Int. J. Speleol. 5 (1973), pp. 219-256.

Branchiobdellids (Annelida: Clitellata) from Some Eastern North American Caves, with Descriptions of New Species of the Genus *Cambarincola*

by

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During the past decade, I have received branchiobdellid material from biospeleologists who are in the process of inventorying cave dwelling animals and investigating their ecology and zoögeography. The branchiobdellids will contribute litte, I fear, to our knowledge of the routes and times of invasion of eastern North American caves by true troglobites.

Nonetheless, there seem to be a few branchiobdellids that are restricted to caves, mainly those known to infest troglobitic asellid isopods. Most, however, are common epigean species that are able to move easily back and forth from epigean to hypogean habitats, and some of these have taken up a life on troglobitic crayfishes. The notorious lack of host specificity on the part of the branchiobdellids (Goodnight, 1940; Hobbs, Holt and Walton, 1967; Holt, 1968a; *inter alia*) and their obvious "preadaptations" to cave life lend credence to these opinions.

I know only one reference to a cave dwelling branchiobdellid: the description of *Cambarincola alienus* Holt, 1963.

Since many speleologists for whom this paper is written, may not know the branchiobdellids and the methods employed in a taxonomic treatment of them, a few remarks may be in order.

The branchiobdellids compose a monotypic order of annelid worms, closely related to the oligochaetes, the acanthodrilids and the hirudineans (Holt, 1965b). Their body is composed of fifteen segments, but only the last eleven, the trunk ones, are numbered, since the first four form a head (the segmentation of the head is still debatable). There are no setae or prostomium; the peristomium and last one or two segments form anterior and posterior suckers. The single spermatheca opens midventrally on (trunk) segment V; the male efferent apparatus by a single midventral pore on segment VI; the ovipores lateroventrally on segment VII. For further anatomical details see Moore, 1895, and Holt, 1949; 1960a; 1965a; 1968a. The animals are uniquely Holarctic in their distribution (*contra* Bishop, 1968) and are known only as epizoites (commensals, parasites, "hitch-hikers") on freshwater crustaceans, principally astacid crayfishes, but they have been reported from isopods (Holt, 1963), freshwater crabs (Hobbs and Villalobos, 1958; Holt, 1964, 1973a) and freshwater shrimp (Liang, 1963), and there is the remarkable case of *Cambarincola vitreus* Ellis, 1919, occurring in the gill chambers of the marine crab,

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Callinectes sapidus Rathbun, 1892, which has become acclimated to freshwater in the bayous of Louisiana (Blackford, 1966).

The methods used in the taxonomic study of branchiobdellids have been described several times and taxonomic characters discussed (Holt, 1960; Hoffman, 1963; other papers by Holt), but it may be appropriate to point out that the material upon which this paper is based was collected entirely by others, mostly in 70% ethanol, and is generally in a poor state of preservation; indeed, some potentially interesting specimens were so macerated that they were discarded.

With the use of a 40X flourite oil immersion objective with a working distance of 1.5 mm, I am able to turn over the slides upon which the animals are mounted entire and unstained and, if necessary, study them from either side. All drawings are so made that the anterior of the worm and illustrated parts are directed towards the reader's right. Measurements, made with an ocular micrometer, are to be considered as approximations only and are given to the nearest 0.1 mm, which accounts for the ranges (presented in parentheses after the average) and the averages of several measurements being the same.

The disposition of material for newly described species is given with the accounts of those species (USNM indicates National Museum of Natural History of the Smithsonian Institution); the remainder are housed at Virginia Polytechnic Institute and State University under my care (indicated by the initials, PCH).

A key to the branchiobdellids known to inhabit caves, either occasionally or permenantly, would be difficult to prepare and of little use at this time: too many undescribed, but similar species are known to inhabit the general area covered in this study. Brief diagnoses, however, of the genera and species treated herein, with the new species fully diagnosed, described and illustrated, are presented along with records of the caves from which they have been taken. Finally, a list of the hosts of cave-dwelling branchiobdellids and a table presenting a summary of them and their hosts listed according to the caves they inhabit are followed by a few remarks concerning the zoögeographical and evolutionary significance of these records. All material at hand, including that so poorly preserved that it is unidentifiable, is listed, except some from southwest Virginia that was discarded before it was cataloged.

