- Cambarus pellucidus testii.—Hay, 1893:283, 285-286, pls. 44, 45: figs. 2, 5, 6, 10-12; 1896:478, 484-485, fig. 4; 1897:209; 1899:959, 966.—Faxon, 1898:647; 1914:415.—Harris, 1903a: 606: 1903b:58, 112, 118, 151, 152, 162.—Banta, 1907:69-73.

87, 90.—Spurgeon, 1915:385-394 [in part].—Creaser, 1932: 336.—R. Rhoades, 1941:144; 1959:400-401.—Daggy and Jacobs, [1949]:4.—Hobbs and Barr, 1972:2, 48, 50, 51, 62.

- ?Cambarus pelucidus.—Eigenmann, 1900:228 [erroneous spelling].
- Cambarus pellucidus testi.—Hay, 1902a:233, 235.—Hobbs and Barr, 1972:50.
- Cambarus (Faxonius) pellucidus.—Ortmann, 1905a:97, 107, 108 [in part]; 1905b:435 [in part]; 1918:848 [by implication, in part].
- Cambarus (Faxonius) pellucidus testi.—Ortmann, 1931:64 [by implication].
- Orconectes pellucidus testii.—Hobbs, 1942a:352 [by implication]; 1948a:19, 20; 1967b:12.—R. Rhoades, 1944:117.— Eberly, 1954:59; 1955:281-282; 1958:3; 1960:30.—Holthuis, 1964:43.—C. W. Hart and D. G. Hart, 1966:8.—Hobbs and Barr, 1972:12, 40, 50-52.—D. G. Hart and C. W. Hart, 1974:115.
- Orconectes (Orconectes) pellucidus testii.—Hobbs, 1942b:154 [by implication].
- Cave crayfish.-Mohr, 1949:1.
- Orconectes pellucidus.—Pennak, 1953:458 [in part], fig. 286.— Eberly, 1958:1, 2 [in part]; 1960:29, 30 [in part].—Barr, 1960:5 [in part].—Arnold, 1961:50.—?M. C. Moore, 1967b: 25; 1971:53.—?D. H. Thompson, 1967:46, 47.—Hobbs and Barr, 1972:22, 40-41, 50, 51 [in part].—Hobbs III, 1972b:10 [in part].
- Cambarus (Cambarus) pellucidus testii.—Balss, 1955:1311.— Hobbs and Barr, 1972:39.
- Cave crayfishes .- Mumford, 1957:286 [in part].
- Orconectes (Orconectes) pellucidus.-Hobbs, 1959:890 [in part].-Hobbs and Barr, 1972:12, 51 [in part].
- Orconectes pellucidus inermis.—R. Rhoades, 1959:401-402 [in part]: 1962:68, 79, 90 [in part].—Nicholas, 1960:133 [in part].—Hart and Hobbs, 1961:176 [in part].—Hobbs and Barr, 1972:51, 52 [in part].
- White crayfish .- Flanders, 1963:48.
- Photograph.-Stenuit and Jasinski, 1964:75 [1966:75].
- Orconectes pellucidus pellucidus.-Krekeler and Williams, 1966:394.
- Orconectes .- Barr, 1968:85 [in part].
- Orconectes pellucidus subspecies.—Hobbs and Barr, 1972:14 [in part].
- Orconectes inermis testii.—Hobbs, 1972b:79, 148, figs. 60f, 61e; 1974b:31, fig. 101.—Hobbs III, 1972a:37, 39, 40; 1973a:12; 1973b:16, 17; 1973c:58, 59; 1973d:182; 1975:277, 280, 284-291, 293, 296-299, figs. 2, 3; 1976:405-411.—Hobbs and Barr, 1972:2, 4, 5, 10, 11, 14, 35, 38, 39, 42, 43, 48-58, 64, 81, figs. 1, 11, 12a,b.—Holt, 1973a:236, 246, 248, 250.
- Orconectes inermis.-Hobbs and Barr, 1972:42, 47, 55, 65 [in part].
- Orconectes (Orconectes) inermis.—Hobbs and Barr, 1972:40 [in part].
- Troglobitic crayfishes .- Hobbs III, 1973c:59.

DIAGNOSIS.—Hobbs and Barr (1972:52):

Albinistic; eyes reduced and without pigment; rostrum without marginal spines or tubercles, acumen not delimited at base from remainder of rostrum; . . . postorbital ridges terminating cephalically without tubercles or spines;



FIGURE 49.—Orconectes inermis testii, topotypes (a, c, f-l, first form male; b, e, second form male; d, female): a, b, mesial view of first pleopods; c, lateral view of carapace; d, annulus ventralis; e, f, lateral view of first pleopods; g, antennal scale; h, epistome; i, dorsal view of carapace; j, basal podomeres of third and fourth pereiopods; k, caudal view of first pleopods; l, dorsal view of distal podomeres of cheliped. (After Hobbs and Barr, 1972, fig. 11.)

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; . . . hooks on ischiopodites of third and fourth pereiopods [of male]. 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.

SIZE.—Carapace length 30.8 mm; postorbital carapace length 26.2 mm.

TYPES.—Syntypes, USNM 17702 (2σ II, ♀), MCZ 7431 (σ II, ♀).

TYPE-LOCALITY.—Mayfield's Cave, SW 1/4, NE 1/4, SW 1/4, Sec. 26, T. 9N, R. 2W, Monroe County, Indiana, U.S.A.

RANGE.—U.S.A. This crayfish is restricted to the subterranean waters of Monroe, Owen, and Greene (?) counties, Indiana. It intergrades with the typical subspecies in the more southern counties of the State.

Indiana. Monroe County: (1) type-locality; (2) Carmichael Cave, NW 1/4, NW 1/4, SW 1/4, Sec. 19, T. 7N, R. 1W (Hobbs and Barr, 1972:55); (3) Eller's Cave, NW 1/4, NW 1/4, SW 1/4, Sec. 15, T. 8N, R. 2W (Blatchley, 1897:141); (4) Hendricks Cave, SW 1/4, NW 1/4, SE 1/4, Sec. 5, T. 8N, R. 2W, 2 Oct 1972, H.H.H. III and J. Keith, coll.; (5) May's Cave, SW 1/4, SE 1/4, NE 1/4, Sec. 24, T. 8N, R. 2W (Eberly, 1955:281); (6) Reeve's Cave, SW 1/4, SW 1/4, NE 1/4, Sec. 34, T. 8N, R. 2W (Hobbs and Barr, 1972:55); (7) Salamander Cave, SW 1/4, SW 1/4, NW 1/4, Sec. 9, T. 8N, R. 2W (Hobbs and Barr, 1972:55); (8) Shaft Cave, NE 1/4, NE 1/4, SE 1/4, Sec. 8, T. 8N, R. 2W (Hobbs and Barr, 1972:55); (9) Truitt's Cave, SW 1/4, SW 1/4, SE 1/4, Sec. 4, T. 8N, R. 2W (Hay, 1891:149); (10) Goode's Cave, SE 1/4, NW 1/4, SE 1/4, Sec. 34, T. 8N, R. 2W (Powell, 1961:82); (11) Ranard School Cave, NE 1/4, NE 1/4, NW 1/4, Sec. 29, T. 9N, R. 2W (Powell, 1961:89); (12) Brinegar's Cave, NW 1/4, NW 1/4, NE 1/4, Sec. 20, T. 8N, R. 2W (Hobbs III, 1975:287); (13) Buckner's Cave, NE 1/4, SW 1/4, SE 1/4, Sec. 17, T. 8N, R. 2W (Love, 1972: 14); (14) Matlock's Cave, NE 1/4, SE 1/4, NE 1/4, Sec. 28. T. 9N, R. 1W (Hobbs III, 1975:288); (15) Saltpeter Cave, SW 1/4, SE 1/4, NW 1/4, Sec. 15, T. 8N, R. 2W (Hobbs III, 1975:288); (16) Smith Spring Cave [= Nudist Cave], SW 1/4, Sec. 2, T. 7N, R. 2W (Hobbs III, 1975:289); (17) Strong's Cave, NW 1/4, SE 1/4, NE 1/4, Sec. 34, T. 9N, R. 2W (Hobbs III, 1975:289); (18) Wayne's Cave, NE 1/4, SE 1/4, NE 1/4, Sec. 17, T. 8N, R. 2W (Arnold, 1961:50). Greene County: (19) Ray's Cave, SE 1/4, NE 1/4, NW 1/4, Sec. 13, T. 7N, R. 4W (M. C. Moore, 1967b:25, sight record). Owen County: (20) Porter's Cave, NE 1/4, SE 1/4, SE 1/4, Sec. 33, T. 12N, R. 2W (Cox, 1973:3, sight record); (21) Sexton Spring Cave [= Deckard or Jones Cave], SW 1/4, SE 1/4, NE 1/4, Sec. 36, T. 7N, R. 3W, 28 Nov 1970, H.H.H. III and M. Moore, coll.

ECOLOGICAL NOTES.—The most comprehensive account of this subspecies available is that of Banta (1907:70-71) in which he made an exhaustive study of the inhabitants of Mayfield's Cave, Monroe County, Indiana.

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 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. (Erebicambarus) laevis Faxon] 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 it[s] 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 cravfish.

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 [sic] 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.

As to the food of *C. pellucidus testii* within the cave, very little has been found out. In captivity it will eat flesh of almost any animal. It does not thrive as well on beef, how-

ever, as does *C. bartoni*, nor does it eat as much. In the cave its food must be very scanty. It certainly could not catch a blind fish, and it seems scarcely likely that it would ever be able to catch the relatively small and active amphipods. The isopods are less active, but are very small to serve as food for so large an animal, which at best could probably catch very few of them. While some decaying organic matter is being continually brought into the cave through sink-holes, it is carried in quantity only at time of high water.

Hobbs III (1973b:17) reported the population in Mayfield's Cave to be 128 ± 33 in the 300 m study area (major stream passage) or 13 crayfish per 30 m. Home ranges of individuals overlap, thus population pressures are exerted as the individuals compete for space, food, and mates.

LIFE HISTORY NOTES.—According to Banta (1907:71), whose observations on molting were made on animals maintained in the laboratory, O. inermis testii molts "two to four or five times a year depending upon the size, the smaller or younger ones molting oftener."

Hobbs and Barr (1972:58) reported that first form males have been collected during the months of January, February, October, and November. No ovigerous females or those carrying young have been reported in the literature, but Banta (1907:72) stated that "very young individuals were seen during February and March, the earliest date being February 17... and at no other time of the year."

REMARKS.—Further details concerning the biology of this species are available in Hobbs III (1973e). Parts of this study are in press, and much of the remainder is in preparation for publication.

Orconectes pellucidus (Tellkampf)

FIGURE 50

- Krebse.-Anonymous, 1843a:49.
- Astacus Bartoni?.—Anonymous, 1843b:175 [not Fabricius, 1798:407].—Putnam, 1872:10.—Hobbs and Barr, 1972:59, 60.
- Astacus pellucidus Tellkampf, 1844a:684; 1844b:383; 1845: 85.—Erichson, 1846:87, 89.—Gibbes, 1850:195.—Dana, 1852a: 522.—Newport, 1855:164, 165, figs. 11-14.—Lucas, 1864:iv.— Hagen, 1870:6, 7, 11.—Faxon, 1885a:10.—R. Rhoades, 1944:112; 1959:399.—Holthuis, 1956b:116.—Hobbs and Barr, 1972:1, 42, 59, 60, 64.
- Cray-fish.-W. M. Thompson, 1844:111-112.
- astacus pellucidus.-Tellkampf, 1845:93.
- Astacus (Cambarus) pellucidus.-Erichson, 1846:95-96.
- Craw-fish .- Silliman, 1851:336.
- Cambarus pellucidus.—Girard, 1952:87, 88.—Hagen, 1870:8, 27, 30-34, 55-56, 97, 101, pl. 1: figs. 68-71, pl. 3: fig. 148, pl. 6; 1872:494-495.—Packard, 1871:750, 751, fig. 131; 1872b:17,

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18, fig. 131; 1873:94 [in part]; 1874:209; 1879:315, fig. 268; 1886:295-297, figs. 263, 264; 1888:8, 10, 12, 19, 38-42, 82, 86, 110, 111, 119, 122, 123, 125, 127 [in part]; 1890:393 [in part].-Cope, 1872a:410; 1879:495.-Smith, 1874:639 [in part]; 1875:477 [in part].-Putnam, 1875a:222; 1875b:198; 1877:16-19.-Hubbard, 1880:38.-Joseph, 1882:12.-Leydig, 1883:38-40 .- Faxon, 1884:139-140 [in part]; 1885a:4, 5, 7-9, 11, 16, 18, 19, 40-46, 59, 82-84, 111, 158, 169, 174, 178, 179 [in part]; 1885b:358; 1890:626, 628; 1898:647 [in part]; 1914:415 [in part], pl. 7: fig. 2a-c.-Underwood, 1886:371 [in part].-Garman, 1889:235, 236; 1924:88, 89.-Parker, 1890:153-155, 157-161, pl. 1: figs. 2-6.-Hovey, 1891:72; 1912:80, 81, 108, 109, 115, 119, 124, 2 figs.-Ortmann, 1892: 11 [in part]; 1902:277-279 [in part]; 1905a:92, 95, 96 [in part]; 1918:838, 848 [in part].-Cunningham, 1893:537.-Stebbing, 1893:208.-Lönnberg, 1894:126; 1895:4-6, 9.-Hay, 1896:485 [in part]; 1897:208-209 [in part]; 1899:959, 966 [in part]; 1902a:226, 228, 230, 235 [in part]; 1902b:436.-Call, 1897:103, 104; 1901:103, 104.-Eigenmann, 1899:60; 1903:169 [in part] .--- ?Price, 1900:155 .-- Steele, 1902:7, 16, 18 [in part].-Harris, 1903a:602, 606; 1903b:58, 67, 70, 80, 112-118, 151, 153, 157, 162, 167 [in part].-Bell, 1906:300, 304, 305 .- Banta, 1907:69-73, 102, 103 [in part] .- Graeter, 1909: 470 [in part] .- Osborn, 1912:923 [in part] .- Spurgeon, 1915: 385-394 [in part] .- Pratt, 1916:392 [in part], fig. 623; 1935:455 [in part], fig. 623; 1948:455 [in part], fig. 623 .--Borradaile, 1923:262, fig. 279 .- Spandl, 1926:95, 141-142, 148 [in part].-Calman, 1927a:51.-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, 1934:104-105 [in part].-Park, 1938:209 .- Mohr, 1939:202 .- R. S. Fleming, 1939:304, 305.-Bouvier, 1940:68.-Park, Roberts, and Harris, 1941:154-171, figs. 1-5.-R. Rhoades, 1941:141, 142, 144.-Hobbs, 1942a:335, 338, 342, 351, 352 [in part]; 1967a:125.-Dearolf, 1942:50; 1953:228-229.-Jeannel, 1943:30, 31, 53, 272, 279.-Balss, 1944:402; 1955:1311, 1312.-Jeannel and Henrot, 1949:21 .- Allee, et al., 1949:559, fig. 196 .- Bott, 1950:25 .- Hobbs and Barr, 1960:19; 1972:37-39, 50, 51, 58, 60-63 [in part].-Vandel, 1964:448, 453, 461, 501, fig. 76; 1965:383, 391, 423, 424, fig. 76 .- Jegla and Poulson, 1968: 280.-Husson, 1970:108.

- Crabs .- Darwin, 1859:137 .- Hobbs and Barr, 1972:60.
- Eyeless Crabs.—Binkerd, 1869:86.—Hobbs and Barr, 1972:60. Cambarus pelulcidus.—Hagen, 1870:106 [erroneous spelling].
- Orconectes pellucidus.—Cope, 1872a:409, 419; 1872b:161, 162, 173, 174; 1879:492, 494 [in part].—Cope and Packard, 1881: 879, 881, 882 [in part].—Wright, 1884:272, 273.—Packard, 1888:24-25, 126, 140, 155[?], pl. 21: fig. 2[?], pl. 22: fig. 7[?]; 1894:735.—Hobbs, 1948a:19; 1967a:125, 130; 1967b:12 [in part]; 1972b:77, 149, figs. 11b, 60a; 1974b:37-38, fig. 102.— Pennak, 1953:458 [in part].—Lübke, 1953, fig. 110.—Eberly, 1954:59; 1958:1-6 [in part]; 1960:29-32 [in part].— Wells, 1959:5-7.—Barr, 1960:5 [in part]; 1967a:160, 161, 186, 187, 192, pl. 46; 1967b:480; 1968:65, 91, fig. 18.—F. A. Brown, 1961:929-930.—Creaser, 1962:3 [in part].—R. Rhoades, 1962:68, 69, 79, 94 [in part].—Fitzpatrick, 1963:60; 1967:141, 142.—Holthuis, 1964:42, 43, 45, 47.—Fingerman, et al., 1964:415, 420.—Vandel, 1964:448, 509, 570, 575 [in part]; 1965:379, 429, 483, 486 [in part].—Mohr, 1964:828.—



FIGURE 50.—Orconectes pellucidus, topotypes (all first form male except b, e, second form male, and h, female): a, b, mesial view of first pleopods; c, lateral view of carapace; d, epistome; e, f, lateral view of first pleopods; g, caudal view of first pleopods; h, annulus ventralis; i, antennal scale; j, dorsal view of carapace; k, ventral view of thoracic region; l, dorsal view of distal podomeres of cheliped. (After Hobbs and Barr, 1972, fig. 14.)

- Poulson, 1964:752, 756, 757, 759, 762, 764; 1966:15.—Moore and Nicholas, 1964:71, 88 [in part].—Frey, 1965:623, 624 [in part].—Mohr and Poulson, 1966:166, 204 [in part].— [?]D. H. Thompson, 1967:46, 47, 51.—Culver, 1967:34.— Jegla and Poulson, 1968:280.—Cooper and Poulson, 1968: 130, fig. 8.—Poulson and Smith, 1969:199-201.—Poulson and Jegla, 1969:193-195.—Anonymous, 1970:120.—Barr and Kuehne, 1971:71, 72.—Hobbs and Barr, 1972:1, 2, 4, 5, 8-14, 22, 37-43, 50, 52, 58-72, 81-83 [in part], figs. 1, 14-16.— Hobbs III and Burdsall, 1972, cover, 4 [in part], fig. 1.—D. G. Hart and C. W. Hart, 1974:71, 74, 116, 136.—Hobbs III, 1975:276, 280, 296, fig. 2.
- Crayfishes .- Putnam, 1875b:191.
- Astacidae.-Shaler, 1875:361 [1876:10].-Hobbs and Barr, 1972:60.
- Cray fish .--- Shaler, 1875:362-363 [1876:11, 12].
- Blind Craw-fish.-Packard, 1879, fig. 269.
- Cambarus typhlobius Joseph, 1880:202 [type-locality: Krain (= Carniola, now northern Yugoslavia), in error, see pp. 8-9 herein].—Faxon, 1884:139; 1885a:7, 45-46; 1914:427.— Underwood, 1886:373.—Hay, 1896:477.—Harris, 1903b:131, 151.—Bouvier, 1940:68.—Van Straelen, 1942:2.—Bott, 1950: 25.—Villalobos F., 1953:348; 1955:11.—Holthuis, 1964:42-47.—Hobbs and Barr, 1972:1, 61-64.
- Cambarus stygius Joseph, 1881:241, 249 [nomen nudum] [not Bundy, 1876:3]; 1882:12 [homonym].—Cope, 1881:882.— Underwood, 1886:373.—Packard, 1888:86, 119, 123, 130.— Faxon, 1914:427 [in part].—Léger, 1924:1206.—Spandl, 1926: 95.—Chappuis, 1927:90, 91.—Stammer, 1932:608.—Wolf, 1934:105.—Bouvier, 1940:68.—Jeannel, 1943:271, 272.—Holthuis, 1964:42-45, 47.—Hobbs and Barr, 1972:1, 52, 61, 63, 64.
- Blind Krebse.—Joseph, 1881:237.
- Cambarus coecus Joseph, 1881:237 [nomen nudum].—Faxon, 1884:139; 1885a:7, 45; 1914:427.—Bouvier, 1940:68.—Holthuis, 1964:42, 45.—Hobbs and Barr, 1972:1, 61, 63, 64.
- Blind crayfish.—Semper, 1881:77.—Packard, 1894:742.—Call, 1901:101.—Holt, 1968:87.—Hobbs and Barr, 1972:62.
- Cambarus (Orconectes) pellucidus.—Hovey, 1882:222 [in part].—Hobbs and Barr, 1972:37, 61 [in part].
- Orconectes.-Hovey, 1882:223 [in part].-Barr, 1968:85 [in part].-Barr and Kuehne, 1971:72, 85, 86.
- Cambarus Stygius.—Faxon, 1884:139; 1885a:iii, 6, 7, 45, 46 [in part].—Bott, 1950:25.
- Camtarus (Orconectes) pellucidus, form inermis.—Packard, 1888:156, pl. 27: fig. 5 [erroneous spelling].—Hobbs and Barr, 1972:61.
- Astacus Cambarus pellucidus.—Rabé, 1890:9.—Hobbs and Barr, 1972:62.
- Astacus Cambarus Stigius.—Rabé, 1890:9 [erroneous spelling].—Hobbs and Barr, 1972:62.
- Cambarus.—Apfelbeck, 1895:24.—Bolivar and Jeannel, 1931: 306, 307, 309.—Vandel, 1964:494, 495, 512; 1965:418, 419, 433.—Hobbs and Barr, 1972:62.
- Colorless crawfish.-Proctor, 1898:658.
- Cambarus pelucidus.—Eigenmann, 1900:228 [erroneous spelling].
- Cambrus Pellucidus .- Price, 1900:155 [erroneous spelling].
- Crayfish.--Call, 1901:100.--Hobbs and Barr, 1972:60, 61, 63, 64.