I am indebted to a number of people. Dr. John R. Holsinger furnished me with much material, particularly most of that from east Tennessee, Virginia and West Virginia, and has helped with the collating of locality and host data. Mr. John E. Cooper and his wife, Martha R. Cooper, have been generous in supplying material and checking host data. Dr. Kenneth Relyea and Mr. Barry Mansell, of Jacksonville, Florida, have supplied me with important collections from caves in Florida. Dr. Horton H. Hobbs III furnished material from Tennessee and Indiana. My colleague, Dr. Harrison R. Steeves III gave me important material. The identification, or confirmation thereof, of isopod hosts was done for me by Dr. Laurence E. Fleming. As always, I am most indebted to Dr. Horton H. Hobbs, Jr., who has contributed specimens, checked host and locality data and read the manuscript, although other friends mentioned above (Martha R. Cooper, John R. Holsinger, Thomas C. Barr, Jr., and Harrison R. Steeves III) have read it. Finally, I must mention Dr. Hobbs,

Jr., again: his key (Hobbs, 1972) to the crayfishes of North America has been used freely, and often without direct citation, in compiling host data.

Cambarincola Ellis, 1912

For synonomies of the genus **Cambarincola**, see Hoffman, 1963, and Holt, 1973a

Diagnosis (from Hobbs, Holt and Walton, 1967: 52). – "Body terete without specialized projections; anterior nephridia opening through common pore on dorsum of segment III; deferent ducts entering ental end of spermiducal gland; prostate and ejaculatory duct both present; penis non-eversible; bursa subpyriform to obcordate; spermatheca never bifid."

Type–species. *Cambarincola macrodontus* Ellis, 1912, by original designation.

Remarks. – Species of the genus *Cambarincola* are the dominant component of the epigean branchiobdellid fauna of North America. This also seems to be true of the cave forms. The range of the genus extends from southern Canada (the northern limits of their astacid hosts) along both sides of the continent to Costa Rica, the southern-most record for any branchiobdellid. Though the genus is believed to be advanced, the order is relatively old (Holt, 1969) and it is not surprising, in view of these facts of distribution and phylogenetic theories, to find members of the genus to be the most common of cave dwelling branchiobdellids.

Cambarincola marthae new species (Fig. 1)

Type-specimens. – Holotype, USNM 49599, one paratype, PCH 2767, taken on *Asellus alabamensis* (Stafford, 1911) in Carter's Cave, Jackson County, Tennessee, by John E. and Martha R. Cooper, September 21, 1968.

Diagnosis. – Small, slender branchiobdellids (about or less than 2.0 mm in length); body outline smooth; upper jaw slightly larger than lower, dental formula (?) 5/4; bursa less than 1/4 body diameter in length; spermiducal gland small, its diameter approximately 1/2 its length; without deferent lobes; prostate non-differentiated, about 5/6 in length, 1/4 in diameter of spermiducal gland, with small, clear ental bulb; spermatheca with ectal duct subequal to bulb in length, total length subequal to body diameter, bulb elongate oval, without ental process.

Etymology. – It is a pleasure to name this species in honor of Martha R. Cooper, its codiscover and herself an authoritative student of the cambarine hosts of most American branchiobdellids.

Descriptions. Specimens of *Cambarincola marthae* are small slender branchiobdellids with the delicate facies of inhabitants of the brood pouches of isopods or the gill chambers of crayfish. The holotype has the following dimensions: *total length*, about 1.8 mm (the animal is fixed in an S-shaped curve and its length is difficult to determine); *greatest diameter*, 0.3 mm; *head length*, 0.2 mm; *head diameter*, 0.2 mm; *diameter, segment*, I, 0.2 mm; *diameter, sucker*, 0.2 mm. The paratype is of approximately the same dimensions.