- Cambarus (Faxonius) pellucidus.—Ortmann, 1905a:97, 107, 108, 111, 114 [in part]; 1905b:435 [by implication]; 1931:64-65 [in part].—Pearse, 1910:10.—Fage, 1931:373 [in part].— Turner, 1935:876.—Hart, 1962:121.
- Blind Crayfish.-Calman, 1927b:53.
- Cityphlobius.—Joleaud, 1939, pl. 14 [lapsus calami for C. typhlobius].—Van Straelen, 1942:2.
- Cambarus caecus.-Bouvier, 1940:68 [erroneous spelling].
- Cambarus (Fexonius) pellucidus.-Rioja, 1941:193 [erroneous spelling].
- Cambarus pellucidus pellucidus.—R. Rhoades, 1941:144.— Hobbs and Barr, 1972:51.
- Cambarus pelludicus.—Dearolf, 1942:50 [erroneous spelling]. Crawfish.—Dearolf, 1942:52.
- Orconectes (Orconectes) pellucidus pellucidus.—Hobbs, 1942b: 154 [by implication].
- Cambarus Pellucidus.-Jackson, 1942:4.
- Orconectes pellucidus pellucidus.—Hobbs, 1942a:352 [by implication]; 1948a:19, 20, figs. 7, 12; 1967a:131; 1967b:7.— R. Rhoades, 1944:112, 113, 115, 117, 120-121; 1959:401; 1962:68, 90 [in part], fig. 8.—Cole, 1959:81.—Eberly, 1960: 30.—Hobbs and Barr, 1960:19; 1972:22, 40, 42, 51, 63, 64.— Nicholas, 1960:133.—Barr, 1961:32; 1968:60.—Hart and Hobbs, 1961:176, 178, 180, 184.—Wolfe and Cornwell, 1964:1467, 1468.—Frey, 1965:624 [in part].—Jegla, Poulson, and Cooper, 1965:639.—C. W. Hart and D. G. Hart, 1966: 8, 9; 1969:167.—Jegla, 1966:346-347, 353.—M. R. Cooper, 1969:205.—D. G. Hart and C. W. Hart, 1974:115.
- Orconectes pellucidus pelluicdus.—Hobbs, 1948a:16 [erroneous spelling]
- Orconectes pellucidus pellucidus pellucidus.—Hobbs, 1948a:19 [lapsus calami].
- Cambarus Coecus.-Bott, 1950:25.
- Cambarus (Cambarus) pellucidus.-Balss, 1955:1311.-Hobbs and Barr, 1972:63.
- Gambarus typhlobius.-Croizat, 1958:908 [erroneous spelling].
- Orconectes (Orconectes) pellucidus.-Hobbs, 1959:890 [in part].-Hobbs and Barr, 1972:12, 51, 64 [in part].
- Crayfishes .- Barr, 1964:79; 1966:15.
- Orconectes pellucidus subspecies.-Hobbs and Barr, 1972:14 [in part].
- Albinistic crayfishes .- Hobbs and Barr, 1972:60 [in part].

DIAGNOSIS .- Hobbs and Barr (1972:65-66):

Albinistic, eyes reduced and without pigment; rostrum with marginal spines or tubercles delimiting base of acumen . . . 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 . . . 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 . . .; central projection small, corneous, flattened in cephalocaudal plane, and directed distad; slight swelling at cephalic base of central projection.

SIZE.—Carapace length 39.1 mm; postorbital carapace length 31.8 mm.

TYPES.—Holotype, ZBM 1562 (d'I).

TYPE-LOCALITY.—Mammoth Cave, Edmonson County, Kentucky, U.S.A.

RANGE.—U.S.A. Orconectes pellucidus is known from the karst area (Pennyroyal Plateau) extending southwestward from Hart County to Trigg County, Kentucky, and Montgomery County, Tennessee.

The following localities, unless accompanied by references or collectors and/or dates, were taken from Hobbs and Barr (1972:68-69).

Kentucky. Barren County: (1) Cave City [= Railroad Cave], in town of Cave City; (2) Diamond Cave, 2 mi (3.2 km) N of Park City on State Rte. 225 (Packard, 1888:39); (3) Twyman Cave, 2 mi (3.2 km) N of Hiseville; (4) Parker Cave, 1.8 mi (2.9 km) SW of Park City, 4 Aug 1975, sight record by J. R. Holsinger. Christian County: (5) Glover's Cave, 4 mi (6.4 km) SW of Trenton. Edmonson County: (6) Mammoth-Flint Ridge Cave System (including Echo River, Roaring River, Styx River, Lake Lethe, Crystal Lake, Floyd Collins Crystal Cave) (Anonymous, 1843a:49); (7) Blowing Spring Cave in Mammoth Cave National Park; (8) Cedar Sink Cave in Mammoth Cave National Park; (9) Long Cave in Mammoth Cave National Park; (10) Stillhouse Hollow Cave in Mammoth Cave National Park; (11) White Cave (Faxon, 1885b:358); (12) Bat Cave, exact location unknown (Packard, 1888:40); (13) ?Ganter's Cave [= Blind Fish Cave, "down the Green River from Mammoth Cave"] (Putnam, 1875b:198); (14) Martin Cave, exact location unknown. Hart County: (15) Bald Knob Cave, 2 mi (3.2 km) W of Hardyville; (16) Buckner Hollow Cave, 1.2 mi (1.9 km) SE of Hinesdale; (17) Horse Cave [= Hidden River Cave], in town of Horse Cave (R. Rhoades, 1944:120); (18) Cave 2 mi (3.2 km) SW of Northtown; (19) Mammoth Onyx Cave on State Rte. 335 (R. Rhoades, 1944:120); (20) Cartmill Cave, 2.5 mi (4.0 km) E of Northtown, 27 Nov 1972, H.H.H. III, coll.; (21) Krump Spring Cave, 2 mi (3.2 km) ESE of Northtown, 1973, B. Ransom(?), coll. Logan County: (22) Cooks Cave, 1 mi (1.6 km) E of Adairville; (23) Mud River Cave, 4 mi (6.4 km) E of Russellville. Trigg County: (24) Cool Spring Cave on Sinking Fork Creek. Warren County: (25) By-Pass Cave, Bowling Green; (26) Lost River Cave, 3 mi (4.8 km) S of Bowling Green; (27) Pruitt Salt Peter Cave, 0.8 mi (1.3 km) SE of Anna; (28) Graham Spring Cave, 6 mi (9.7 km) ENE of Bowling Green, 21 Oct 1972, H.H.H. III, coll.

Tennessee. Montgomery County: (29) Sink Hole Cave on Austin Peay College Farm at Clarksville; (30) Bellamy Cave, 3.0 mi (4.8 km) S of Oakwood, lat. 36°29'39"N, long. 87°34'14"W.

ECOLOGICAL NOTES.—The majority of specimens of Orconectes pellucidus in collections were taken in the Mammoth-Flint Ridge Cave System. Although this species has been sampled from some 20 additional caves in seven counties of central Kentucky and north-central Tennessee, the following descriptions are based upon the comparatively well-known Mammoth-Flint Ridge complex of passages. This system is the longest linear cave system known to man and is developed in the St. Louis and Ste. Genevieve Mississippian limestones (Barr, 1967a:147). Five or six levels of passages are developed, and the abundance and permanence of aquatic habitats increase markedly in the lower levels (Barr, 1967a:149). Considerable effort has been made to understand the complex hydrology of the system (R. F. Brown, 1966; Hendrickson, 1961; Hess, Wells, and Brucker, 1974; White, Watson, Pohl, and Brucker, 1970).

Summarizing our present understanding, catchment from local precipitation (minus evaporation and transpired water) vanishes into sinkholes on the Mammoth-Flint ridges after short epigean courses. Where the sandstone cap has been breached, the water finds its way underground, and is ultimately funneled to two major streams which drain the cavern system: the Styx River (flowing SSE) undoubtedly receiving, in addition, backwaters of the Green River; and Echo-Roaring River (flowing WNW) deriving much of its recharge from the Sinkhole Plain located south of the Mammoth Cave Plateau. During major floods, the flow in both of these underground streams is reversed. Based on investigations by Barr and Kuehne (1971:70-74), the subterranean aquifers exhibit maximal flow during late winter and spring, and by late summer or early autumn, many small subsurface streams disappear. According to Barr and Kuehne (1971:72-73):

The cave rivers occupy the floor of galleries which are quite similar to the dry upper passages in dimensions and contours. Except under extreme flood conditions the rivers appear much like the surface streams with long pools and short riffles. In the Echo system the largest pools may exceed 100 m in length, but widths seldom surpass 10 m. Styx River is first seen through a floor window (the "Dead Sea"), and can be followed for about 100 m before its channel becomes heavily silted, when most of the flow apparently takes place in inaccessible lateral conduits. Residual pools in the silted area ("Lake Lethe") exhibit little or no flow in late autumn, and are normally less than 1 m deep, although two of them are approximately 3 m deep even at low water. In the Echo system, pool depths of 3 to 4 m are common. Occasionally siphons carry the rivers beneath rubble or dipping ceiling beds, and it is as impenetrable siphons that they debouche into the narrow valley of Green River. Echo-Roaring River is less depositional in character than Styx River, and finer sediments are usually restricted to deep pools, backwater and gradually sloping banks. In summer the streams are extremely clear and without appreciable flow, but they become badly roiled by even small rises, and have high turbidity virtually all winter.

When flooding is extensive, filling the river passages and inundating even normally dry portions of the cave, organisms are displaced sometimes considerable distances. As floodwaters subside, isolated pools often remain high above mean water level. Consequently, crayfishes and other aquatic forms are stranded until high waters return or die as the pools become desiccated. "Several specimens were obtained from places where the pools were nearly or quite dried up, and it was observed that in such places the crayfish had dug for itself a hole or had crawled under a stone and was making preparations to remain. They were already in a semi-dormant condition and in a few days would doubtless have died" (Hay, 1902a:231).

Numerous aquatic habitats exist as the result of surface seepage and accumulation of water in areas well above maximum inundation levels. Pool depth and permanence are related to surface precipitation, ceiling drip, and evaporation rates. Commonly, these pools are accompanied by various types of speleothems actively forming directly above at the ceiling level. Barr and Kuehne (1971:71) note:

The largest known body of water situated above flood levels in Mammoth Cave is Crystal Lake in the Frozen Niagara section. It fills the bases of two narrowly connected domepits and is ponded to a maximum depth of about 3.5 m by a flowstone dam at one end, artificially grouted and cemented. Surface area is about 120 m³. Water is supplied only by ceiling drip and wall flow after heavy surface precipitation. Levels are highest in late winter and slowly fall about 0.3 to 0.5 m by the following autumn. The lake contains no macroscopic organic material; bottom sediments are free of odor when brought to the surface. Enrichment is assumed to be meager, coming mainly from cricket guano and soil microorganisms carried into the cave by ground water ... Two Orconectes pellucidus were observed on most visits.

Physico-chemical data are sparse for virtually all spelean environments and, even when available, rarely are they known for annual or even seasonal periods. Of exceptional value, therefore, is this study by Barr and Kuehne (1971:53-61) in which they presented limnological data obtained from October 1961 to November 1962 for Crystal Lake,

Echo-Roaring, and Styx rivers in the Mammoth-Flint Ridge System. The annual range of variability in the cave was much smaller than for surface waters, and the rate of change was greatest at the beginning of winter. The physico-chemical characteristics of Echo-Roaring River and Styx River are markedly affected by backflooding from Green River during winter, producing abrupt decreases in temperature and pH, commonly producing increases in dissolved oxygen, and variously affecting methyl orange alkalinity. As they point out, these sharp variations may serve as cues for triggering certain biological processes in aquatic troglobites; however, considerable effort will be required to determine accurately what effects these environmental fluctuations have upon cavernicoles. In contrast, Crystal Lake maintains a relatively low oxygen content (generally below 9 ppm), higher pH and total alkalinity, and a more stable temperature. Zooplankton populations fluctuate qualitatively and quantitatively in all three habitats, but are consistently less variable in Crystal Lake, which also demonstrates a much lower density of bottom microand macrofaunas.

Orconectes pellucidus, like numerous cavernicoles, is an opportunist in respect to its food habits and feeds upon organic material transported into the cave or upon the dead bodies of organisms, sometimes on "Crangonyx and other minute crustacea" (Hovey, 1891:72). Hovey (1912:114) further substantiates this by mentioning that the species "feeds on aquatic crustacea which it deftly extracts with its pincerlike claws from under flat stones." Barr and Kuehne (1971:94) indicate its position in the trophic levels of Mammoth Cave by stating:

The "Shrimp Pools" of the Roaring River Passage of Mammoth Cave are an example of a moderately complex aquatic community based on bacterial decomposition of stream detritus; protozoans and other microfauna feed on the bacteria and are in turn eaten by isopods, amphipods, and atyid shrimps; crayfishes and amblyopsid fishes represent the higher trophic levels in this community.

Even though O. pellucidus is situated at the upper trophic position, it is not immune from predation. Jegla, Poulson, and Cooper (1965:639) reported that predation by fishes [probably Amblyopsis spelaea] may reduce population density, thus indicating that at least in some caves, fishes may act to restrict maximum growth of populations. "The tracks of a cave rat, several excavations made by

him, and the remains of a crayfish showed that even in the vastnesses of their subterranean home the crayfishes have enemies to which they sometimes fall victims" (Hay, 1902a:231).

Injury, resulting in mutilation (by autotomy or otherwise), and regeneration occur frequently as the result of interspecific or intraspecific contacts, predation by fishes, "flash-flooding," or other factors. "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" (Hobbs and Barr, 1972:71).

The behavior and activity of *O. pellucidus* has been well documented over the years. Hay (1902a: 230–231) visited Mammoth Cave in August 1901 and reported the following:

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. While thus resting, the only movement observable was a slight waving to and fro of the antennae. Sometimes an individual was seen on a submerged rock mass resting in the same way; such individuals appeared to have no difficulty in running rapidly over the rough surfaces. When alarmed in any way, the crayfish would begin to show signs of uneasiness by moving slightly about in various directions, and then dart away, propelled by the vigorous strokes of its tail fan. There seemed to be no ability on the part of the animal to select a safe haven of refuge from a distance, for the flight for safety was apt to end anywhere; the course was usually laid for deeper water, but if a rock or the wall of the pool was encountered the crayfish would quickly conceal itself in a crevice and retreat beyond reach of danger. Several individuals, when repeatedly chased across a small pool, became either too exhausted or too enraged to retreat and showed a readiness to fight by rising high on the front walking legs and waving their chelae about in the direction of the danger. Their movements were very quick, probably more rapid than those of outside species, and it was difficult to touch their antennae and escape a nip from their chelae.

Disturbances at the water's surface did not appear to frighten the crayfishes and he deduced "that in this creature the senses of sight and hearing have entirely disappeared." Giovannoli (1933a: 618) augmented Hay's account of the species:

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 aboveground 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 toward deeper water, but if startled they swim blindly backward just as any crayfish does.

Park, Roberts, and Harris (1941:159-165) reported this species to be photonegative and presented data to indicate an arhythmic activity pattern. Re-examination of these data by F. A. Brown (1961:929) "indicated a statistically significant . . . 24-hr. rhythm of activity to be present . . . with minimum activity about 9:00 a.m. and maximum about 7:00 p.m." Jegla and Poulson (1968:280) reviewed both works of Park, Roberts, and Harris, and Brown and concluded that the data cannot "be used to distinguish between endogenously and exogenously controlled rhythms." Also, in discussing the photonegative responses of O. pellucidus, Poulson (1964:755-756) stated: "Light stimulation of the brain area, reduced eye stalk, or 6th abdominal ganglion results in negative reaction to light," and he noted that a "kinetic component is found . . . since they turn away when illuminated on one side."

LIFE HISTORY NOTES .- Data on molting and reproductive cycles of this species are relatively few. First form males have been observed during every month of the year except January, September, and December, exceptions probably reflecting the limited collections made during these months; thus, breeding males probably occur throughout the year. Eigenmann (1899:60) collected a single female carrying young in Mammoth Cave on 23 November 1898. To date, this is the only report of females with young. Hobbs and Barr (1972:72) recorded a female carrying eggs, collected from Bald Knob Cave, Hart County, Kentucky, on 11 September 1965. These reports do not support the conclusion of Hay (1902a:232), however, that copulation occurs in the early fall and that eggs "are said to be laid during the winter." Poulson (1964:752) pointed out that fall breeding "precedes low water by one to two months, and high water, with maximum organic inwash, by four to six months."

Genus Procambarus

Astacus.—Harlan, 1830:464 [not Fabricius, 1775:413]. Camborus.—Williamson, 1899:47 [erroneous spelling]. Cambarus.—Ortmann, 1905a:96 [not Erichson, 1846:95].