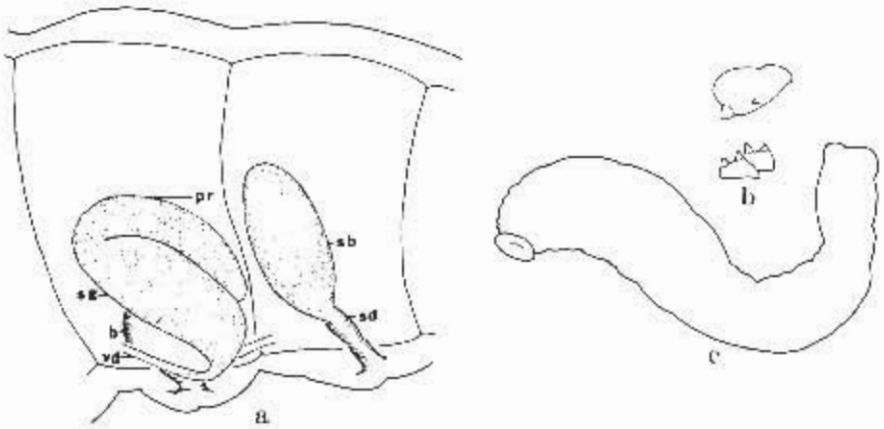

Fig. 1. *Cambarincola marthae*, new species. *a*, reproductive system of holotype; *b*, same, lateral aspects of jaws; *c*, same, outline of holotype. Abbreviations: *b*, bursa; *pr*, prostate; *sb*, spermathecal bulb; *sd* spermathecal ectal duct; *sg*, spermiducal gland; *vd*, vas deferens.

The peristomium appears to be entire, *i.e.*, it is not divided into dorsal and ventral lips: this may be an artifact of fixation. An undeterminable number of oral papillae are present in the paratype, but none can be detected, though their presence may be assumed, in the holotype.

Other than a shallow peristomial sulcus, there are no external furrows that encircle the head; internally there is one somewhat obscure pharyngeal sulcus.

The jaws are difficult to interpret. The upper jaw is only slightly greater in dimensions than the lower one (the ratio of their respective anteroposterior lengths is 11/9), but is much more massive in appearance, presumably because of a greater thickness of its base and tooth-bearing border. The upper jaw appears, in the holotype, to have only three teeth, with the median one large and distinct and the lateral ones small and indistinct; in the paratype there is a suggestion of five teeth on it. The lower jaw, in both type-specimens, bears four relatively small, but clearly distinct and sharply pointed teeth. Parenthetically, variability in number of teeth in species with jaws that are large in proportion to the size of the teeth is known in other species of the genus.

The spermiducal gland, as is true of the entire male reproductive system, is relatively small, without deferent lobes, and is otherwise unremarkable. The prostate is approximately 5/6 the length and 1/4 the diameter of the spermiducal gland, is non-differentiated (that is, it is histologically similar to the latter) and possesses a small, but clear, ental bulb.

The ejaculatory duct is a distinct muscular tube that is concordant in size with other components of the male system.

The pyriform bursa is small, about 120 by 83 microns in length and greatest diameter respectively. Although the penial sheath portion is relatively short and the atrial fold is obscure (possibly both features are related to the organ's small size),

the bursa is in general appearance similar to those of most species of the genus.

The spermatheca lies obliquely in its segment in the holotype. Its ectal duct curves under and to the side of the gut. If extended, it and the approximately equal in length spermathecal bulb are subequal to the diameter of segment V in total length. The elongated oval bulb lacks any suggestion of an ental process.

Variation. – Only the types of *Cambarincola marthae* are known and nothing can be added to the account of the differences between them that is noted above. The differences are of such a nature that they do not raise doubts as to the conspecificity of the types.

Affinities. – *Cambarincola marthae* and the other three isopod inhabiting troglobitic branchiobdellids belong to a group of species with a non-differentiated prostate. There are a number of such species, particularly among those of western North America, but the only ones that have been formally described are *C. alienus* Holt, 1963, eight species named by Hoffman (1963) and nine others from Mesoamerica (Holt, 1973a).

It is not possible at this time to determine which of these species is most closely related to *C. marthae*. But, discounting the possibility of parallel evolution, the closest relative of *C. marthae* perhaps should be sought among those species with a non-differentiated prostate, without dorsal ridges on the anterior annuli of the trunk segments, with an ental bulb of the prostate and without an ental process of the spermatheca. There are three such species, two of which are Mesoamerican (Holt, 1973a). One of the latter two, *C. acudentatus* Holt, 1973, from Grutas de Quintero, eleven kilometers southwest of Ciudad Mante, Tamulipas, México, is a cave inhabitant known only from the troglobitic isopods *Speocirolana bolivari* (Rioja, 1943) and *S. pelaezi* (Bolivar y Pieltain, 1950). It is readily distinguishable from *C. marthae* by the 7/6 dental formula and prominent sharp teeth; by the deferent lobes of the spermiducal gland which are absent in *C. marthae*; and by the larger proportionate size of the prostate, subequal to the spermiducal gland. The other close Mesoamerican relative of *C. marthae* is *C. susanae*, Holt, 1973, a species whose type locality is La Cueva Chica, El Pujal, three kilometers northeast of Valles, San Luis Potosí, México. This species cannot be suspected of being a true troglobite: it is known not only from caves, but from surface waters in five states in México from the Río Grande drainage in Nuevo León to western Campeche on the Yucatan Peninsula. It differs from *C. marthae* in the much greater disparity between upper and lower jaws; its upper jaw is almost twice as large as the lower and is otherwise distinctive in that the teeth are borne on a prominently raised ridge on the jaw; in the long reflexed spermiducal gland; and in the proportionately much shorter prostate that is only 1/2 the length of the spermiducal gland. Finally, *C. demissus* Hoffman, 1963, possesses those features considered above that indicate a relationship to *C. marthae*. *Cambarincola demissus* may be a gill inhabitant on the host crayfish and is known only from Wise and Tazewell Counties, Virginia, and a cave in Greenbrier County, West Virginia. It differs from *C. marthae* most notably in the disproportionately much greater diameter of the posterior segments which confers a cuneate appearance to the animals in lateral aspect; in the 3/3 or 1/1 dental formula; and in the remarkably small proportional size of the reproductive

organs, including the spermatheca, the length of which is only about one-half the diameter of segment V.

None of the three species considered above can be regarded with any certainty as closely related to *C. marthae*. Indeed, the great possibility of parallelism in the origin of many minor characters that separate members of the genus renders plausible the contrary view that the closest relative of *C. marthae* should be sought among those species without an ental bulb of the prostate.

Host. – *Asellus alabamensis.*
Distribution. – Known only from the type-locality.
Material examined. – The type-series.

Cambarincola steevesi, new species (Fig. 2)

Type-specimens. – Holotype, USNM 49680, two paratypes, USNM 49681 and one paratype, PCH 1883, taken on *Asellus alabamensis* in Glover's Cave, Todd County, Kentucky, by R. M. Norton, April 17, 1964; one paratype, USNM 49682 (PCH 1884), taken on *Asellus alabamensis*, in Brown Cave, Barren County, Kentucky, by R. M. Norton, September 25, 1965.

Diagnosis. – Small slender branchiobdellids (about 1.0 to 2.4 mm in length); body outline smooth; upper jaw slightly larger than lower, dental formula 5/4; bursa somewhat less than 1/4 body diameter in length; spermiducal gland small, its diameter 1/2 its length; prostate non-differentiated, slender, subequal to spermiducal gland in length, 1/6 latter in diameter, without ental bulb; spermatheca relatively long, its length often equal to body diameter, bulb oval to spatulate, without ental process.

Etymology. – It is an honor to dedicate this species to my friend and colleague, Dr. Harrison R. Steeves III, who gave me specimens of the first cavernicolous branchiobdellid from an isopod, *Cambarincola alienus*, and the material upon which this species is based.