- Procambarus Ortmann, 1905b:435, 437 [proposed originally as subgenus elevated to generic rank by Hobbs, 1942a:341; type-species: Cambarus digueti Bouvier, 1897:225].
- Paracambarus Ortmann, 1906:1 [proposed originally as subgenus, elevated to generic rank by Hobbs, 1942a:344, but returned to subgeneric status by Hobbs, 1972a:3; typespecies: Cambarus (Paracambarus) paradoxus Ortmann, 1906:3].
- Ortmannicus Fowler, 1912:341 [proposed originally as substitute name for Ortmann's (1905a:96) subgenus Cambarus, placed in synonomy with Ortmann's Procambarus by Hobbs, 1942a:342, but employed as subgenus by Hobbs, 1972a:8; type-species: Astacus Blandingii Harlan, 1830:464].
- Cambarellus.—Creaser, 1933:21 [lapsus for Cambarus] [not Ortmann, 1905a:106].
- Cambaus.-Okada, 1948:133 [erroneous spelling].
- Pracambarus.-Villalobos F., 1953:352 [erroneous spelling].
- Paracamburus .--- Villalobos F., 1953:354 [erroneous spelling].
- Procambrus.-Sukô, 1961:37 [erroneous spelling].
- procambarus .- Padgett, 1970:19.
- Subgenus Girardiella Lyle, 1938:76 [type-species: Cambarus hagenianus Faxon, 1884:141].
- Subgenus Ortmanmanicus.—Hobbs, 1942a:342 [erroneous spelling].
- Subgenus Acucauda Hobbs, 1972a:5 [type-species: Procambarus fitzpatricki Hobbs, 1971c:461].
- Subgenus Austrocambarus Hobbs, 1972a:5 [type-species: Procambarus vazquezae Villalobos F., 1954:328].
- Subgenus Capillicambarus Hobbs, 1972a:6 [type-species: Cambarus (Cambarus) hinei Ortmann, 1905b:401].
- Subgenus Hagenides Hobbs, 1972a:7 [type-species: Astacus advena LeConte, 1856:402].
- Subgenus Leconticambarus Hobbs, 1972a:7 [type-species: Cambarus barbatus Faxon, 1890:621].
- Subgenus Lonnbergius Hobbs, 1972a:8 [type-species: Cambarus acherontis Lönnberg, 1895:6].
- Subgenus Mexicambarus Hobbs, 1972a:8 [type-species: Cambarus (Cambarus) bouvieri Ortmann, 1909:159].
- Subgenus Pennides Hobbs, 1972a:10 [type-species: Procambarus natchitochae Penn, 1953:5].
- Subgenus Remoticambarus Hobbs, 1972a:11 [type-species: Procambarus pecki Hobbs, 1967b:2].
- Subgenus Scapulicambarus Hobbs, 1972a:11 [type-species Cambarus clarkii paeninsulanus Faxon, 1914:369].
- Subgenus Tenuicambarus Hobbs, 1972a:12 [type-species: Procambarus tenuis Hobbs, 1950:194].
- Subgenus Villalobosus Hobbs, 1972a:12 [type-species: Paracambarus riojae Villalobos F., 1944:161].

DIAGNOSIS.—Third maxilliped not enlarged, reaching little, if at all, beyond apex of rostrum, and bearing teeth on mesial margin of ischium. Branchial count 17 + ep. Male with or without boss on caudomesial angle of coxa of fourth pereiopod; hooks on ischia of third, fourth, or third and fourth pereiopods; first pleopods symmetrical or asymmetrical and terminating in 2 to 4 parts, if only 2, never bent at right angle to shaft of appendage, and, if shoulder present on cephalic surface, always situated far proximal to base of central projection or cephalic process. Female with annulus ventralis freely movable and with moderately well-developed first pleopods.

RANGE.—North and Middle America and West Indies. The piedmont and coastal plain provinces from New Jersey to Florida, westward in the coastal plain from Florida to Texas and northward in the Mississippian Embayment through western Tennessee and Kentucky, and from Ohio, southern Wisconsin, and Minnesota southwestward through eastern Colorado and New Mexico, and Mexico (mostly along the eastern slopes of the latter) to Honduras; also on Cuba and Isla de Pinos. Introduced into California (including Baja California), Costa Rica, Hawaii, Japan, and Kenya.

NUMBER OF SPECIES AND SUBSPECIES.—There are 128 of which 12 are troglobitic.

Subgenus Austrocambarus

- Subgenus Cambarus.—Ortmann, 1905a:97 [in part] [not Erichson, 1846:95].
- Subgenus Procambarus Ortmann, 1905b:437 [in part].
- Subgenus Austrocambarus Hobbs, 1972a:5, figs. 2b, 5, 20a [type-species: Procambarus vazquezae Villalobos F., 1954: 328].

DIAGNOSIS.—First form male with simple hooks on ischia of third pereiopods only; coxa of fourth pereiopod without caudomesial boss. First pleopods symmetrical, with strong shoulder on cephalic surface proximal to terminal elements; subapical setae absent; terminal elements consisting of welldeveloped distolaterally directed, tapering or flattened mesial process; prominent cephalodistally directed central projection; and caudal knob (accessory cushion-like prominence also present in *P*. (*A.*) *niveus*); cephalic and/or caudal processes often absent. Females with distinct preannular plate.

RANGE.—Middle America and West Indies. The Atlantic slope, from the Cordillera Volcánica Transversal of Mexico southward to Honduras (Mexicanus Group) and on Cuba and Isla de Pinos (Cubensis Group).

NUMBER OF SPECIES AND SUBSPECIES.—There are 18, of which 4 are troglobitic.

Procambarus (Austrocambarus) niveus Hobbs and Villalobos F.

FIGURE 51

Procambarus niveus Hobbs and Villalobos F., 1964:308, 314,



FIGURE 51.—Procambarus (Austrocambarus) niveus (a, c, f-l, holotypic first form male; b, e, topotypic second form male; d, allotypic female): a, b, mesial view of first pleopods; c, lateral view of carapace; d, annulus ventralis; e, f, lateral view of first pleopods; g, dorsal view of carapace; h, basis and ischium of third pereiopod; i, epistome; j, antennal scale; k, caudal view of first pleopods; l, dorsal view of distal podomeres of cheliped. (Except b and e, redrawn from Hobbs and Villalobos F., 1964, pls. 5, 6.)

318, 342-346, pls. 5, 6.—Chace and Hobbs, 1969:5, 14, 24, 34, 38, 117, 120, fig. 31d.—Straskraba, 1969:19.— Hobbs, 1969b:161; 1971a:12.—Hobbs and Barr, 1972:1, 4.— Botosaneanu, 1973:211.—Caine, 1974a:488.—Holthuis, 1974b: 240-242.—Silva T., 1974:23, 47-48.—Cooper and Cooper, 1975:3.

Procambarus (Austrocambarus) niveus.-Hobbs, 1972a:6; 1972b:38, 151; 1974b:45, 126, fig. 186.-Hobbs III, 1975:276.

DIAGNOSIS.—Albinistic, but eyes pigmented and with facets. Areola constituting 33.2 to 33.6 percent of total length of carapace (41.7 to 42.0 percent of postorbital carapace length). Epistome produced laterally in small lobes. First pleopod of first form male with mesial process flattened, not tapering, and directed more laterally than distally; central projection with small acute accessory tooth extending cephalodistally; and caudal element provided with cushion-like cephalolateral prominence.

SIZE.—Carapace length 25.3 mm; postorbital carapace length 20.4 mm.

TYPE.—Holotype and allotype, USNM 109076, 109077 (GI, Q).

TYPE-LOCALITY.—Cuevas de Santo Tomás, Sierra de los Organos, cerca de Ponce, Pinar del Río, Cuba.

RANGE.—Cuba. Known only from the typelocality.

ECOLOGICAL NOTES.—Holthuis (1974b:240-241) described the type-locality as follows:

The Gran Caverno [= Caverna] de Santo Tomás is the largest cave of Cuba and even of Latin America, consisting of a system of galleries situated on various horizontal levels, one above the other. On the lowest level there is a permanent subterranean stream. The next higher level contains the Cueva del Segundo Cauce, which only receives water from the subterranean stream after heavy rains, when the flooding of the river makes it possible to reach this higher level. The galleries at still higher levels are entirely dry. The Cueva del Segundo Cauce is situated at an altitude of about 150 m and is a large, almost straight gallery. A part of it, which bears the name "Cueva de las Represas," is characterized by that it contains a great number of permanent pools, the bottom and sides of which consist of rough hardened calcareous mud, sometimes covered with a layer of soft mud. The pools are of various shapes, and their depth varies from 2-5 cm to 1.5-2 m. The temperature of the water is 20° to 21° C. In the dry season these permanent pools are isolated, separated from each other by barriers of calcified mud. But when after heavy rains the subterranean river penetrates this level of the caves, it forms a connection between the several pools. The pools hold enough water to last them from one flood to another; they also receive water coming down through the ceiling as is shown by the presence of stalactites in these caves.

The crayfish are found in the large to very large pools,

sometimes single, sometimes in small groups. There are large and small specimens . . . A count was made of the crayfishes in this gallery and a total of 50 were noted. The same kind of crayfish was also observed (but not collected) in a subterranean stream which runs at a lower level, viz., in the active zone of the cave.

LIFE HISTORY NOTES.—The holotypic male, form I, and allotype were obtained on 24 December 1956. Holthuis (1974b:240) recorded a collection of 6 males and 2 females made by Botosaneanu, Domingo Deas, and José M. Marrero on 12 April 1973; two of the males were first form. Ovigerous females have not been reported.

REMARKS.—Holthuis (1974b:241) stated that the color of the crayfish is quite variable but that the eyes are always black.

Procambarus (Austrocambarus) oaxacae oaxacae Hobbs

FIGURE 52

Procambarus (Austrocambarus) oaxacae oaxacae Hobbs, 1973a: 29-33, 38, figs. 3-5.—Reddell, in press. Blind crayfish.—Reddell, 1973b:90.

DIAGNOSIS .- Body with markedly reduced pigmentation, virtually albinistic but often with slight tan suffusion on abdomen; eyes reduced in size with or without traces of facets, frequently with few ommatidia bearing reddish purple pigment, but with pigmented area not sharply margined. Areola constituting 35.8 to 37.8 percent of total length of carapace (43.7 to 46.1 percent of postorbital carapace length). Cervical spine obsolete. Antennal scale broadest distal to midlength. Coxa of fifth pereiopod lacking corneous caudomesial boss. First pleopod of first form male with mesial process not strongly flattened, tapering distally, and directed more distally than laterally; central projection lacking accessory tooth; and caudal element lacking cushion-like prominence.

SIZE.—Carapace length 30.9 mm; postorbital carapace length 25.4 mm.

TYPES.—Holotype, allotype, and morphotype, USNM 144341, 144342, 144348 (GI, Q, GI); paratypes, IBM, TTM, USNM.

TYPE-LOCALITY.—Cueva del Guano, 10 km NE of Valle Nacional, Oaxaca, Mexico.

RANGE.—Mexico. Known only from the typelocality.

ECOLOGICAL NOTES .- The types were collected



FIGURE 52.—Procambarus (Austrocambarus) oaxacae oaxacae (all from holotypic first form male except c, g, from morphotypic second form male, and l from allotypic female): a, lateral view of carapace; b, c, mesial view of first pleopods; d-f, mesial, caudal, and lateral view of distal part of first pleopod; g, h, lateral view of first pleopods; i, dorsal view of carapace; j, basal podomeres of third, fourth, and fifth pereiopods; k, antennal scale; l, annulus ventralis; m, dorsal view of distal podomeres of cheliped; n, caudal view of first pleopods; o, epistome. (After Hobbs, 1973a, fig. 3.)

from a stream within the cave (Reddell, 1973b:90). He also reported that the crayfish "were eagerly collected by our guides for their supper." This crayfish shares the cave with *Neopalaemon nahuatlus*. The large populations of both species are perhaps due to the large quantity of guano that is deposited in the stream (Reddell, in press).

LIFE HISTORY NOTES.—Among the 14 specimens collected on 28 December 1972, 4 are first form males. No females with eggs or young have been observed.

Procambarus (Austrocambarus) oaxacae reddelli Hobbs

FIGURE 53

Procambarus (Austrocambarus) oaxacae reddelli Hobbs, 1973a: 33-38, figs. 6-8.—Reddell, in press.

Troglobitic crayfish.-Reddell, 1973b:89.

Procambarus oaxacae reddelli.-Hobbs, 1973b:73.

DIAGNOSIS.—Body without pigment or with tan suffusion on abdomen; eyes with distinct black pigmented faceted area. Areola constituting 33.2 to 35.7 percent of total length of carapace (42.0 to 44.4 percent of postorbital carapace length). Cervical spine present. Antennal scale broadest distal to midlength. Coxa of fifth pereiopod lacking prominent sclerotized caudomesial boss. First pleopod of first form male with mesial process not strongly flattened, tapering distally, and directed more distally than laterally; central projection lacking accessory tooth; and caudal element lacking cushionlike prominence.

SIZE.—Carapace length 37.4 mm; postorbital carapace length 30.5 mm.

TYPES.—Holotype, allotype, and morphotype, USNM 144346, 144347, 144348 (σ I, ρ , σ II); paratypes, IBM, TTM, USNM.

TYPE-LOCALITY.—Cueva del Nacimiento del Río San Antonio, 10 km SSW of Acatlán, Oaxaca, Mexico.

RANGE.—Mexico. This crayfish is known with certainty only from the type-locality. Atypical representatives were found in Cueva del Guayabo, 12 km NE of Valle Nacional, Oaxaca, exhibiting characteristics suggesting a possibility of gene flow between this and the nominate subspecies.

ECOLOGICAL NOTES.—A description of the cave from which this crayfish was described is presented by Reddell (1973b:89). In the type-locality, the crayfish "were extremely abundant throughout the length of this large cave. They tended to congregate especially about small areas of guano left by bats which roosted in small groups on the ceiling. The crayfish in this cave are also used for food by local inhabitants" (Reddell, in press). See "Ecological Notes" for Macrobrachium villalobosi.

LIFE HISTORY NOTES.—Of the 16 specimens from the type-locality collected on 26 December 1972, 2 are first form males. No females carrying eggs or young have been observed.

Procambarus (Austrocambarus) rodriguezi Hobbs

FIGURE 54

- Procambarus rodriguezi Hobbs, 1943:198, 203-206, figs. 15-26; 1966:71; 1969b:161; 1971a:3, 12, 30, 31.—Villalobos F., 1948:182; 1953:346, 356, 364, 365, 372; 1954:303, 306, 321-323, 363; 1955:2, 20, 160, 161, 176-178, 218.—Rioja, 1953a: 288, 289, 292; 1971:530.—Nicholas, 1962:173.—Hobbs and Villalobos F., 1964:313.—Reddell, 1971a:25; 1971b:217, 219.—Hobbs and Barr, 1972:1, 4.—D. G. Hart and C. W. Hart, 1974:22.
- Paracambarus rodriguezi,—Rioja, 1953a:293 [erroneous combination].
- Procambarus (Austrocambarus) rodiguezi.—Hobbs, 1972a:6 [erroneous spelling].
- Procambarus (Austrocambarus) rodiguezi.—Hobbs, 1972a:6 152, fig. 22c; 1973a:25, 38; 1974b:45, 123, fig. 174.—Hobbs 111, 1975:276.

DIAGNOSIS.—Body without pigment or pale orange; eyes with small pigment spot but no facets. Areola constituting 35.8 to about 37.5 percent of total length of carapace (43.5 to 44.3 percent of postorbital carapace length). Cervical spine present. Antennal scale broadest distal to midlength. Coxa of fifth pereiopod lacking prominent, sclerotized caudomesial boss. First pleopod of first form male with mesial process strongly flattened, tapering distally, and directed more distally than laterally; central projection lacking accessory tooth; and caudal element lacking cushion-like prominence.

SIZE.—Carapace length 33.7 mm; postorbital carapace length 27.4 mm.

TYPES.—Holotype, allotype, and "morphotype," USNM 81302 (&I, Q, &II); paratypes, USNM, MCZ.

TYPE-LOCALITY.—Cueva de Ojo de Agua Grande, WNW of Hacienda Potrero Viejo, Paraje Nuevo, Córdoba, Veracruz, Mexico. Visits by several persons to Cueva de Ojo de Agua Grande attempting



FIGURE 53.—Procambarus (Austrocambarus) oaxacae reddelli (all from holotypic first form male except c, g, from morphotypic second form male, and k from allotypic female): a, lateral view of carapace; b, c, mesial view of first pleopods; d-f, mesial, caudal and lateral views of distal part of first pleopod; g, h, lateral view of first pleopods; i, dorsal view of carapace; j, basal podomeres of third, fourth, and fifth pereiopods; k, annulus ventralis; l, antennal scale; m, dorsal view of distal podomeres of cheliped; n, caudal view of first pleopods; o, epistome. (After Hobbs, 1973a, fig. 8.)

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to obtain additional specimens of this species have disclosed only a single juvenile crayfish, and, as pointed out by Reddell (in press), the brief description of the stream presented by Hobbs (1943:206)



FIGURE 54.—Procambarus (Austrocambarus) rodriguezi (a, f-l, holotypic first form male; b, e, morphotypic second form male; c, d, allotypic female): a, b, mesial view of the first pleopods; c, lateral view of carapace; d, annulus ventralis; e, f, lateral view of first pleopods; g, epistome; h, dorsal view of carapace; i, caudal view of first pleopods; j, antennal scale; k, dorsal view of chela; l, basal podomeres of third, fourth, and fifth pereiopods.

hardly applies to the "rapid rock-floored stream" in Cueva de Ojo de Agua Grande! See Sbordoni and Argano (1972:18-19) for a description of this cave.

RANGE.—Mexico. Known only from the type-locality.

ECOLOGICAL NOTES.—The subterranean stream "consisted of pools joined by shallow narrows, and the crayfish were found in water about four inches [10.2 cm] deep" (Hobbs, 1943:206).

LIFE HISTORY NOTES.—Of the 10 specimens collected on 24 December 1940, only one was a first form male. No females carrying eggs or young have been reported.

Subgenus Leconticambarus

Subgenus Cambarus.—Ortmann, 1905a:97 [in part] [not Erichson, 1846:95].

Subgenus Ortmannicus Fowler, 1912:341 [in part].

Subgenus Ortmanmanicus.—Hobbs, 1942a:342 [in part] [erroneous spelling].

Subgenus Leconticambarus Hobbs, 1972a:7, figs. 1m, 2f, 9, 20d [type-species: Cambarus barbatus Faxon, 1890:621].

DIAGNOSIS.—First form male with simple hooks on ischia of third and fourth pereiopods; coxa of fourth pereiopod lacking caudomesial boss. First pleopods asymmetrical with sloping shoulder on cephalic surface proximal to terminal elements; subapical setae present; terminal elements comprising distally directed, slender, sinuous, mesial process; prominent slender, acute cephalic process arising from cephalomesial surface of appendage and directed distally; and rounded caudal knob bearing corneous, distally directed, lanceolate central projection on cephalomesial surface.

RANGE.—U.S.A. From the southeastern part of South Carolina southward to the Florida Keys and westward to the southern Escambia and Perdido basins in Alabama and Florida.

NUMBER OF SPECIES.—Of the 17 species, only one is troglobitic.

Procambarus (Leconticambarus) milleri Hobbs

FIGURE 55

- Procambarus milleri Hobbs, 1971b:115-118, 121-123, figs. 1-11, 16.—Hobbs and Barr, 1972:4.—Caine, 1974a:490-491.— Relyea and Sutton, 1975c:8.
- Procambarus (Leconticambarus) milleri.—Hobbs, 1972a:7 [by implication], 8; 1972b:51, 151, fig. 11f; 1974b:51-52, 130.

fig. 203; 1975a:14.—Hobbs III, 1975:276. Crayfish.—Peck, 1974b:31 [in part].

DIAGNOSIS.—Same as that for the subgenus. In addition, albinistic, eyes reduced but with pigmented area bearing facets.

SIZE.—Carapace length 13.8 mm; postorbital carapace length 11.4 mm.

TYPES.—Holotype and morphotype, USNM 131257, 131258 (JI, JI); paratypes, USNM.

TYPE-LOCALITY.—Well at Little Bird Nursery and Garden Store at 8427 Bird Road, Miami, Dade County (Sec. 15, T. 54S, R. 40E), Florida, U.S.A.

RANGE.—U.S.A. Known only from the typelocality.

ECOLOGICAL NOTES.—The specimens were obtained from a trap at the outlet of a motorized pump installed in a well 22 feet (6.7 m) deep.