Description. – Members of *Cambarincola steevesi* are small, slender worms with the thin body wall and delicate appearance of other branchiobdellids that infest isopods. The holotype has the following dimensions: *total length*, 2.1 mm; *greatest diameter* 0.5 mm; *head length*, 0.3 mm; *head diameter*, 0.2 mm; *diameter, segment I*, 0.2 mm; *diameter, sucker*, 0.2 mm. The average dimensions of the type-series, including the holotype, are as follows: *total length*, 1.7 mm (1.0-2.4 mm); *greatest diameter*, 0.4 mm (0.2-0.5 mm); *head length*, 0.3 mm (0.2-0.5 mm); *head diameter* 0.2 mm (0.2-0.3 mm); *diameter, segment I*, 0.2 mm (0.2-0.2 mm); *diameter, sucker*, 0.2 mm (0.2-0.2 mm). Other specimens from Trigg County, Kentucky, are of similar general dimensions.

The peristomium, in most specimens, is divided into upper and lower lips: in some specimens the lateral indentations of the peristomium that divide it into lips are undetectable. There are no observable oral papillae. With the exception of the peristomial sulcus, the head has no external indications of segmentation and the one internal pharyngeal sulcus is obscure.

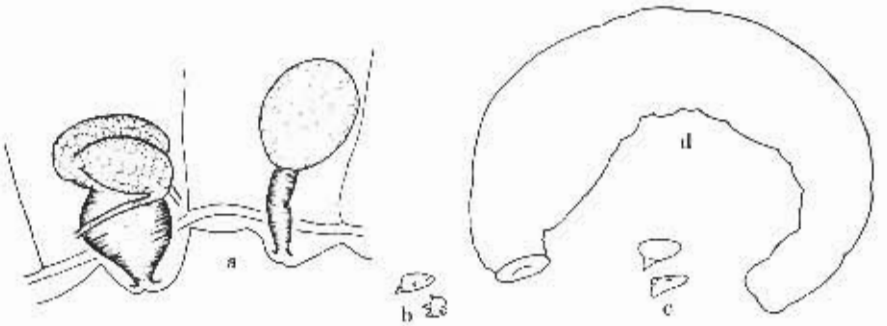

Fig. 2. *Cambarincola steevesi*, new species. *a*, reproductive systems of holotype; *b*, same, oblique view of jaws; *c*, same, lateral view of jaws of paratype; *d*, same, outline of holotype.

The jaws are always medium brown and obvious with the upper one slightly the larger and a dental formula of 5/4. Although perhaps proportionately small, they are typical of those of most species of the genus.

The spermiducal gland is small, about twice or rather less, its diameter in length, and lies laterally to the ental portion of the bursa and extends dorsally beyond the ventral border of the gut. The non-differentiated prostate is somewhat shorter than the spermiducal gland, but is only 1/6 to 1/5 the diameter of the latter. In some specimens, its ental end appears to be composed of thickened, non-glandular cells, but there is no distinct ental bulb, *i.e.*, a clear fluid filled space with a thin-walled, non-glandular covering. Other than their disproportionately small size, characteristic of the male reproductive system as a whole, there is nothing of note presented by the ejaculatory duct or bursa.

The spermatheca, provided with a long ectal duct, lacks an ental process and the oval to spatulate bulb often reaches the dorsal body wall.

Variation. — The jaws are less prominent in smaller (younger) specimens, but are always colored and visible. The spermathecal bulb may vary somewhat in shape, but no more than that found at various degrees of maturity in other species. There is never any indication, even in animals with a spatulate (presumably incompletely distended) spermathecal bulb, of an ental process of the spermatheca. Though not apparent in the holotype and some other specimens, the ental end of the prostate is probably normally characterized by thickened non-glandular cells.