LIFE HISTORY NOTES .- From Hobbs (1971b:122):

First form males were collected in February, March, and May. The holotype was collected on May 2, 1968 when it was in the first form. It was placed in an aquarium where it molted on October 22 to second form, increasing its carapace length only 0.4 mm. It molted again on November 25, returning to the first form, with an increase in carapace length of 1.2 mm. It died on March 17, 1969. These observations were made by Mr. Miller who preserved the exuvia[e] Second form males were obtained in January, February, March, July, and August. The only female that has been found is a juvenile taken on January 27, 1968.

Subgenus Lonnbergius

- Subgenus Cambarus.—Ortmann, 1905a:97 [in part] [not Erichson, 1846:95].
- Subgenus Ortmannicus Fowler, 1912:340, 341 [in part].
- Subgenus Ortmanmanicus.—Hobbs, 1942a:342 [in part] [erroneous spelling].
- Subgenus Lonnbergius Hobbs, 1972a:8, figs. 2g, 10, 20e [type-species: Cambarus acherontis Lönnberg, 1895:6].

DIAGNOSIS.—First form male with bituberculate hooks on ischia of third and fourth pereiopods. Coxa of fourth pereiopod with prominent, vertically disposed caudomesial boss. First pleopod symmetrical, subapical setae absent; terminal elements comprising mesial process directed distally but not reaching nearly so far as level of apex of central projection; cephalic process rudimentary or absent; caudal process prominent, flanked by protuberance on ridge of caudal knob; and prominent, subacute, distally directed central projection. Females lacking preannular plate. Annulus ventralis



FIGURE 55.—Procambarus (Leconticambarus) milleri, holotypic first form male (except b, d, morphotypic second form male): a, b, mesial view of first pleopods; c, lateral view of carapace; d, e, lateral view of first pleopods; f, epistome; g, basal podomeres of third and fourth pereiopods; h, dorsal view of carapace; i, dorsal view of distal podomeres of cheliped; j, caudal view of first pleopods; k, antennal scale. (After Hobbs, 1971b, figs. 1–11.)

as long as broad with cephalolateral portions hidden beneath multituberculate sternum.

RANGE.—U.S.A. Vicinity of Lake Brantley and Palm Springs, Seminole County, Florida.

NUMBER OF SPECIES.—Monotypic.

Procambarus (Lonnbergius) acherontis (Lönnberg)

FIGURE 56

Cambarus acherontis Lönnberg, 1894:125-127; 1895:6-12, figs. 1-5b.—Faxon, 1898:646 [in part]; 1914:413-414.—Hay.



FIGURE 56.—Procambarus (Lonnbergius) acherontis, from Palm Springs (a, c, f-l, first form male; b, e, second form male; d, female): a, b, mesial view of first pleopods; c, lateral view of carapace; d, annulus ventralis; e, f, lateral view of first pleopods; g, epistome; h, dorsal view of carapace; i, caudal view of first pleopods; j, antennal scale; k, dorsal view of distal podomeres of cheliped; l, basal podomeres of third, fourth, and fifth pereiopods.

1899:959, 966; 1902b:436.—Ortmann, 1902:277; 1918:839.— Harris, 1903a:606; 1903b:58, 67, 150, 152, 162 [in part].— Banta, 1907:73.—Spandl, 1926:95 [in part].—Chappuis, 1927: 91 [in part].—Wolf, 1934:104.—Hobbs, 1938:91; 1940:387-394, fig. 15; 1942b:8, 9, 92; 1972a:2, 8; 1974a:15.—Jeannel, 1943:272.—Hobbs and Barr, 1972:38, 63[?].

- Cambarus archerontis.-Hay, 1902b:437 [erroneous spelling].
- Cambarus (Cambarus) acherontis.—Ortmann, 1905a:102; 1918:848 [by implication].—Balss, 1955:1311.
- Cambarus (Ortmannicus) acherontis.—Fowler, 1912:341 [by implication].
- Procambarus acherontis.—Hobbs, 1942a:342 [by implication]; 1942b:12, 13, 21, 28, 83, 91-92, 120, 121, figs. 86-90; 1943:202; 1944:8; 1945:69, fig. 13; 1959:884; 1969b:160; 1971b:123, fig. 12.—Pennak, 1953:458.—Walton and Hobbs, 1959:118.—Nicholas, 1960:133.— Warren, 1961:7, 10.—Hobbs and Barr, 1972:4, 62.—Holt, 1973b:88.—D. G. Hart and C. W. Hart, 1974:123.—Caine, 1974a:490.
- Procambarus (Lonnbergius) acherontis.—Hobbs, 1972a:8, figs. 2g, 10; 1972b:36, 150, fig. 11d; 1974b:52, 133, fig. 215; 1975a:15.—Hobbs III, 1975:276.
- Lonnbergius .- Hobbs, 1972a: fig. 20e.
- Crayfish.-Peck, 1974b:31 [in part].

DIAGNOSIS.—Same as that for subgenus Lonnbergius. In addition, body and eyes without pigment.

SIZE.—Carapace length 26.6 mm; postorbital carapace length 21.5 mm.

TYPES.—Holotype, ZIAS 1/4412 (1 specimen).

TYPE-LOCALITY.—Subterranean rivulet about 42 feet (12.7 m) from the surface, near Lake Brantley, Seminole County, Florida, U.S.A.

RANGE.—U.S.A. Known only from Florida.

Seminole County: (1) type-locality; (2) Palm Springs, about 12 miles N of Orlando (Hobbs, 1940:393).

ECOLOGICAL NOTES.—Other than the two specimens recorded by Lönnberg (1894:126) from the type-locality, the only others known to us are those taken from Palm Springs, where

we found more than two score of white crayfishes lying in the algae over the bottom of a pool formed by the spring. This pool (walled-up for swimming purposes) measures about 60 by 20 feet [18.2 by 6.1 m]; most of it is approximately 6 feet [1.8 m] deep. The walls and bottom were covered with a thick algal growth and deposited on it was a sediment characteristic of sulphur springs. The water had a pH of 7.6. Mr. Marchand caught most of the 44 specimens that we secured by diving to the bottom and capturing them with his hands. They were extremely sluggish, many lying in the algae on their backs with their feet turned up toward the surface as though dead. Even after they were bagged there was little sign of life [Hobbs, 1940:388].

Lönnberg's account points out the fact that this species does not confine itself to the mouths of springs or sinks but occurs in at least one underground stream, evidenced by his specimens found in a well dug near Lake Brantley. "At first they were fairly numerous, but later on, when I had heard about it and tried to obtain some specimens, I could only procure two males" (Lönnberg 1894b [1895]:4) [Hobbs, 1942b:92].

LIFE HISTORY NOTES.—Among the 44 specimens collected on 11 November 1938 in Palm Springs, were 3 first form males. No females carrying eggs or young have been reported. According to Warren (1961:7), many specimens have been collected in Palm Springs. Perhaps he intended this to mean others than the 44 just mentioned, but by whom and when they were collected or what became of them is unknown to us.

Subgenus Ortmannicus

- Subgenus Cambarus.—Ortmann, 1905a:97 [in part] [not Erichson, 1846:95].
- Subgenus Ortmannicus Fowler, 1912:341 [in part].-Hobbs, 1972a:9-10, figs. 2i, 12, 20a [type-species: Astacus Blandingii Harlan, 1830:464].
- Subgenus Ortmanmanicus.—Hobbs, 1942a:342 [in part] [erroneous spelling].

DIAGNOSIS.—First form male with simple hooks on ischia of third and fourth pereiopods. Coxa of fourth pereiopod with conspicuous caudomesial boss. First pleopods strongly asymmetrical, often with rounded hump on cephalic surface proximal to terminal elements; subapical setae present; terminal elements comprising subspiculiform mesial process directed caudally or caudodistally, cephalic process hooding or situated lateral to central projection, caudal element represented by longitudinal ridge (caudal knob and caudal process absent), and central projection narrow and elongate or beaklike with apex directed caudally or caudodistally. Female lacking preannular plate; annulus ventralis with sinuous sinus crossing midlength; sternum immediately cephalic to annulus with or without tubercles.

RANGE.—North America and Middle America. New Jersey to Florida, northwestward to Wisconsin and Iowa, and southwestward to Puebla, Mexico.

NUMBER OF SPECIES AND SUBSPECIES.—There are 47, of which 6 are troglobitic.

Procambarus (Ortmannicus) erythrops Relyea and Sutton

FIGURE 57

?Procambarus pallidus.—Hobbs, 1971b:123 [in part, Suwannee County].



FIGURE 57.—Procambarus (Ortmannicus) erythrops (all holotypic first form male except b, d, from morphotypic second form male, and j from allotypic female): a, b, mesial view of first pleopods; c, basal podomeres of third, fourth, and fifth pereiopods; d, e, lateral view of first pleopods; f, lateral view of carapace; g, epistome; h, antennal scale; i, dorsal view of carapace; j, annulus ventralis; k, caudal view of first pleopods; l, dorsal view of distal podomeres of cheliped. (From Relyea and Sutton, 1975c, fig. 1.)

Troglobitic Procambarus.—Relyea and Sutton, 1975a:174. Procambarus erythrops Relyea and Sutton, 1975b:234-235 [nomen nudum].—Cooper and Cooper, 1975:4.

- Procambrus erythrops.—Relyea and Sutton, 1975b:234 [erroneous spelling].
- Procambarus (Ortmannicus) erythrops Relyea and Sutton, 1975c:8-14, figs. 1, 2.—Hobbs, 1975a:15.—Cooper and Cooper, 1975:5.

DIAGNOSIS.—Integument white to pale tan. Eyes reduced, lacking facets, but with red pigment spot. Areola 35.3 to 38.7 percent of total length of carapace. Single pair of cervical spines present. Postorbital ridges without spines or spiniform tubercles caudally. Hook on ischium of fourth pereiopod of male not overreaching basioischial articulation and not opposed by tubercle on basis; first pleopod with cephalic process partially hooding central projection. Female lacking caudally directed prominences on caudal margin of sternum immediately cephalic to annulus ventralis.

SIZE.—Carapace length 45.6 mm; postorbital carapace length 36.1 mm.

TYPES.—Holotype, allotype, and morphotype, USNM 133471, 133472, 133473 (JI, Q, JI); paratypes, RNHL, USNM.

TYPE-LOCALITY.—Sim's Sink, 1 mi (1.6 km) W of junction of U.S. Highways 27 and 129, and 0.1 mi (0.16 km) S of Highway 27, Suwannee County (Sec. 24, T. 6S, R. 14E), Florida, U.S.A.

RANGE.—U.S.A. Known only from Florida.

Suwannee County: (1) type-locality; (2) unnamed sink [? = Bufo Sink (Franz and Sutton, in press)] 0.2 mi (0.32 km) S of type-locality (Relyea and Sutton, 1975c:13); (3) Quarry Sink (Franz and Sutton, in press); (4) Hildreth Cave, 7 mi (11.3 km) E of Branford, 10 Mar 1962, R. D. Warren, coll. The latter locality, based on a juvenile male, should be confirmed.

ECOLOGICAL NOTES.—The following excerpts are taken from Relyea and Sutton (1975b:234–235).

[This crayfish was] found both at the bottom of the sink . . . and in crevices on the vertical limestone walls of the pool. We have observed and captured individuals from near the water's edge to a depth of about 13 m in the cave. The bottom of the sink is composed of decaying logs and detritus. A fine black silt in the cave may be a preferred substrate. The edge of the pool of water has a floating layer of decaying leaves which may afford cover and, ultimately, food. We suspect that the artificial roof allows the crayfish to use what once was a lighted and less suitable portion of the aquatic system of the sink. It seems likely that *P. erythrops* would retreat into deeper areas if the roof were not there.

They indicated that the population at Sim's Sink,

estimated to consist of 200 to 300 individuals, appeared to be largely concentrated in the area near the mouth of the cave "which probably reflects the energy funnel effect of sink holes such as this." They observed the crayfish feeding on detritus and referred to it as an "opportunist with respect to obtaining food." Frogs and toads have been observed in the sink and are believed by Relyea and Sutton to be important sources of "energy input," along with insects and rodents, into the subterranean habitat. The water temperature of the sinkhole remained at 22° C throughout January and February, and the water levels are reported to be "low through the winter months into May or June, when, with increasing rain, water level rises. We suspect that juveniles are dropped in conjunction with rising water. This would afford maximum dispersal of young as well as coincide with maximum organic input." They believe that males "patrol a territory while females seek protected areas" Copulation was observed in the laboratory with pairs remaining together as long as 12 hours. The only macroscopic troglobites known to be associated with P. erythrops are Troglocambarus maclanei which "is found in greater abundance deeper in the cave system, resulting in minimal overlap with P. erythrops," and a "troglobitic isopod [= amphipod, pers. comm. from Relyea], Crangonyx hobbsi"

LIFE HISTORY NOTES.—First form males have been collected from January to July and copulation was observed from March through July (Franz and Sutton, in press); no females carrying eggs or young have been observed.

Procambarus (Ortmannicus) horsti Hobbs and Means

FIGURE 58

Procambarus horsti Hobbs and Means, 1972:393, 401-408, fig. 2.-Relyea and Sutton, 1975c:14, fig. 3.

Procambarus (Ortmannicus) horsti.—Holt, 1973a:246, 248.— Hobbs, 1974b:56, 137, fig. 230; 1975a:15.—Caine, 1974a:490 [by implication].—Hobbs III, 1975:276.

Crayfish.-Peck, 1974b:31 [in part].

DIAGNOSIS.—Body white or colorless. Eyes reduced, lacking facets and pigment. Areola 40.2 to 41.8 percent of total length of carapace. Cervical spines multiple. Postorbital ridges with 2 or 3 spiniform tubercles caudally. Hook on ischium of

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fourth pereiopod of male overreaching basioischial articulation and opposed by low swelling on basis;

first pleopod with cephalic process situated lateral to central projection. Female with caudally di-



FIGURE 58.—Procambarus (Ortmannicus) horsti (a, c, j-l, holotypic first form male; b, e, morphotypic second form male; d, allotypic female): a, b, mesial view of first pleopods; c, lateral view of carapace; d, annulus ventralis; e, j, lateral view of first pleopods; g, epistome; h, dorsal view of carapace; i, caudal view of first pleopods; j, antennal scale; k, dorsal view of distal podomeres of cheliped; l, basal podomeres of third, fourth, and fifth pereiopods. (From Hobbs and Means, 1972, fig. 2.)

rected prominences on caudal margin of sternum immediately cephalic to annulus ventralis.

SIZE.—Carapace length 41.1 mm; postorbital carapace length 33.0 mm.

TYPES.—Holotype, allotype, and morphotype, USNM 132043, 132044, 132045 (σ I, φ , σ II); paratypes, USNM.

TYPE-LOCALITY.—Big Blue Springs (tributary to the Wacissa River), 2.2 miles (3.5 km) south of the cross-roads in the town of Wacissa, Jefferson County (SE 1/4, NW 1/4, Sec. 12, T. 2S, R. 3E), Florida, U.S.A.

RANGE.—U.S.A. Known only from the typelocality. "A single male collected from a 'welldigging rig' on the farm of Mr. Pichard, 4.5 mi [7.2 km] east of Tallahassee on the old St. Augustine Road, is tentatively assigned to this species" (Hobbs and Means, 1972:407).

ECOLOGICAL NOTES.—Quoting from a letter from Michael N. Horst, Hobbs and Means (1972:406) noted:

With underwater lights and safety lines, we entered the cave source going straight down, pulling ourselves in, as the water exiting the spring source has a great deal of force. The hard limestone bottleneck which we had entered was about ten feet [3 m] in length and opened into a small room which contained several branches The floor of this room was white with crayfish; a huge population In spite of the direct beams of our diving lights, the crayfish exhibited no variation in behavior. They extend throughout the entire spring, at least as far as we have been able to go with our diving gear, maximum depth being 70-80 feet [21-24 m]. I saw little in the way of food, aside from many intact gastropod shells In collecting the specimens, we encountered two individuals with some brown hue to their carapace Also, we noted in collecting the crayfish in the cave that they seem quite weak In general, they are inactive during the day and extremely active at night I found two or three specimens in protected areas of the "bowl," completely out of the cave itself, but near auxiliary entrances.

LIFE HISTORY NOTES.—First form males were found in October. No females carrying eggs or young have been observed.

Procambarus (Ortmannicus) lucifugus lucifugus (Hobbs)

FIGURE 59

Cambarus lucifugus.—not Packard, 1888:82 [lapsus for Crangonyx lucifugus Hay].—Hobbs, 1942c:56 [in part]; 1962:274 [in part]. White crawfish.-Hubbard, 1894:395 [in part].

- Cambarus acherontis.—Faxon, 1898:645-646, 692 [in part], pl. 62: figs. 1-5; 1914:368[?].—Harris, 1903b:67, 150 [in part].— Chappuis, 1927:91 [in part].—Wolf, 1934:104.—Mohr, 1939:202.—Hobbs, 1940:401; 1942b:8; 1962:273.—Hobbs and Barr, 1972:63.
- Cambarus lucifugus lucifugus Hobbs, 1940:387, 389, 393, 394, 397-403, 405, 406 [in part], fig. 17; 1942a:343; 1942b:8, 9.
- Procambarus lucifugus lucifugus.—Hobbs, 1942a:343, 349; 1942b:12, 13, 21, 31, 129–131, 134–137, 139, 147, figs. 151– 155; 1944:8; 1958a:160; 1958b:73, 77, 79, 81, 83, 86, 87 [by implication], fig. 14; 1962:282, 285, 286, fig. 41; 1971b:123, fig. 13.—Nicholas, 1960:134.—Warren, 1961:7, 10.—Hobbs and Barr, 1972:4, 63.—Relyca and Sutton, 1974:32.
- Procambarus lucifugus.—Pennak, 1953:458 [in part].—Hobbs, 1959:884 [in part].—Barr, 1968:65 [in part].—Peck, 1974c:56 [in part].—Relyea and Sutton, 1975b:235 [in part].— Cooper and Cooper, 1975:5 [in part].
- Procambarus (Orimannicus) lucifugus lucifugus.—Hobbs, 1972a:9-10; 1972b:54, 151, figs. 11e, 45b; 1974b:58, 137, fig. 228; 1975a:15.—Holt, 1973a:229, 246, 248.—Caine, 1974a:490 [by implication].—Relyea and Sutton, 1975c:8, 13, 14 [by implication].—Hobbs III, 1975:276.

Crayfish.-Peck, 1974b:31 [in part].

DIAGNOSIS.—Albinistic. Eyes reduced and without pigment or facets. Areola 38.0 to 40.0 percent of total length of carapace. Single pair of cervical spines present. Postorbital ridges without spines or spiniform tubercles caudally. Hook on ischium of fourth pereiopod of male not overreaching basioischial articulation and not opposed by tubercle on basis; first pleopod with cephalic process hooding central projection. Female lacking caudally directed prominences on caudal margin of sternum immediately cephalic to annulus ventralis.

SIZE.—Carapace length 41.1 mm; postorbital carapace length 34.1 mm.

TYPES.—Holotype, allotype, and "morphotype," USNM 77916, 77917, 77918 (JI, Q, JI); paratypes, MCZ, USNM.

TYPE-LOCALITY.—Gum Cave [= Sweet Gum Cave; Bat Cave], about 7 miles (11.3 km) SW of Floral City, Citrus County (NW 1/4, NE 1/4, Sec. 36, T. 20S, R. 19E), Florida, U.S.A.

RANGE.—U.S.A. Citrus and Hernando counties northward to Marion County, Florida, where intergrading with P. (O.) lucifugus alachua.

Florida. Citrus County: (1) type-locality (Hubbard, 1894:395). Hernando County: (2) unnamed cave, 14 mi (22.5 km) N of Weekiwachee (Hobbs, 1940:402). Lake County: (3) Eustis, no other locality data available (Faxon, 1914:368); this locality is included with reservation, for the specimens from it are not typical. Marion County: (4) Indian Cave



FIGURE 59.—Procambarus (Ortmannicus) lucifugus lucifugus (a, c, f-m, holotypic first form male; b, e, morphotypic second form male; d, allotypic female): a, b, mesial view of first pleopods; c, lateral view of carapace; d, annulus ventralis; e, f, lateral view of first pleopods; g, dorsal view of carapace; h, antennal scale; i, caudal view of distal part of first pleopod; j, basal podomeres of third, fourth, and fifth pereiopods; k, dorsal view of distal podomeres of cheliped; l, epistome; m, caudal view of first pleopods.

[= Last Resort Cave], about 7 mi (11.3 km) SW of Ocala, Sec. 36, T. 15S, R. 20E (Hobbs, 1940:406); (5) Waldo Cave, about 4 mi (6.4 km) SW of Ocala, Sec. 26, T. 15S, R. 21E (Hobbs, 1942b:139); (6) Eichelburger's Cave, 1.2 mi (1.9 km) W and 1 mi (1.6 km) S of Bellview, NW 1/4, Sec. 2, T. 17S, R. 22E, 23 Sep 1952, R. B. Cumming, coll.; (7) Roosevelt Cave, 2 mi (3.2 km) S of Ocala, 19 Oct 1960, R. D. Warren, coll. (Warren, 1961:7); (8) Steeple Cave (Franz and Sutton, in press); (9) Sunday Sink (Franz and Sutton, in press).

ECOLOGICAL NOTES.—The only notes available are on the type-locality, where, according to Hobbs (1942b:136),

at a depth of 75 feet [22.7 m] from the cave entrance several large pools of apparently still water occupy the major portion of the cave bottom. The pool from which most of the crayfish were taken is about 50 by 7 feet [15 by 2 m] and from 12 to 56 feet [3.6 to 17 m] deep. The water is very clear and has a temperature of 70° F [21.1°C]. The surface film is often thick with detritis, and the bottom of the pool has a layer of dark muddy silt which contains an abundance of insect parts. Roaches and beetles (Dermestidae) are common in the cave, but a large amount of the insect fragments are probably derived from the bat droppings, and the dead beetles and roaches which wash into the water provide a comparatively abundant food supply.

The only crayfish associate in Gum Cave is *Troglocambarus maclanei*. In Eichelburger's Cave, a crayfish tentatively identified as *P*. (O.) pallidus was found with it.

LIFE HISTORY NOTES.—First form males have been collected from February to May and in August. No females carrying eggs or young have been observed.

Procambarus (Ortmannicus) lucifugus alachua (Hobbs)

FIGURES 4, 60

Cambarus lucifugus alachua Hobbs, 1940:387, 389, 398, 402-406, fig. 18; 1942b:9; 1942c: pl. 1: figs. 7, 8.

- Cambarus lucifugus.-Hobbs, 1940:394 [in part]; 1942c:56 [in part]; 1962:274 [in part].
- Procambarus lucifugus alachua.—Hobbs, 1942a:343, 349; 1942b:12, 13, 21, 31, 129, 130, 134, 136-141, 147, figs. 156-160; 1943:206; 1944:8; 1958a:160; 1958b:73, 77, 79-81, 83, 86, 87 [by implication], fig. 16; 1962:282, 285, 286, fig. 42; 1969b:161; 1971b:123, fig. 14; 1975a:15.—Hoff, 1944:340.— Hart, 1959:204.—Walton and Hobbs, 1959:118, 119.—Hobbs and Barr, 1960:13; 1972:4.—Nicholas, 1960:134.—Warren, 1961:7, 9, 10.—M. R. Cooper, 1969:203, 204, 206, fig. 1.— Franz, 1970:74.—Holt, 1973a:229.—Relyea and Sutton, 1974:32.—D. G. Hart and C. W. Hart, 1974:128, 131.
- Procambarus lucifugus.-Hobbs, 1959:884 [in part].-D. S. Lee, 1969:211.-Peck, 1974c:56 [in part].-Relyea and

Sutton, 1974:32; 1975b:235 [in part].-Cooper and Cooper, 1975:4, 5 [in part].

- Procambarus (Ortmannicus) lucifugus alachua.—Hobbs, 1972a:10; 1972b:54, 151, fig. 45a; 1974b:58, 136, fig. 227; 1975a:15.—Holt, 1973a:229, 246, 248.—Caine, 1974a:490 [by implication].—Relyea and Sutton, 1975c:8, 14 [by implication].—Hobbs III, 1975:276.
- Troglobitic crayfishes .- Relyea and Sutton, 1972:14-15.

Crayfish .- Peck, 1974b:31 [in part].

DIAGNOSIS.—Albinistic, sometimes with brownish coloration on abdomen. Eyes reduced, lacking facets, but with black pigment spot. Areola 37.9 to 39.0 percent of total length of carapace. Single pair of cervical spines present. Postorbital ridges without spines or spiniform tubercles caudally. Hook on ischium of fourth pereiopod of male not overreaching basioischial articulation and not opposed by tubercle on basis; first pleopod with cephalic process hooding central projection. Female lacking caudally directed prominences on caudal margin of sternum immediately cephalic to annulus ventralis.

SIZE.—Carapace length 45.2 mm; postorbital carapace length 37.1 mm.

TYPES.—Holotype, allotype, and "morphotype," USNM 76592 (σ I, φ , σ II); paratypes, USNM.

TYPE-LOCALITY.—Hog Sink, about 10 miles (16 km) W of Gainesville, Alachua County (Sec. 24, T. 10S, R. 18E), Florida, U.S.A.

RANGE.—U.S.A. Southwestern Alachua and western Gilchrist counties, Florida, intergrading with P. (O.) l. lucifugus in Marion County.

Florida. Alachua County: (1) type-locality; (2) Goat Sink, about 11 mi (18 km) W of Gainesville, Sec. 20, T. 9S, R. 18E (Hobbs, 1942b:137); (3) Squirrel Chimney, about 11 mi (18 km) NW of Gainesville, Sec. 21, T. 9S, R. 18E (Hobbs, 1942b:137); (4) Dudley's Cave, about 13 mi (21 km) W of Gainesville, Sec. 32, T. 9S, R. 18E (Hobbs, 1942b:137); (5) Protheroe Sink, Sec. 24, T. 108, R. 18E (Warren, 1961:8); (6) Cueva Frio, about 10 mi (16 km) W of Gainesville, Sec. 24, T. 10S, R. 18E, adjacent to Hog Sink, 23 Mar 1941, L. J. Marchand and H.H.H., Jr., coll.; (7) Bat Cave, Sec. 18, T. 9S, R. 17E, 21 May 1972, B. F. Mansell and F. Hurt, coll.; (8) Martin's Cave, 5 mi (8.1 km) N of Newberry (Relyea and Sutton, 1974:32); (9) Seven Chimneys, Sec. 17, T. 9S, R. 17E (Franz and Sutton, in press). Gilchrist County: (10) Robert's Cave, Sec. 11, T. 95, R. 14E (Warren, 1961:8); (11) Bat Hole (Franz and Sutton, in press).

ECOLOGICAL NOTES.—This crayfish has been found in a variety of sinks several of which were described by Hobbs (1942b:138-139). In some of them, the pools supporting the crayfish are in total darkness, and, in others, varying degrees of light reach the area occupied by the crayfish. In at least one,



FIGURE 60.—Procambarus (Ortmannicus) lucifugus alachua (a, c, f-l, holotypic first form male; b, e, morphotypic second form male; d, allotypic female): a, b, mesial view of first pleopods; c, lateral view of carapace; d, annulus ventralis; e, f, lateral view of first pleopods; g, dorsal view of carapace; h, epistome; i, antennal scale; j, dorsal view of distal podomeres of cheliped; k, caudal view of distal part of first pleopod; l, basal podomeres of third, fourth, and fifth pereiopods.

Goat Sink, the pool receives direct light, reduced only by the steep sides of the sink and the overhanging trees. As pointed out by Hobbs (1942b:19), "these underground waters, at least throughout the peninsula, show very little variation in either temperature or pH, being around 70° [F] [21.1° C] and 7.1 respectively." In several of the localities, rather

large populations were present in the areas receiving organic materials through rain wash into the sinks, and in those pools open to filtered or direct light where tree litter falls directly into the water. Relyea and Sutton (1974:32) reported a large specimen of P. (O.) l. alachua from the stomach of a catfish, Ictalurus natalis, collected in Martin's Cave.

LIFE HISTORY NOTES.—First form males have been collected from October to April, and Franz and Sutton (in press) stated that copulation had been observed from March through July. No females carrying eggs or young have been reported.

Procambarus (Ortmannicus) orcinus Hobbs and Means

FIGURE 61

- Procambarus pallidus.—Hobbs, 1958b:81 [in part]; 1971b:123 [in part].—Hobbs and Hart, 1959:149.—Warren, 1961:8 [in part].
- Procambarus orcinus Hobbs and Means, 1972:393-401, 408, fig. 1.-Holt, 1973a:229.
- Procambarus (Ortmannicus) orcinus.—Holt, 1973a:226, 246, 248.—Caine, 1974a:490 [by implication].—Hobbs, 1974b:58–59, 137, fig. 231; 1975a:15.—Relyea and Sutton, 1975c:14, fig. 4 [by implication].—Hobbs III, 1975:276.

Crayfish.-Peck, 1974b:31 [in part].

DIAGNOSIS.—Albinistic, often with subcuticular tissues pinkish orange. Eyes reduced, lacking facets, but with red pigment spot. Areola 31.0 to 35.6 percent of total length of carapace. Cervical spines multiple. Postorbital ridges with 2 to 5 spines caudally. Hook on ischium of fourth pereiopod of male overreaching basioischial articulation and opposed by tubercle on basis; first pleopod with cephalic process situated lateral to central projection. Female with caudally directed prominences on caudal margin of sternum immediately cephalic to annulus ventralis.

SIZE.—Carapace length 25.3 mm; postorbital carapace length 19.1 mm.

TYPES.—Holotype, allotype, and morphotype, USNM 132031, 132032, 132033 (JI, Q, JI); paratypes, USNM. TYPE-LOCALITY.—Gopher Sink, 3.1 mi (5 km) SW of Florida Road 61 and 0.2 mi (0.5 km) E of Florida Road 369, Leon County (SW 1/4, NW 1/4, NE 1/4, Sec. 16, T. 2S, R. 1W), Florida, U.S.A.

RANGE.—U.S.A. Restricted to the panhandle of Florida between the Apalachicola and Aucilla rivers. The following localities are from Hobbs and Means (1972:399).

Florida. Leon County: (1) type-locality; (2) Osgood Sink, NE 1/4, Sec. 11, T. 2S, R. 1E; (3) Culley's Cave, SE 1/4, Sec. 17, T. 2S, R. 1W. Wakulla County: (4) Wakulla Springs, Sec. 11, T. 3S, R. 1W.

ECOLOGICAL NOTES.—Sinkholes and subterranean streams serve as habitats for this crayfish. In the type-locality, according to Hobbs and Means (1972: 400–401), they

were found clinging upside-down to the ceiling and head down on the vertical sidewalls. The first individuals seen were about 25 feet [8 m] from the mouth of the cavern, and sightings became more frequent with increasing penetration to about 150 feet [45 m], beyond which no collections were made, although crayfish were observed deeper in the cavern. Light was just perceivable 150 feet [45 m] from the mouth, indicating that these animals are abundant in the twilight zone. Individuals were most numerous along the walls, especially where there were cracks and fissures near the floor. When disturbed, they swam toward the bottom. If pursued, the majority came to rest partially buried in the bottom sediments On one occasion, an isopod was apparently eaten by a crayfish within 10 minutes after being brought to the surface. Dead and injured crayfish were usually cannibalized if not removed from containers shortly after arrival at the surface.

Other animals observed in the twilight zone of the cavern were Palaemonetes paludosus, the eel Anguilla rostrata, and the minnow Hybopsis harperi.

LIFE HISTORY NOTES.—First form males were collected in February and April. No females carrying eggs or young have been observed; however, a copulating pair was seen at the type-locality on 3 April 1971 (Hobbs and Means, 1972:400).

Procambarus (Ortmannicus) pallidus (Hobbs)

FIGURES 4, 62

Cambarus acherontis .- Hobbs, 1937:154.

- Cambarus acherontis pallidus Hobbs, 1938:90-91 [nomen nudum].
- Cambarus pallidus Hobbs, 1940:387, 389, 394-398, fig. 16; 1942b:9; 1942c:56, pl. 1: figs. 11, 12.
- Procambarus pallidus.-Hobbs, 1942a:343, 349; 1942b:12, 21, 31, 129, 130, 134, 135, 137-142, 147, figs. 161-165; 1944:8;



FIGURE 61.—Procambarus (Ortmannicus) orcinus (a, c, f-l, holotypic first form male; b, e, morphotypic second form male; d, allotypic female): a, b, mesial view of first pleopods; c, lateral view of carapace; d, annulus ventralis; e, f, lateral view of first pleopods; g, dorsal view of carapace; h, epistome; i, caudal view of first pleopods; j, antennal scale; k, dorsal view of distal podomeres of cheliped; l, basal podomeres of third, fourth, and fifth pereiopods. (From Hobbs and Means, 1972, fig. 1.)



FIGURE 62.—Procambarus (Ortmannicus) pallidus (a, c, f-m), holotypic first form male; b, e, morphotypic second form male; d, allotypic female): a, b, mesial view of first pleopods; c, lateral view of carapace; d, annulus ventralis; e, f, lateral view of first pleopods; g, caudal view of distal part of first pleopod; h, dorsal view of carapace; i, caudal view of first pleopods; f, epistome; k, antennal scale; l, dorsal view of distal podomeres of cheliped; m, basal podomeres of third, fourth, and fifth pereiopods.

1958a:160; 1958b:73, 77, 79, 81, 83, 86, 87, fig. 20; 1959:884; 1962:286, fig. 43; 1971b:114-115, 123, figs. 15, 19b.— Pennak, 1953:458.—Chace, 1954:322.—Walton and Hobbs, 1959:119.—Hobbs and Hart, 1959:149.—Nicholas, 1960: 134.—Warren, 1961:8, 10.—Mohr and Poulson, 1966:135, 204.—Franz, 1970:74.—Hobbs and Barr, 1972:4.—Hobbs and Means, 1972:393, 408.—D. G. Hart and C. W. Hart, 1974:131.—Peck, 1974c:56.—Relyea and Sutton, 1975a:173-174; 1975b:235.—Cooper and Cooper, 1975:4.

Procambarus (Ortmannicus) pallidus.—Hobbs, 1972a:10; 1972b:54, 151, figs. 9b, 45c; 1974b:59, fig. 229; 1975a:15.— Caine, 1974a:490 [by implication].—Relyea and Sutton, 1975c:8, 14 [by implication].—Hobbs III, 1975:276.

Crayfish.-Peck, 1974b:31 [in part].

Procambrus pallidus.—Relyea and Sutton, 1975a:174, fig. 1 [erroneous spelling].

DIAGNOSIS.—Albinistic, eyes reduced, lacking facets and pigment. Areola 38.0 to 43.0 percent of total length of carapace. Single pair of cervical spines present. Hook on ischium of fourth pereiopod of male overreaching basioischial articulation but not opposed by tubercle on basis; first pleopod of first form male with cephalic process partially hooding central projection, latter beaklike. Female with caudally directed prominences on caudal margin of sternum immediately cephalic to annulus ventralis.

SIZE.—Carapace length 39.6 mm; postorbital carapace length 32.5 mm.

TYPES.—Holotype and allotype, USNM 76591 (σ I, φ); "morphotype," USNM 79350 (σ II); paratypes, MCZ, USNM.

TYPE-LOCALITY.—Warren's Cave, 11 miles (17.7 km) NW of Gainesville, Alachua County (Sec. 13, T. 9S, R. 18E), Florida, U.S.A.

RANGE.—U.S.A. Known only from Florida where it occurs in the northwestern part of Alachua County, southwestern Columbia County, and western Suwannee County. Tentatively assigned to the species are specimens from southern Marion and eastern Madison counties.

Florida. Alachua County: (1) type-locality; (2) Hog Sink, Sec. 24, T. 10S, R. 18E (Hobbs, 1942b:140); (3) Devil's Hole, Sec. 18, T. 10S, R. 18E (Hobbs, 1942b:140); (4) Pallidus Sink, Sec. 15, T. 8E, R. 17E (Hobbs, 1942b:140); (5) High Springs Cave, Sec. 2, T. 8S, R. 17E (Hobbs, 1942b:140); (6) Squirrel Chimney, Sec. 21, T. 9S, R. 18E (Hobbs, 1942b:140); (7) Protheroe Sink, Sec. 24, T. 10S, R. 18E (Warren, 1961:8); (8) Still Sink, Sec. 29, T. 9S, R. 18E (Warren, 1961:8); (9) Pumped from well, 150 feet (45 m) deep, across road from Four O'Clock Church [= Fort Clark Church], W of Gainesville, 11 Nov 1954, Babb and Pirkle, coll.; (10) Chimney

Sink, 0.5 mi (0.8 km) N of Newberry on U. S. Highway 41, 6 May 1939, W. M. McLane and H.H.H., Jr., coll.; (11) Hornsby Sink near High Springs, 26 Dec 1968, W. Hulet, coll.; (12) Goat Sink, about 11 mi (18 km) W of Gainesville, Sec. 20, T. 9S, R. 18E (Franz and Sutton, in press). Columbia County: (13) River Bed Cave, 3 mi (4.8 km) W of High Springs on U.S. Highway 27, Sec. 13, T. 7S, R. 16E (Hobbs, 1940:398). Madison County: (14) Suwanacoochee Spring, Ellaville, 4 Jul 1971, S. Maegerlein, coll. Marion County: (15) Eichelburger's Cave, 1.2 mi (2 km) W and 1 mi (1.6 km) S of Bellview, NW 1/4, Sec. 2, T. 17S, R. 22E, 23 Sep 1952, R. B. Cumming, coll. Suwannee County: (16) unnamed sink in Peacock Slough system, about 3 mi (5 km) E of Lauraville, 9 Jul 1970, W. F. Smith-Vaniz, coll.

Localities cited previously for Leon and Wakulla counties, Florida, are based on erroneous determinations of *P*. (*Ortmannicus*) orcinus. See the synonomy for the latter.

ECOLOGICAL NOTES .- Descriptions of several habitats in which this crayfish occurs are presented by Hobbs (1942b:140-142), who indicated that only in one locality had the species been reported to have been present in numbers, and it was not seen or was very rare there (Devil's Hole) when he visited it on subsequent occasions. Devil's Hole is different from any other habitat in which the species was found by us in that the water is frequently coffeecolored rather than being clear; only after extended periods without rain does the dark coloration disappear. "It is an open sink with an overhanging wall of limestone; the water is exposed to sunlight, and it is very dark in color as compared with water in which all of the rest of my cavernicoles have been taken, and it is distinctly stagnant. Scattered over the muddy bottom of the pool which is shallow near the edge and progressively deeper under the overhanging wall are many rocks, dead tree trunks, and limbs" (Hobbs, 1942b:142).

Procambarus (O.) pallidus was the first troglobitic crayfish to be collected by one of us (Hobbs, Jr.), and it was discovered in a small solution cavity in an abandoned course of the Santa Fe River in Columbia County, Florida, in March 1935. In "River Bed Cave," when first visited by me in company with my father, access to the water was limited to a subcylindrical narrow passage that could be negotiated only in a prone position. This tunnel, some two meters in length and disposed at an angle of 45 degrees to the surface, intersected the water table where there was no room for turning around. Equipped with a flashlight and a coffee strainer, I entered the tunnel head first and ob-

Procambarus .- Mohr and Poulson, 1966:136-140.

procambarus pallidus .- Padgett, 1970:19.