Affinities. — Among the members of the genus with a non-differentiated prostate without an ental bulb, *Cambarincola steevesi* lacks the large size of the prostate or the obvious deferent lobes of all those described by Hoffman (1963). An ental bulb of the prostate clearly separates *C. marthae* from *C. steevesi* which lacks this feature. The physiological significance of this structure and the relationship between it and the thickened non-glandular cells of the ental end of the prostate are not known and, indeed, *C. marthae* may be the closest relative of *C. steevesi* (see the discussion of the affinities of *C. marthae*). All the features that

separate *C. marthae* from the Mesoamerican worms with which the latter is compared apply to *C. steevesi* except for the prostatic ental bulb, but all are markedly different from those of *C. steevesi* in various ways and need not be further considered here. But *C. alienus*, which infests isopods and is an apparent troglobite, should be. The latter differs from *C. steveesi* in its greatly reduced, almost colorless, jaws and prominent ental process of the spermatheca. If, as has been previously postulated (Holt, 1969: 193-194), the ental process of the spermatheca is primitive and the non-glandular ental end of the prostate of *C. steevesi* is a step in the evolution of an ental bulb of the latter, then *C. steevesi* and *C. alienus* would each have features expected in the ancestral stock that gave rise to all three of the isopod infesting, troglobitic branchiobdellids: *C. alienus*, *C. marthae* and *C. steevesi*. This must stand as sheer speculation, but it seems reasonable to suspect a relationship among these species and, in some respects (the ental bulb of the prostate and the absence of an ental process of the spermatheca), *C. marthae* is the most specialized of the three. Although *C. alienus* is obviously specialized in the extreme reduction of its jaws, on balance it may be closer to a hypothesized ancestral stock of all three species.

Host. – *Asellus alabamensis.*

Distribution. – *Cambarincola steevesi*, in addition to the type-locality, is known from Taylor Cave, Trigg County, Kentucky, and Brown Cave, Barren County, Kentucky.

Material examined. – The type-series (four specimens); six specimens, PCH 1884, from Barren County, Kentucky.

Cambarincola leoni new species (Fig. 3)

Type-specimens. – Holotype, USNM 49676 and one paratype, USNM 49677, on *Procambarus (Ortmannicus) orcinus* Hobbs and Means, 1972, taken from Gopher Sink, Leon County, Florida, by D. Bruce Means and Joseph Halusky, April 3, 1971 (PCH 2757); five paratypes, PCH 2756, on *P. orcinus* taken from Gopher Sink, Leon County, Florida, by D. B. Means and J.F. Berry, February 26, 1971.

Diagnosis. – Moderately large branchiobdellids (about 2.8 mm to 5.3 mm in length); minor annulations subequal to major (anterior) ones in diameter; intra-segmental furrows prominent; jaws dark brown, subequal in size, dental formula 1/2; bursa elongate, pyriform; spermiducal gland slender, 1/3 to 1/2 non-glandular; prostate non-differentiated, with small, obscure ental bulb; spermatheca with very large ovoid bulb, without ental process.

Etymology. – For the Spanish conquistador, Ponce de León, discoverer of Florida.

Description. – Members of the species *Cambarincola leoni* are moderately large branchiobdellids. The holotype and four other mature specimens yield the following average dimensions: *total length*, 3.8 mm (2.8-5.3 mm); *greatest diameter*, 0.7 mm (0.6-0.8 mm); *head length*, 0.6 mm (0.4-0.7 mm); *head diameter*, 0.4 mm (0.3-0.5 mm); *diameter, segment I*, 0.4 mm (0.3-0.5 mm); *diameter, sucker*, 0.4 mm (0.3-0.5 mm).

The lips are entire; there are no detectable oral papillae; the peristomial sulcus is prominent. Externally, there is a very shallow encircling sulcus of the head, corresponding to a single internal pharyngeal one.

Supernumary muscles of the anterior annulations of the trunk segments are poorly developed, so that the body outline is relatively smooth, although the posterior annulations are prominent by virtue of relatively deep intra- and