136 served some 6 to 10 crayfish at rest or moving

slowly about just beyond arm's length. When my light was trained directly upon an animal, it moved away from the beam, but, within a few minutes, I discovered that if the spot of light was placed in front of one of them, it moved slowly toward the illuminated spot. By keeping the lighted area several centimeters in front of the crayfish, I succeeded in attracting the animal close enough so that I was able to pin it to the silty substrate with my strainer and transfer it to a container. The commotion involved in catching this specimen apparently caused the other crayfish to move well out of range and no others could be enticed to move toward me. Ironically, to get out of the "hole" with the crayfish, my father had to pull me out by my heels! On a subsequent visit to the cave, better access to this exposed pool was made possible by enlarging another entrance, whereupon additional specimens were obtained.

In none of the caves that supported populations of this species was a current detected in the water. Surely there must be channels in the porous limestone galleries at lower levels, and the fact that the single female from Madison County assigned to this species came from Suwanacoochee Spring near Ellaville suggests that the species is not confined to lentic habitats.

One specimen of P. (O.) pallidus was taken from the stomach of a catfish, *Ictalurus natalis*, collected in Chimney Sink (see locality 10 above), and another was obtained from a well 150 feet (45 m) deep (see locality 9 above). Squirrel Chimney is described in "Remarks" (p. 140).

LIFE HISTORY NOTES.—First form males have been collected in March, April, July, October, and December. The only ovigerous female known is that reported by Relyea and Sutton (1975a:173– 174), which was collected in Squirrel Chimney, Alachua County, in November 1971, and maintained in the laboratory where it was estimated to lay approximately 130 eggs on 1 or 2 March 1972. The eggs were described as being white and having a diameter of approximately 2 mm. The eggs did not hatch; most dropped from the pleopods on March 7 after which the female was preserved. No females carrying young have been reported.

Subgenus Remoticambarus

Subgenus Remoticambarus Hobbs, 1972a:11, figs. 2m, 16, 20b [type-species, Procambarus pecki Hobbs, 1967b:2].

DIAGNOSIS.—Male with simple hooks on ischia of third pereiopods; coxa of fourth pereiopod with prominent, bulbous, caudomesial boss. First pleopods symmetrical, with strong shoulder on cephalic surface proximal to terminal elements; subapical setae absent; terminal elements consisting of welldeveloped mesial process directed distolaterally, obscuring central projection in caudal aspect, and acute central projection; caudal knob, cushion-like prominence, caudal process, and cephalic process absent. Female lacking preannular plate; annulus ventralis with short, curved sinus on caudal wall; sternum immediately cephalic to annulus unadorned.

RANGE.—U.S.A. Restricted to the Tennessee River basin in Colbert, Lauderdale, and Morgan counties, Alabama.

NUMBER OF SPECIES .- Monotypic.

Procambarus (Remoticambarus) pecki Hobbs

FIGURE 63

- Procambarus pecki Hobbs, 1967b:2-8, 10-15, figs. 1-12, 18, 21g; 1969b:119, 130; 1972a:11; 1974a:15; 1974b:65.—Hobbs and Barr, 1972:1, 4, 52, 65.—Caine, 1974a:488.—Cooper and Kuchne, 1974:492.
- New troglobitic form .- Cooper and Cooper, 1970:23.
- Procambarus (Remoticambarus) pecki.—Hobbs, 1972a:11, figs. 2m, 16; 1972b:31, 32, 151, figs. 11g, 22b, 23a; 1974a:15; 1974b:65, fig. 279.—Holt, 1973a:231, 246, 248.—Hobbs III, 1975:276.

DIAGNOSIS.—Same as that for subgenus. In addition, albinistic, eyes reduced and without pigment.

SIZE.—Carapace length 31.0 mm; postorbital carapace length 24.2 mm.

TYPES.—Holotype, allotype, and morphotype, USNM 117684, 117685, 117686 (*J* I, *Q*, *J* II); paratypes, MCZ, TU, USNM.

TYPE-LOCALITY.—McKinney Pit Cave, about 2.5 miles (4 km) W of Tuscumbia, Colbert County (Sec. 10, T. 4S, R. 12W), Alabama, U.S.A.

RANGE.—U.S.A. Same as for subgenus.

Alabama. Colbert County: (1) type-locality. Morgan County: (2) Cave Spring Cave, SE 1/4, NE 1/4, SW 1/4, Sec. 4, T. 6S, R. 3W (Hobbs, 1967b:7). Lauderdale County: (3) Key Cave, SE 1/4, NW 1/4, SW 1/4, Sec. 35, T. 3S, R. 12W (Hobbs, 1967b:7).

ECOLOGICAL NOTES.—Cooper and Kuehne (1974: 492) describe the habitat and associates in Key Cave. The following notes are available on the type-locality (Hobbs, 1967b:5):


FIGURE 63,—Procambarus (Remoticambarus) pecki (all holotypic first form male except b, d, from morphotypic second form male, and g from allotypic female): a, b, mesial view of first pleopods; c, dorsal view of carapace; d, e, lateral view of first pleopods; f, epistome; g, annulus ventralis; h, basis and ischium of third pereiopod; i, antennal scale; j, caudal view of first pleopod; k, basal podomeres of third, fourth, and fifth pereiopods and first pleopods; l, dorsal view of distal podomeres of cheliped. (From Hobbs, 1967b, figs. 1–12.)

The entrance to the cave is a vertical sinkhole some 30 feet [9.1 m] in depth, located at the foot of a ravine. After the initial drop, the level of the cave descends gradually to an irregular pool of standing water approximately 150 square feet in area and ranging in depth from one to four feet [0.3-1.2 m]. The bottom is covered with a heavy layer of silt. The far end of this pool connects with extensive channels of deeper water. Following heavy rains, much debris from the surface apparently washes into the cave.

LIFE HISTORY NOTES.—First form males have been collected in March, April, July, and December. Females with eggs or young have not been observed.

Genus Troglocambarus

Troglocambarus Hobbs, 1942a:345 [type-species: Troglocambarus maclanei Hobbs, 1942a:345].

Trolgocambarus.-Vandel, 1964:603 [erroneous spelling].

DIAGNOSIS.—Third maxilliped greatly enlarged, reaching much beyond apex of rostrum, and lacking teeth on mesial margin of ischium. Branchial count 16 + ep. Male with coxa of fourth pereiopod bearing caudomesial boss; hooks on ischia of third and fourth pereiopods; first pleopods asymmetrical and terminating in 4 distinct parts. Female with annulus ventralis freely movable and with rudimentary first pleopods.

RANGE.—U.S.A. Restricted to Florida. NUMBER OF SPECIES.—Monotypic.

Troglocambarus maclanei Hobbs

FIGURES 4, 64, 65

White crawfish.—Hubbard, 1894:395 [in part].
Troglocambarus maclanei Hobbs, 1942a:345–350, pls. 1, 2; 1942b:7, 9, 12, 13, 21, 28, 138, 141, 146–149, pls. 1, 10: figs. 171–175; 1944:8; 1958b:87; 1959:883; 1963:8; 1971b:122, figs. 17, 19a; 1972b:18, 152, figs. 5b, 9a; 1974a:16, fig. 11; 1974b: 68, fig. 294; 1975a:14; 1976:547.—Pennak, 1953:458, 462.—Eberly, 1954:59.—Chace, 1954:322.—Nicholas, 1960:134.—Warren, 1961:8–10.—Barr, 1968:64, 65, fig. 17.—Mohr and Poulson, 1966:136–141, 204.—Holt, 1968:87; 1973a:229, 246, 248.—D. S. Lee, 1969:211.—Franz, 1970:74.—Hobbs and Barr, 1972:4.—Peck, 1974c:55–56.—Relyea and Sutton, 1975b:235; 1975c:13.—Cooper and Cooper, 1975:4, 5.
Troglocambarus.—Balss, 1957:1574.

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T[roglocambarus] Maclanei.—Franz, 1970:74.

Crayfish.-Peck, 1974b:31 [in part].

DIAGNOSIS.—Identical to that of Genus Troglocambarus. SIZE.—Carapace length approximately 15.5 mm; postorbital carapace length 13.0 mm.

TYPES.—Holotype, allotype, and "morphotype," USNM 79385, 79386, 79387 (♂I, ♀, ♂II); paratypes, MCZ, USNM.

TYPE-LOCALITY.—Squirrel Chimney, about 11 miles (18 km) northwest of Gainesville, Alachua County (Sec. 21, T. 9S, R. 18E), Florida, U.S.A.

RANGE.—U.S.A. Citrus to Suwannee counties, Florida.

Florida. Alachua County: (1) type-locality; (2) Goat Sink, about 11 mi (18 km) W of Gainesville, Sec. 20, T. 9S, R. 18E (Hobbs, 1942a:350). Citrus County: (3) Gum Cave [= Sweet Gum Cave; Bat Cave], about 5 mi (8 km) SW of Floral City, NW 1/4, NE 1/4, Sec. 36, T. 20S, R. 19E (Hobbs, 1942a:350). Marion County: (4) Indian Cave [= Last Resort Cave], 7 mi (11.3 km) SW of Ocala, Sec. 36, T. 15S, R. 20E, 6 Qct 1962, R. D. Warren, coll.; (5) Sunday Sink (Franz, pers. comm.). Suwannee County: (6) Sin's Sink, 1 mi (1.6 km) W of junction of U.S. Highways 27 and 129, and 0.1 mi (0.2 km) S of Highway 27, Sec. 24, T. 6S, R. 14E (Relyea and Sutton, 1975b:235).

ECOLOGICAL NOTES .- This crayfish appears to be confined to subterranean pools where it is usually found clinging ventral-side-up to submerged limestone ceilings. Most of the specimens collected were plucked by hand from their pendant position; only a few have been found on the floor of pools in company with larger troglobitic species of the genus Procambarus (Figure 4). In all of the caves from which this crayfish has been reported, the water was clear, with a temperature of 20° to 21° C. In most of the caves, the bottoms of the pools were coated with fine silt; in some, they were covered by debris consisting mostly of tree litter, interspersed with large limerock outcrops. Rarely are loose limerock masses present in the pools. According to Mohr and Poulson (1966:138), this crayfish has been observed striking, with its third maxillipeds, at a floating fruit fly in a manner reminiscent of a praying mantis; however, the crayfish was not successful in capturing the fly.

Frequently the antennae are brought toward the mouth and drawn through the setae-studded third maxillipeds. Suspecting that *T. maclanei* was a filter feeder, on the basis of these tremendously enlarged appendages and the way in which they were positioned to filter water passing forward from the gill chamber, one of us (Hobbs, Jr.) placed two individuals in an aquarium, leaving them together overnight. The following morning, the larger of



FIGURE 64.—Troglocambarus maclanei, dorsal view of first form male from Squirrel Chimney. (From Hobbs, 1942b, pl. 1.)

the two was in the process of devouring the smaller!

Relyea and Sutton (1975b:235) pointed out: "The only other large troglobite associated with *P.* erythrops [in Sim's Sink] is the crayfish *Troglocam*barus maclanei. The latter is found in greater abundance deeper in the cave system, resulting in minimal overlap with *P. erythrops. Troglocambarus* maclanei is a coinhabitant of other Florida caves with *Procambarus pallidus* and *P. lucifugus*.... In these situations *T. maclanei* also probably occupies lower energy zones."

LIFE HISTORY NOTES.—First form males have been reported as collected only in March, July, August, and September. Females carrying eggs or young have not been observed.

REMARKS.—To our knowledge, the first specimen of the species to be collected was a female obtained by W. T. Swingle, H. J. Webber, and H. G. Hubbard in Gum Cave, Citrus County, Florida, in July 1894. This crayfish, in the collection of the Smithsonian Institution, was in a jar also containing *Procambarus* (O.) *lucifugus lucifugus* and was not recognized until examined by Martha R. Cooper about a decade ago.

Mohr and Poulson's (1966:136-141) rather detailed account of the "rediscovery" of Troglocam-



FIGURE 65.—Troglocambarus maclanei, (types from Squirrel Chimney): a, dorsal view of anterior region; b, mesial view of first pleopod of first form male; c, mesial view of first pleopod of second form male; d, lateral view of first pleopod of second form male; e, lateral view of first pleopod of first form male; f, ventral view of third maxillipeds; g, annulus ventralis; h, basal podomeres of third, fourth, and fifth pereiopods of first form male.

barus maclanei by McLane and Hobbs and of subsequent early collections of this crayfish is not entirely accurate, and it seems appropriate here to recount the events as Hobbs, Jr., remembers and has recorded some of them. Before doing so, however, it is pertinent to quote the original description of the type-locality (Hobbs, 1942a:347, 349): Squirrel Chimney, as its name indicates, is a circular solution cavity with almost vertical walls, the latter supporting a luxuriant growth of liverworts, mosses, and small ferns. The "chimney" penetrates the surface soil and limestone to a depth of approximately 50 feet [15 m] where it strikes the water table. Debris has fallen into the sink and has accumulated at the water level so that a little less than half the opening contains water, the rest of it being covered over with fallen leaves which are supported by dead tree

trunks and limbs. Within six to eight feet [2 to 2.4 m] of the bottom a small opening about three feet [1 m] in diameter leads out into a fissure about 25 yards [23 m] long and four feet [1.2 m] wide, the whole bottom of which is filled with water ranging in depth from a few inches to 30 feet [9 m] at the deepest place sounded. The light is very dim inside of the fissure, even at the opening, and a short distance away, to the eye it is completely dark. The water is very clear; however, the surface film sometimes supports a coat of fine silt and debris. The bottom consists of mud, sand, and silt with large limerock outcrops.

Excellent photographs of this solution cavity are presented by Mohr and Poulson (1966:184–186).

A common interest in cave faunas shared by Professor H. B. Sherman (a student of Chiroptera) and me (Hobbs, Ir.) led us to undertake a survey of the caves in the Gainesville, Florida, area. We borrowed from the County Agent aerial photographs of Alachua County that had been made during the winter months and made photostatic copies which could be taken into the field. With these in hand, we rode along the section lines in the county, stopping to inspect any area indicated by a dark spot on the map. Such spots were usually indicative of the presence of nondeciduous trees growing in depressions (sinkholes) or around the mouths of caves. Since that part of Florida is mostly flat, the roads along the section lines are almost straight and nowhere along them is one more than one-half mile (0.8 km) away from any likely looking spot within the mile-square areas. On 19 March 1941, Professor Sherman, James J. Friauf, the late William A. McLane, and I visited Goat Sink and also examined several areas that appeared on the photographs as possible sinkholes. It was late in the afternoon, and McLane and I left the car for a quick look at a possible sinkhole near the road. The spot we had stopped to examine proved to be nothing more than a shallow depression, but on our way back to the car where Professor Sherman and Jim Friauf were awaiting us, we saw a subcylindrical solution cavity, which we dubbed "Squirrel Chimney," because on our approach a squirrel scurried up the wall into a nearby tree. We hastened back to the car for a rope, and the two of us dropped off into the pit, Professor Sherman and Jim awaiting us at the surface. As we approached the debris-littered bottom, we saw several albinistic crayfish among the submerged tree trunks and limbs. Upon entering the opening leading to the fissure, we spied a number of comparatively large troglobitic forms that I assumed to be *Procambarus* pallidus. With that conviction, I said to McLane, "Billy, if you catch one of them and it's a new one, I'll name it for you." In any case, he jumped into the water at the shallow end of the fissure, flourishing a net in an attempt to bag one or more of the crayfish in view. Following a few passes with the net, the water became so clouded I suggested that we leave. Not until we had scaled the rope and reached the surface did McLane hand me a vial containing a crayfish, saying, "Sorry, Doc, I missed the big ones but here is a little one." He himself had not seen the animal and its capture in the net was purely accidental!

Even without a hand lens it was obvious to me that he had collected something startling in the way of a crayfish, and if not a "freak" an animal that would bear his name. It was too late to go back into the chimney that afternoon. The following day, however, an attempt was made to organize a small "expedition" to return to Squirrel Chimney. Most of my usual caving companions were involved in classes (at the University of Florida), and only A. C. Chable could get away. We were in the car, ready to leave, when my old friend and collecting companion on many forays, Lewis J. Marchand, was seen walking across the campus toward the Chemistry Building. Being aware of his weakness for "water goggling" (diving without snorkel or reserve air supply), I hailed him with "Why don't you go with us out to this new cave?" and added, with some reluctance, "It's a wonderful place for water goggling!" That was enough to cause him to postpone studying for an organic examination the following day.

Once within the fissure off the chimney and a little miffed by my misleading account of the "wonderful place for water goggling," he good-naturedly entered the water and made short forays to the bottom of the pool, collecting a number of specimens of *Procambarus pallidus*. Becoming somewhat more familiar with the immediate surroundings, he swam farther away from the fissure while Chable and I, straddling it, trained our light so that he could find his way back to where he might surface. After repeated dives and failure to find the new crayfish, he was ready to abandon the project but agreed to make one more dive. This time, upon approaching the fissure, he rolled onto his back and his light struck the submerged ceiling where he saw and collected a specimen of the species that was to be called *Troglocambarus maclanei*, the second specimen that I had seen. Four more specimens were plucked from the submerged ceiling of Squirrel Chimney by him that afternoon.

As pointed out by Mohr and Poulson (1966:136), it is probable that the activity of McLane in attempting to catch specimens of P. pallidus caused the little second form male caught by him to become "dislodged" from the adjacent ceiling. The only specimen collected by me was one that was thus dislodged when, on a later date, Marchand jumped into the water, and I saw it drifting toward the bottom and was able to net it.

Section ANOMURA

Family AEGLIDAE

Genus Aegla

Galathea.-Latreille, 1818, pl. 308:fig. 2 [not Fabricius, 1793:471].

Aegla Leach, 1821:49 [type-species: Galathea laevis Latreille, 1818:4, pl. 308: fig. 2.].

Aeglea .- Desmarest, 1825:187 [erroneous spelling].

DIAGNOSIS.—Body depressed. Branchial region of carapace marked by complex arrangement of sutures. Second and third pereiopods nonchelate, fifth pereiopod conspicuously smaller than second, third, and fourth, its coxa situated mesial and slightly caudal to that of fourth pereiopod. Telson with median longitudinal suture. Basal segment of uropod at least half as long as lateral ramus.

RANGE.—South America. Between 20°30'S and 40°28'S (Schmitt, 1942:431).

NUMBER OF SPECIES.—Approximately 25 species, only one of which is troglobitic (Burns, 1972:596).

Aegla cavernicola Türkay

FIGURE 66

Aegla cavernicola Türkay, 1972:415-417, fig. 1, pl. 1: figs. 1, 2.

DIAGNOSIS.—Eyestalks conical, narrowing distally; cornea distinctly smaller than in other species of the genus. Rostrum highly keeled and clearly overreaching eyestalks. Only first hepatic lobe of carapace clearly delimited. (Adapted from Türkay, 1972:415.) SIZE.—Carapace length 15 mm; carapace width 13 mm (Türkay, 1972:417).

TYPES.—Holotype (Q) NMG.

TYPE-LOCALITY.—"Grutas das Areias," São Paulo, Brazil.

RANGE.—Brazil. Known only from the type-locality.

ECOLOGICAL NOTES.—The single specimen known was taken from a freshwater basin with a slight current more than 300 m within the cave.

LIFE HISTORY NOTES .- None available.

Section BRACHYURA

Family PSEUDOTHELPHUSIDAE

Genus Potamocarcinus

Telphusa.-Latreille, 1825a:564 [not Latreille, 1825a:561].

Potamia.—Randall, 1839:120 [not potamia Latreille, 1831:338]. Potamocarcinus H. Milne Edwards, 1853:208 [type-species:

- Potamocarcinus armatus H. Milne Edwards, 1853:208]. Potomocarcinus.—H. Milne Edwards, 1853:208 [erroneous
- spelling].
- Boscia H. Milne Edwards, 1853:208 [in part] [type-species: Telphusa dentata Latreille, 1825a:564].
- Pseudothelphusa.—Smith, 1870:146 [in part] [not Pseudo-Thelphusa de Saussure, 1857:305].
- Rathbunia Nobili, 1896:1 [type-species: Rathbunia Festae Nobili, 1896:2].
- Hypolobocera Ortmann, 1897:323 [type-species, Polamia chilensis H. Milne Edwards and Lucas, 1843:22; originally proposed as genus, utilized by Bott (1967b:365) as subgenus].
- Kingsleya Ortmann, 1897:324 [type-species: Potamia latifrons Randall, 1839:120; originally proposed as genus, utilized by Bott (1967a:302) as subgenus].
- Typhlopseudothelphusa Rioja, 1953a:291 [nomen nudum]; 1953b:217 [type-species: Typhlopseudothelphusa mociñoi Rioja, 1953b:218].
- Typhloseudothelphusa.-Rioja et al., 1955:313 [erroneous spelling].
- Subgenus Megathelphusa Smalley, 1964b:9 [type-species: Pseudothelphusa magna Rathbun, 1895:377].
- Subgenus Anaphyromos Smalley, 1964c:651 [type-species: Pseudothelphusa tuberculata Rathbun, 1897a:60].
- Typhlopseudotelphusa.-Vandel, 1964:183; 1965:142 [erroneous spelling].
- Subgenus Raddaus Pretzmann, 1965:2 [type-species: Pseudothelphusa similis Rathbun, 1905:295].
- Guinotia Pretzmann, 1965:3 [in part] [type-species: Telphusa dentata Latreille, 1825a:564].
- Subgenus Moritschus Pretzmann, 1965:3 [type-species: Pseudothelphusa ecuadorensis Rathbun, 1897a:58].
- Subgenus Phyllothelphusa Pretzmann, 1965:8 [type-species: Pseudothelphusa lindigiana Rathbun, 1897a:59].



FIGURE 66.—Aegla cavernicola, holotype: a, dorsal view; b, ventral view. (Courtesy of Michael Türkay.)

Strengeria Pretzmann, 1965:7 [type-species: Pseudothelphusa Conradi Nobili, 1897:3].

- Neostrengeria Pretzmann, 1965:7 [type-species: Boscia macropa H. Milne Edwards, 1853:208].
- Hypolocera.-Bott, 1967b:367 [erroneous spelling].

Radaus .- Bott, 1967c:376 [erroneous spelling].

- Anaphrymos.-Bott, 1967c:376 [erroneous spelling].
- Elsalvadoria Bott, 1967c:380 [type-species: Pseudothelphusa z. zurstrasseni Bott, 1956:232].
- Typhlopseudotehlphusa.—Rodríguez and Smalley, 1972:92 [erroneous spelling].

DIAGNOSIS.—First gonopod of male straight and strong; margin straight. Surface bearing apical spines directed cephalically or disposed at right angle to axis of gonopod. Strong mesial process or apical or subapical lobule always present. Lateral suture and margin forming apical lobule, which in some species prolonged beyond apex of gonopod. (Free translation from Rodríguez and Smalley, 1972:70).

RANGE.—Western Hemisphere. Southern Mexico and Lesser Antilles to Chile and Brazil.

NUMBER OF SPECIES.—At least 24 species and subspecies, only one of which is troglobitic.

Subgenus Typhlopseudothelphusa

- Typhlopseudothelphusa Rioja, 1953a:291 [nomen nudum]; 1953b:217 [type-species: Typhlopseudothelphusa mociñoi Rioja, 1953b:218].
- Typhloseudothelphusa.—Rioja et al., 1955:313 [erroneous spelling].
- Typhlopseudotelphusa.--Vandel, 1964:183; 1965:142 [erroneous spelling].

- Subgenus Typhlopseudothelphusa.-Pretzmann, 1965:2.
- Subgenus Typhlopseudotelphusa.—Rodríguez and Smalley, 1972:92 [erroneous spelling].
- Subgenus Typhlopseudotehlphusa.—Rodriguez and Smalley, 1972:92 [erroneous spelling].

DIAGNOSIS.—Eyes reduced, devoid of pigment and lacking facets. Pereiopods very long and slender.

RANGE.—Mexico. Known only from the State of Chiapas.

NUMBER OF SPECIES.—Monotypic.

Potamocarcinus (Typhlopseudothelphusa) mocinoi (Rioja)

FIGURES 67, 68

Typhlopseudothelphusa n.g. n.sp. Rioja, 1953a:291-293 [nomen nudum]. Typhlopseudothelphusa mociñoi Rioja, 1953b:218-225, figs. 1-12; 1971:548.

Cangrejo ciego.-Rioja, 1953c:11, fig. 2.

- Typhloseudothelphusa mociñoi.-Rioja, et al., 1955:313 [erroneous spelling].
- Typhlopseudothelphusa mocinoi.—Nicholas, 1962:174.—Hartnoll, 1964a:164; 1964b:78.
- Typhlopseudotelphusa mocinoi.—Vandel, 1964:183; 1965:142 [erroneous spelling].
- Potamocarcinus (Typhlopseudothelphusa) mocinoi.—Pretzmann, 1965:2 [by implication]; 1972:7, 64 [by implication], 81, figs. 19, 730-732.—Smalley, 1970:102.—Reddell, 1971a: 26; 1971b:217, 219.—Reddell and Mitchell, 1971a:2.— Sbordoni, Argano, and Zullini, 1973:9.

- Potamocarcinus (Typhlopseudothelphusa).—Smalley, 1970:103, 105.
- Potamocarcinus (Typhlopseudothelphusa) mociñoi.-Rodríguez and Smalley, 1972:72, 92, figa. 3, 25, 26.



FIGURE 67.—Potamocarcinus (Typhlopseudothelphusa) mocinoi, dorsal view. (Redrawn from Rioja, 1953b, fig. 1.)

Cave crab.-Barr, 1968:82.



FIGURE 68.—Potamocarcinus (Typhlopseudothelphusa) mocinoi, first pleopod of male: a, lateral view of distal part; b, caudomesial view of same; c, cephalolateral view of same; d, anterolateral view; e, caudolateral view. $(a-c, \text{Redrawn from Rodríguez and Smalley, 1972, fig. 3; d, e, redrawn from Rioja, 1953b, figs. 9, 10.)$

Potamocarcinus (Typhlopseudotelphusa) mociñoi.--Rodríguez and Smalley, 1972:92 [erroneous spelling].

Potamocarcinus (Typhlopseudotehlphusa) mociñoi.-Rodríguez and Smalley, 1972:92 [erroneous spelling].

Potamocarcinus mocinoi.-Sbordoni, Argano, and Zullini, 1973:26.

DIAGNOSIS.—Same as that of subgenus.

Size.—Carapace length 22 mm, width 32.5 mm (Rioja, 1953b:220).

TYPES.—Holotype (3) IBM; paratypes, IBM, USNM.

TYPE-LOCALITY.—Cueva del Tío Ticho, approximately 3 km S of Comitán, Chiapas, Mexico.

RANGE.—Mexico. Known from only three localities in the State of Chiapas.

Chiapas: (1) type-locality; (2) Cueva de Los Murciélagos, 14 km ESE of San Cristóbal de Las Casas, 29 Aug 1972, J. Cooke, W. Russell, and R. Mitchell, coll.; (3) Cueva de Los Llanos, 15 km ESE of San Cristóbal de Las Casas, 29 Aug 1972, J. C., W. R., and R. M., coll. Specimens from the latter two localities are in the Smithsonian Institution.

ECOLOGICAL NOTES.—According to Sbordoni, Argano, and Zullini (1973:26), the cave, Cueva del Tío Ticho, also known as Cueva de la Toma de Agua, is essentially a sinkhole located at an altitude of 1700 m. The cavity intercepts a stream, 110 m below the surface, that furnishes water to the city of Comitán. "From the beginning of the decent, everywhere is completely covered with mud." At the bottom, which is very muddy, a small stream flows in a narrow channel feeding a pool of very turbid water. The air temperature at the bottom was 19.3° C and "halfway down was 18.8° C." According to local residents, the crabs are more frequently found during flood periods.

Rioja (1953b:225) conjectured that this crab probably feeds on isopods, insects, arachnids, and other cavernicoles that live with it in the cave.

LIFE HISTORY NOTES.—There are no published data. Reddell (in press) reported that "a female with 75 eggs and another with 57 young were collected on 21 August 1967 on a mud slope along the cave stream."

Family GRAPSIDAE

Genus Sesarma

- Sesarma Say, 1817:76 [type-species, Ocypode reticulatus Say, 1817:73].
- Pachysoma de Haan, 1833:5; 1835:33 [type-species: Grapsus (Pachysoma) bidens de Haan, 1835:53, 60-61; not Pachysoma MacLeay, 1821, a genus of Coleoptera].
- Chiromantes Gistel, 1848:x [type-species: Grapsus (Pachysoma) bidens de Haan, 1835:33, 60-61].
- Holometopus H. Milne Edwards, 1852:187 [type-species: Grapsus (Pachysoma) hematocheir de Haan, 1835:62].
- Holograpsus H. Milne Edwards, 1854:158 [lapsus calami for Holometopus].
- Subgenus Sesarma de Man, 1895:143 [type-species: Grapsus (Pachysoma) hematocheir de Haan, 1835:62].
- Subgenus Episesarma de Man, 1895:165 [type-species: Cancer tetragonus Fabricius, 1798:341].
- Subgenus Parasesarma de Man, 1895:181 [type-species: Cancer quadratus Fabricius, 1798:341].
- Subgenus Perisesarma de Man, 1895:208 [type-species: Grapsus (Pachysoma) bidens de Haan, 1835:33, 60-61].

DIAGNOSIS.—Carapace quadrate or subquadrate and convex dorsally; front large and inclined; pterygostomian and lateral regions with granules and short hairs arranged in reticulate lines. Antennules folded beneath front. Antennae situated in orbital hiatus. Third maxillipeds with oblique hairy ridges on exposed surface. Epistome not projecting beyond edge of front.



FIGURE 69.—Sesarma (Sesarma) verleyi, dorsal view of male from St. Claire Caves, St. Catherine Parish, Jamaica.

RANGE.—Widespread in tropical and temperate regions.

NUMBER OF SPECIES.—Approximately 35 to 40 American species and subspecies, only one species of which is troglobitic.

Subgenus Sesarma

DIAGNOSIS.—Lateral margins of carapace with tooth posterior to external orbital tooth; upper surface of propodus of cheliped almost always without pectinate ridge, when present always longitudinal.

RANGE.—Same as that for genus.

NUMBER OF SPECIES.—Approximately 12 American species, only one of which is troglobitic.

Sesarma (Sesarma) verleyi Rathbun

FIGURES 69, 70

- Sesarma (Sesarma) verleyi Rathbun, 1914:123-124, pl. 6; 1918:285, 288-289, pl. 76.—Hartnoll, 1965:113.—Chace and Hobbs, 1969:191.
- Sesarma verleyi.—Hartnoll, 1964a:145, 164–166, 168, fig. 14B; 1964b:78; 1965:113; 1971:260–262.—Chace and Hobbs, 1969: 14, 26, 34, 38, 157.—Peck, 1975:308, 312, fig. 4.

Sesarma .- Peck, 1974b:34.

DIAGNOSIS .- Integument thin and without pig-

ment. Eyestalks tapering distally, bearing reduced pigmented corneal area. Walking legs conspicuously longer than those of its congeners.



FIGURE 70.—Sesarma (Sesarma) verleyi, first pleopod of male from St. Claire Caves, St. Catherine Parish, Jamaica: a, anterior view; b, lateral view of distal part; c, posterior view.

SIZE.—Carapace length 21 mm (Chace and Hobbs, 1969:191); width 24 mm (Hartnoll, 1964a: 165).

TYPES.—Holotype (9) USNM 24940.

TYPE-LOCALITY.—Mulgrave, Saint Elizabeth Parish, Jamaica.

RANGE.—Jamaica. Endemic on the Island where inhabiting several subterranean drainage systems.

Saint Elizabeth Parish: (1) type-locality. Saint Mary Parish: (2) Limestone cave at Lucky Hill (Hartnoll, 1964a:164). Saint Catherine Parish: (3) limestone cave at Worthy Park (Hartnoll, 1964a:164); (4) St. Claire Cave, Edwarton. Saint Ann Parish: (5) Cricket Cave, Douglas Castle. Specimens from the latter two localities were collected by S. B. and J. Peck in December 1972.

ECOLOGICAL NOTES.—In discussing the distribution of this crab, Hartnoll (1964a:164–165) related that in the cave at Lucky Hill there is a slowly flowing stream some 60 feet (18.2 m) below the surface that courses over a finely silted substrate. There the crab was found both in the water and under rocks in a damp area some distance from the stream. In the cave at Worthy Park, the crabs were found in and on the muddy banks of a sluggish river flowing from a series of rimstone pools. Individuals on the banks crawled quickly into the water when disturbed.

LIFE HISTORY NOTES.—According to Hartnoll (1964a:166), the largest male he examined measured 20.5 mm and had "partly mature gonads."

Females were obtained up to 25 mm., and puberty occurs between 18 and 21 mm. . . . No berried females or larvae were obtained, but the ovaries of the females were examined. In the most mature of these, the ova exceed 1 mm. in diameter, showing that when laid the eggs will be large, doubtless resulting in a modified larval phase like that described for the other species.

Appendix 1

American Non-troglobitic Decapods Reported

Although no intensive search has been made to determine the decapod species that inhabit caves as accidentals, trogloxenes, or troglophiles, the following is a list of species together with the first reference to their occurrence in caves (in each country and state or province) that we have encountered. Also included are several records based on unpublished observations.

North America

UNITED STATES

Alabama

- Cambarus (Cambarus) bartonii (Fabricius, 1798:407) [Cambaridae]; personal communication from Martha R. Cooper.
- Cambarus (Depressicambarus) striatus Hay (1902b:437 [Cambaridae]; personal communication from Martha R. Cooper.
- Cambarus (Erebicambarus) tenebrosus Hay (1902a:232) [Cambaridae]; reported by Rhoades (1941:148) as C. (C.) cahni Rhoades (1941:146).
- Orconectes virilis (Hagen, 1870:63) [Cambaridae]; personal communication from Martha R. Cooper.

Arkansas

Orconectes meeki brevis Williams (1952:348) [Cambaridae]; specimens in USNM collected by J. H. Black.

Florida

- Macrobrachium carcinus (Linnaeus, 1758:631) [Palaemonidae]; reported by Holthuis (1952:124).
- Palaemonetes paludosus (Gibbes, 1850:197) [Palaemonidae]; reported by Hobbs and Means (1972:401).
- Procambarus (Ortmannicus) fallax (Hagen, 1870:45) [Cambaridae]; observed by Hobbs, Jr.
- Procambarus (Scapulicambarus) paeninsulanus (Faxon, 1914: 369) [Cambaridae]; specimens in USNM collected by John E. and Martha R. Cooper.

Georgia

Cambarus (C.) bartonii; reported by Cooper and Iles (1971:46) as Cambarus bartoni cavatus Hay (1902b:435); specimens in USNM collected by Walter Auffenberg and John Crenshaw. Cambarus (Depressicambarus) latimanus (LeConte, 1856:402) [Cambaridae]; reported by Holsinger and Peck (1971:30).

Cambarus (D.) striatus; reported by Holsinger and Peck (1971:30) as "Cambarus sp."

Indiana

- Cambarus (Erebicambarus) laevis Faxon (1914:391) [Cambaridae]; reported by Hay (1891:147) as Cambarus bartonii (Fabricius, 1798:407).
- Orconectes immunis (Hagen, 1870:71) [Cambaridae]; reported by Hobbs III (1975:279).
- Orconectes propinguus (Girard, 1852:88) [Cambaridae]; reported by Hobbs III (1975:280).

Kentucky

- Cambarus (E.) laevis; personal communication from Martha R. Cooper.
- Cambarus (E.) ornatus Rhoades (1944:144) [Cambaridae]; specimen in collection of USNM obtained by Rendell Rhoades.
- Cambarus (E.) tenebrosus; reported by Silliman (1851:336) as "large-eyed and colored crawfish."

Missouri

- Orconectes luteus (Creaser, 1933:7) [Cambaridae]; reported by Creaser (1933:9).
- Orconectes neglectus neglectus (Faxon, 1885c:142) [Cambaridae]; reported by Williams (1954:904).
- Orconectes punctimanus (Creaser, 1933:1) [Cambaridae]; personal communication from Martha R. Cooper.

New York

Cambarus (Puncticambarus) robustus Girard (1852:90) [Cambaridae]; specimens in USNM collected by S. B. Peck.

Oklahoma

- Orconectes meeki brevis Williams (1952:348) [Cambaridae]; reported by Black (1971:10).
- Orconectes neglectus neglectus; reported by Black (1971:10).
- Orconectes palmeri longimanus (Faxon, 1898:655) [Cambaridae]; reported by Black (1971:10).
- Procambarus (Girardiella) simulans simulans (Faxon, 1884: 112) [Cambaridae]; reported by Black (1971:10). Specimens

assigned to *Procambarus simulans* were found in Wild Woman Cave, Murray County, Oklahoma (Harrel, 1960;31).

Tennessee

Cambarus (E.) tenebrosus; reported by Hart and Hobbs (1961:178).

Texas

Orconectes palmeri longimanus (Faxon, 1898:655) [Cambaridae]; reported by Penn and Hobbs (1958:474).

Procambarus (G.) simulans simulans; reported by Penn and Hobbs (1958:474).

Procambarus (Orimannicus) acutus acutus (Girard, 1852:91) [Cambaridae]; reported by Reddell (1965:161).

Procambarus (Scapulicambarus) clarkii (Girard, 1852:91) [Cambaridae]; reported by Reddell (1965:161).

Virginia

- Cambarus (Cambarus) bartonii; reported by Holsinger (1964: 62) as Cambarus bartonii bartonii.
- Cambarus (Jugicambarus) dubius Faxon (1884:114) [Cambaridae]: reported by Holsinger (1964:62) as Cambarus carolinus (Erichson).
- Cambarus (Cambarus) sp. [Cambaridae]; reported by Holsinger (1964:62) as "Cambarus bartonii ssp."

West Virginia

Cambarus (C.) bartonii; reported by Hobbs (1964:189) as Cambarus bartonii bartonii.

Middle America

MEXICO

Chiapas

Macrobrachium carcinus; collected by the Italian Expedition of 1971 and identified by Hobbs, Jr.

- Procambarus (Austrocambarus) mirandai Villalobos (1954:355) [Cambaridae]; reported by Rioja (1953a:291) as "Procambarus n. sp."
- Procambarus (Austrocambarus) species [new], Hobbs (in press) [Cambaridae]; reported by Sbordoni, Argano, and Zullini (1973:32) as "crayfishs."

Hidalgo

Procambarus (Ortmannicus) toltecae Hobbs (1943:198) [Cambaridae]; reported by Hobbs (1971a:37).

Puebla

Procambarus (Villalobosus) xochitlanae Hobbs (1975b:16) [Cambaridae]; reported by Hobbs (1975b:19).

San Luis Potosí

- Macrobrachium carcinus; reported by Breder (1942:11) as Macrobrachium jamaicensis (Herbst).
- Procambarus (Ortmannicus) acutus cuevachicae (Hobbs, 1941a:1) [Cambaridae]; reported by Bridges (1940:84) as crayfish.
- Procambarus (O.) toltecae; reported by Hobbs (1971a:57).
- Procambarus (Ortmannicus) villalobosi Hobbs (1969a:41) [Cambaridae]; reported by Hobbs (1969a:41).
- Smalley (1972:77) [Pseudothelphusidae]; reported by Rodríguez and Smalley (1972:77).

Sonora

Pseudothelphusa (Pseudothelphusa) sonorae Rodríguez and Smalley (1972:90) [Pseudothelphusidae]; reported by Rodríguez and Smalley (1972:90).

Tamaulipas

Procambarus (O.) toltecae; reported by Hobbs (1971a:37).

COSTA RICA

Potamocarcinus (Megathelphusa) magnus magnus (Rathbun, 1895:377) [Pseudothelphusidae]; reported by Rathbun (1895:377) as Pseudothelphusa magna.

GUATEMALA

- Isabellagordonia (Isabellagordonia) longipes Pretzmann (1972: 91) [Pseudothelphusidae]; reported by Pretzmann (1972:92).
- Isabellagordonia (Phrygiopilus) acanthophallus (Smalley, 1970:98) [Pseudothelphusidae]; reported by Smalley (1970: 98) as Phrygiopilus acanthophallus.
- Sesarma (Holometopus) roberti H. Milne Edwards (1853:182) [Grapsidae]; reported by Reddell (in press).

West Indies

BONAIRE

Macrobrachium faustinum lucifugum Holthuis (1974b:233) [Palaemonidae]; reported by Rathbun (1919:324) as M. olfersii. [M. faustinum lucifugum has been reported from epigean and hypogean waters. It is possible that the epigean records are based on erroneous determinations, and that this shrimp is confined to subterranean habitats.]

CUBA

La Habana

Cardisoma guanhumi Latreille (1825b:685) [Gecarcinidae]; reported by Acevedo G. (1967:51).

SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY

Las Villas

- Epilobocera armata armata (Smith, 1870:151) [Pseudothelphusidae]; reported by Pretzmann (1972:111).
- Epilobocera gertraudae Pretzmann (1972:112) [Pseudothelphusidae]; reported by Pretzmann (1972:113).
- Gecarcinus ruricola (Linnaeus, 1758:626) [Gecarcinidae]; reported by Hardy (1963:160).

Cardisoma guanhumi; reported by Silva T. (1974:23).

Oriente

Macrobrachium faustinum lucifugum; reported by Holthuis (1974b:234).

Cardisoma guanhumi; reported by Viña B. (1970:5).

Gecarcinus lateralis (Freminville, 1835:224) [Gecarcinidae]; reported by Viña B. (1970:5).

Gecarcinus ruricola; reported by Viña B. (1970:5).

Sesarma sp. [Grapsidae]; reported by Viña B. (1970:5).

Pinar del Río

Macrobrachium faustinum lucifugum; reported by Holthuis (1974b:234).

CURACAO

Macrobrachium faustinum lucifugum; reported by Holthuis (1974b:238).

DOMINICAN REPUBLIC

Macrobrachium faustinum lucifugum; reported by Chace (1975:35) as Macrobrachium crybelum Chace (1975:30).

AMAICA

- Atya innocous (Herbst, 1792:62) [Atyidae]; reported by Peck (1975:308).
- Atya lanipes Holthuis (1963a:61) [Atyidae]; reported by Peck (1975:308).
- Xiphocaris elongata (Guérin-Méneville, 1855, pl. 2) [Atyidae]; reported by Peck (1975:308) as Xiphocharis [sic] elongata.
- Macrobrachium carcinus; reported by Peck (1975:308) as Mecrobrachium [sic] carcinus.
- Macrobrachium faustinum lucifugum; reported by Holthuis (1974b:237).

- Macrobrachium heterochirus (Wiegmann, 1836:149) [Palaemonidae]; reported by Peck (1975: 308).
- Cardisoma guanhumi; reported by Peck (1975:308).
- Gecarcinus ruricola; reported by Peck (1975:308).
- Sesarma (Holometopus) miersii Rathbun (1897b:91) [Grapsidae]; reported by Peck (1975:308) as Sesarma miersii.
- Sesarma (Sesarma) bidentatum Benedict (1892:77) [Grapsidae]: reported by Peck (1975:308) as Sesarma bidentatum.

PUERTO RICO

- Xiphocaris elongata Guérin-Méneville (1855, pl. 2: fig. 16, 16a) [Atyidae]; reported by Nicholas (1966:131, photograph). ?Macrobrachium faustinum lucifugum; reported by Nicholas
- (1966:138) as M. faustinum. Epilobocera sinuatifrons (A. Milne-Edwards, 1866:205) [Pseu-
- dothelphusidae]; reported by Rathbun (1905:319). Cardisoma guanhumi; reported by Nicholas (1966:137).

South America

BRAZIL

- Euryrhynchus burchelli Calman (1907:297) [Palaemonidae]; reported by Calman (1907:297).
- Aegla strinatii Türkay (1972:417) [Aeglidae]; reported by Türkay (1972:418).

ECUADOR

Macrobrachium brasiliense (Heller, 1862:419) [Palaemonidae]; specimens in USNM collected by S. and J. Peck.

FRENCH GUIANA

Caridinopsis brevinaris Holthuis (1956a:56) [Atyidae]; reported by Holthuis (1956a:56). Euryrhynchus wrzeniowskii; reported by Miers (1877:662).

GUYANA

Euryrhynchus wrzeniowskii Miers (1877:662) [Palaemonidae]; reported by Holthuis (1956a:68).

SURINAM

Euryrhynchus wrzeniowskii; reported by Holthuis (1956a:68).

Appendix 2

Symbionts of American Troglobitic Decapods

Metazoan symbionts have been reported for none of the American troglobitic decapods except crayfishes. The known symbionts include annelids belonging to the family Branchiobdellidae, entocytherid ostracods, and a copepod of the family Canthocamptidae. All of the species of these three families which have been reported to infest troglobitic crayfishes are listed below together with the host species and the first reference to the association in each of the geographic areas recognized.

UNITED STATES

Alabama

- Cambarincola sheltensis Holt (1973a:229) [Branchiobdellidae]; reported by Holt (1973a) on Orconectes australis australis (p. 229), Cambarus (A.) hamulatus (p. 231), C. (A.) jonesi (p. 231), and Procambarus (R.) pecki (p. 231).
- Sagittocythere barri (Hart and Hobbs, 1961:174) [Entocytheridae]; reported by Hart and Hobbs (1961:174) on O. a. australis and C. (A.) jonesi.

Florida

- Cambarincola leoni Holt (1973a:226) [Branchiobdellidae]; reported by Holt (1973a) on Procambarus (O.) orcinus (p. 226), P. (O.) lucifugus x alachua (p. 229).
- Uncinocythere ambophora (Walton and Hobbs, 1959:115) [Entocytheridae]; reported by Walton and Hobbs (1959:118) on Procambarus (L.) acherontis.
- Uncinocythere equicurva (Hoff, 1944:337) [Entocytheridae]; reported on Procambarus (O.) lucifugus alachua by Hoff (1944:340); identity of ostracod questioned by Walton and Hobbs (1959:118).
- Uncinocythere lucifuga (Walton and Hobbs, 1959:118) [Entocytheridae]; reported by Walton and Hobbs (1959:118) on P. (O.) l. alachua.

Georgia

Uncinocythere warreni Hobbs and Walton (1968:250) [Entocytheridae]; reported by Hobbs and Walton (1968:251) on Cambarus (J.) cryptodytes.

Indiana

- Cambarincola dubius Holt (1973a:234) [Branchiobdellidae]; reported by Holt (1973a:234) on Orconectes inermis testii.
- Dactylocythere susanae Hobbs III (1971a:140) [Entocytheridae]; reported by Hobbs III (1975:283) on O. i. testii and O. inermis inermis.
- Donnaldsoncythere donnaldsonensis (Klie, 1931:334) [Entocytheridae]; reported by Hobbs III (1975:283) on O. i. testii and O. i. inermis.
- Sagittocythere barri; reported by Hart and Hobbs (1961:176) on O. i. inermis; and by Hart and Hart (1966:8) on O. i. testii.
- Uncinocythere xania (Hart and Hobbs, 1961:181) [Entocytheridae]; reported by Hobbs III (1975:283) on O. i. inermis and O. i. testii.
- Atthyella pilosa Chappuis (1929:53) [Canthocamptidae]; reported by Hobbs III (1973e) on O. i. inermis.

Kentucky

- Dactylocythere prionata (Hart and Hobbs, 1961:178) [Entocytheridae]; reported by Hart and Hobbs (1961:180) on Orconectes australis packardi.
- Dactylocythere steevesi (Hart and Hobbs, 1961:174) [Entocytheridae]; reported by D. G. Hart and C. W. Hart (1974: 71) on Orconectes pellucidus and O. a. packardi.
- Dactylocythere susanae; reported by Hobbs III (1971a:140) on O. i. inermis and O. a. packardi.
- Dactylocythere ungulata (Hart and Hobbs, 1961:177) [Entocytheridae]; reported by D. G. Hart and C. W. Hart (1974: 74) on O. pellucidus and O. a. packardi.
- Sagittocythere barri; reported by Hart and Hobbs (1961:176) on O. i. inermis, O. a. packardi, and O. pellucidus.
- Sagittocythere stygia Hart and Hart (1966:9) [Entocytheridae]; reported by Hart and Hart (1966:9) on O. pellucidus.

Missouri

- Uncinocythere pholetera (Hart and Hobbs, 1961:181) [Entocytheridae]; reported by Hart and Hobbs (1961:182) on Cambarus (E.) hubrichti.
- Uncinocythere xania (Hart and Hobbs, 1961:181) [Entocytheridae]; reported by Hart and Hobbs (1961:181) on Cambarus (J.) setosus.

Tennessee

Dactylocythere steevesi; reported by Hart and Hobbs (1961:

180) on O. p. pellucidus [= O. a. australis] and by D. G. Hart and C. W. Hart (1974:71) on O. a. australis.

- Dactylocythere ungulata; reported by Hart and Hobbs (1961: 178) on O. a. australis and O. p. pellucidus [= O. a. australis].
- Donnaldsoncythere tuberosa (Hart and Hobbs, 1961:182) [Entocytheridae]; reported by Hart and Hobbs (1961:184) on O. p. pellucidus [= O. a. australis] and by D. G. Hart and C. W. Hart (1974:82) on O. a. australis.
- Sagittocythere barri; reported by Hart and Hobbs (1961:175) from Carter Cave where O. incomptus is the only crayfish known to be present.

West Virginia

- Cambarincola demissus Hoffman (1963:365) [Branchiobdellidae]; reported by Holt (1973a:238) on Cambarus (P.) nerterius.
- Cambarincola philadelphicus (Leidy, 1851:209) [Branchiob-

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dellidae]; reported by Holt (1973a:240) on C. (P.) nerterius.

Mexico

Oaxaca

- Entocythere claytonhoffi Rioja (1942:201) [Entocytheridae]; reported by Hobbs (1973a:33) on Procambarus (A.) o. oaxacae.
- Ankylocythere maya Hobbs (1971a:34) [Entocytheridae]; reported by Hobbs (1973a:33) on P. (A.) o. oaxacae.
- Ankylocythere bidentata; reported by Hobbs (1973a:38) on P. (A.) o. reddelli.

Veracruz

Ankylocythere bidentata (Rioja, 1949:320) [Entocytheridae]; reported by Hobbs (1971a:30) on Procambarus (A.) rodriguezi.

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Glossary

(See Figures 1 and 2 for illustrations of morphological characters, some of which are not defined below.)

- ABDOMEN. That portion of the body posterior to the cephalothorax, consisting of the telson and six body segments or somites; the "tail."
- ACUMEN. The apical part of the rostrum frequently delimited basally by marginal spines.
- ALLOCHTHONOUS. Organic matter introduced into subterranean waters from epigean environments.
- ANCHIALINE. Referring to saltwater or brackish pools fluctuating with the tides but with no surface connection to the sea.
- ANNULUS VENTRALIS. Seminal receptacle of cambarids, consisting of a median sclerite between the fourth and fifth pereiopods.
- ANTENNAL SCALE. The plate-like exopod of the antenna.
- ANTENNAL SPINE. A spine on, or adjacent to, the anterior margin of the carapace, immediately ventral to the orbit.
- ANTENNULAR PEDUNCLE. The proximal segments of the antennule, from which the flagella arise.
- APPENDIX INTERNA. A slender rodlike structure on the mesial border of the endopod of the second through fifth pleopods of shrimps; terminal and/or subterminal hooked setae allow the mesial joining of two pleopods of a pair.
- APPENDIX MASCULINA. A setiferous lobe or rodlike structure situated between the appendix interna and the mesial margin of the mesial ramus (endopod) of the second pleopod of male shrimps. Often an important taxonomic character, the presence or absence of an appendix masculina is the easiest means of distinguishing males and females of most freshwater shrimps.
- AREOLA. The dorsomedian area of the thoracic part of the carapace of crayfishes, bounded laterally by paired arched (branchiocardiac) grooves.
- ARTHROBRANCH. A gill arising from the articular membrane at the proximal base of the coxa of an appendage.
- BASIS. The second segment from the proximal end of a segmented appendage.
- BRANCHIAL COUNT. The number of gills and epipodites present on one side of the cephalothorax.
- BRANCHIOSTEGAL SPINE. A short spine located on or near the anterior margin of the carapace, ventral to the antennal spine in shrimps; in crayfishes, immediately ventral to the anterior extremity of the cervical groove.
- CARAPACE. The "head shield" overlying the cephalothoracic somites of the body.
- CARAPACE LENGTH. In shrimps, the distance from the posterior margin of the orbit to the mid-caudodorsal margin of the carapace; in crayfishes, the distance from the tip of the rostrum to the mid-caudodorsal margin of the carapace.
- CARPUS. The fifth segment from the proximal end of a

segmented appendage; in some shrimps, consisting of several articles (that of the second pereiopod of alpheids and hippolytids consisting of a number of articles).

- CENOTE. A depression or sinkhole in karst areas, having a pool at the bottom; associated with Yucatán, Mexico.
- CEPHALOTHORAX. That portion of the body bearing the eyes and all of the appendages through the fifth pereiopod.
- CERVICAL GROOVE. The major arc-like suture on the carapace of a crayfish, dividing it into cephalic and thoracic regions.
- CERVICAL SPINE. Spine on the lateral surface of the carapace immediately posterior to the cervical groove in crayfishes.
- CHELA. A forceps-like structure consisting of the two distalmost podomeres of a pereiopod.
- CHELIPED. A pereiopod bearing a chela; in crayfishes, the first pereiopod.
- CORNEA. The terminal cap of the eye, faceted except in most troglobites.
- coxA. The first (proximal) segment of a segmented appendage.
- DACTYL. The distalmost segment of a usually 7-segmented appendage.
- DETRITIVORE. An animal that feeds on detritus.
- ENDITE. A mesial lobe-like extension of a podomere or such an extension from the axial part of an unsegmented appendage.
- ENDOPOD. The mesial ramus of a biramus appendage, having its origin on the basis.
- EPEIRIC. A shallow sea extending over large areas of a continental mass.
- EPIGEAN. Referring to the surface of the earth, as opposed to hypogean.
- EPIPODITE. A lateral plate-like extension from the coxa often bearing gill filaments.
- EPISTOME. A transverse plate situated anterior to the mouth.
- EURYPHAGOUS. Employing a wide range of living and decaying animal and plant matter as food.
- EXOPOD. The lateral ramus of a biramous appendage, having its origin on the basis.
- EXTENSOR SURFACE. The unopposed surface of a flexed podomere of an appendage.
- FINGER. One of the rami of the chela; the movable finger consisting of the dactyl and the immovable finger of the opposable part of the propodus.
- FIRST FORM MALE (31). The sexually functional male cambarid, most readily recognized by the possession of at least one corneous terminal element on the first pleopod.
- FLAGELLAR LOBULE. A slender process extending from the distomesial angle of the lateral major lobe of the first maxilliped.

- FLAGELLUM. The multiarticulate, typically filamentous part of an antennule or antenna.
- FLEXOR SURFACE. The opposable surface of a flexed podomere of an appendage.
- HEPATIC AREA. In crayfishes, paired cephalolateral regions of the carapace between the orbit and cervical groove.
- HEPATIC LOBE. One of three pairs of lobes on the cephalolateral margin of the carapace of aeglids delimited anteriorly and posteriorly by emarginations.
- HEPATIC SPINE. A spine located near the anterior margin of the hepatic area of the carapace of certain shrimps, or on the hepatic area of cambarids.
- HYPOGEAN. Refers to beneath the surface of the earth; subterranean.
- HYPORHEIC ZONE. The interstices formed in coarse sand, gravel, and rocks comprising the substrate of a stream.
- INCISOR PROCESS. The cutting (as opposed to the molar or grinding) lobe of the mandible.
- ISCHIOPODITE. The third segment from the base of a segmented appendage.
- ISCHIUM. See ischiopodite.
- KABST. A terrain underlain by extensively leached carbonate rock, typified by numerous sinkholes and subsurface solution cavities.
- LENTIC. Refers to standing water.
- LOTIC. Refers to running water.
- MANDIBLE. One of a pair of heavily calcified jaws situated anterodorsal to other gnathal appendages.
- MAXILLA. One of a pair of two sets of appendages lying immediately posterior to the mandible.
- MAXILLIPED. One of a pair of three sets of appendages lying immediately posterior to the maxilla.
- MERUS. The fourth segment from the proximal end of a segmented appendage.
- MONOTYPIC. The status of a taxon consisting of a single subordinate taxonomic unit.
- ORBIT. One of a pair of excavations on the anterior margin of the carapace in which the eye is situated.
- ORBITAL HIATUS. The gap in the orbital margin at its ventromesial angle.
- PALM. The broadened portion of the propodus of a chela proximal to the fingers.
- PALP. The comparatively slender 2- or 3-segmented part of the mandible.

- PEREIOPOD. One of the five posterior pairs of appendages (legs) supporting the cephalothorax.
- PLEOPOD. One of five pairs of appendages borne on the first five abdominal segments.
- PLEUROBRANCH. A gill situated on the body wall dorsal to the articulation of an appendage.
- PODOBRANCH. A gill borne on the coxa of an appendage.
- PODOMERE. A single segment of an appendage.
- POSTANNULAR PLATE. A median sclerite (plate) immediately caudal to the annulus ventralis.
- POSTORBITAL CARAPACE LENGTH. The distance from the orbit to the mid-caudodorsal margin of the carapace.
- PREANNULAR PLATE. A broad plate situated immediately anterior to the annulus ventralis in certain cambarids.
- PROPODUS. The sixth or penultimate segment of a segmented appendage.
- PTERYGOSTOMIAN REGION. The paired anteroventral area of the carapace lateral to the mouth area.
- PTERYGOSTOMIAN SPINE. A spine borne on the anteroventral margin of the carapace, ventral to the branchiostegal spine (in shrimps).
- RETINACULAR HOOKS. The curved hooks on the appendices internae serving to link paired pleopods.
- ROSTRUM. The anterior projection of the cephalothorax between the eyes.
- SCAPHOCERITE. See antennal scale.
- SECOND FORM MALE (δ II). The sexually nonfunctional male cambarid, most easily recognized by the lack of a corneous terminal element on the first pleopod.
- SPELEAN. Referring to subterranean habitats.
- SPELEOTHEM. Crystaline deposit that develops in subsurface cavities of limestone formations (stalactites and stalagmites).
- STERNUM. The midventral surface of the body, between the coxae of the appendages.
- SUPRAORBITAL SPINE. A spine on the carapace situated posterodorsal to the orbit.
- TELSON. The terminal (posterior) unit of the abdomen.
- TROGLOBITE. An obligate inhabitant of subterranean habitats.
- TROCLOPHILE. A facultative occupant of subterranean environments able to complete its life history underground.
- TROGLOXENE. An inhabitant of subterranean environments that is unable to complete its life history underground.
- UROPOD. Part of "tail fan"; a paired biramous appendage borne on the sixth abdominal somite.

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