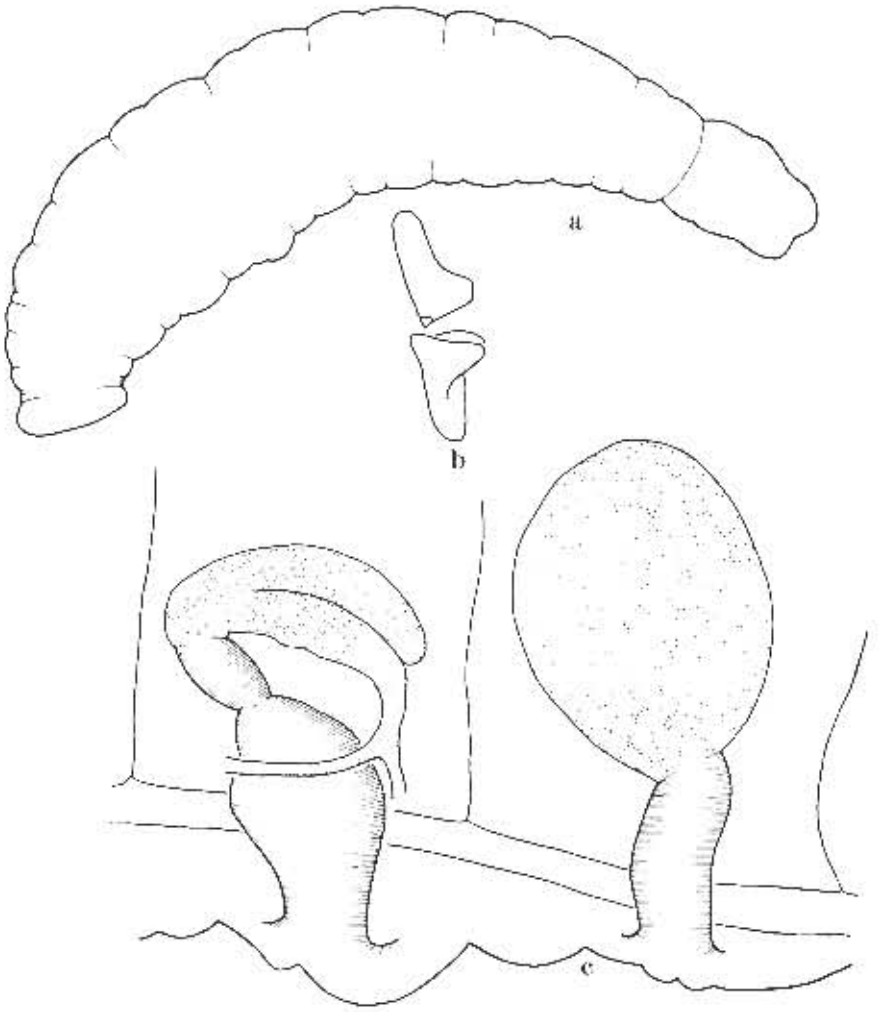

Fig. 3. *Cambarincola leoni*, new species. *a*, outline of holotype; *b*, same, lateral view of jaws; *c*, same, reproductive systems.

intersegmental furrows. The anterior nephridiopore is obscure in my relatively well preserved material. The clitellum is especially prominent on segment VII.

The jaws are unsual and diagnostic. Subequal in size, dark brown, they have large dorsally and ventrally directed bases, respectively, with shorter logitudinally oriented flanges, which confer an approximately L-shaped appearance (inverted for the lower jaw) upon them in lateral view. The teeth are blunt and obscure in all my specimens, but the dental formula appears to be 1/2.

The spermiducal gland is small and slender, but its truly distinctive feature is the non-glandular nature of its ental portion which comprises from 1/4 to 1/2 of its total length, and is composed of the type of epithelial cells which characterize the deferentia. This non-glandular portion is hardly greater in diameter than that of one of the two vasa deferentia. The ectal 1/2 to 3/4 of the gland is hardly more than twice the diameter of the slender ental part.

The prostate in non-differentiated; is subequal in diameter and approximately 2/3 the length of the spermiducal gland. It possesses a small, obscure ental bulb. The ejaculatory duct and bursa present no noteworthy features, though the bursa is somewhat more elongated than is common in the genus. It has a prominent atrial fold at its midlength.

The spermathecal ectal duct is approximately 1/3 the total length of the organ, that, in its entirety, is subequal in length to the body diameter. The spermathecal bulb is proportionately huge, ovoid, thin-walled, with only a mere suggestion, produced by somewhat thicker epithelial cells at its apex, of an ental process.

The sucker is provided with a number of prominent unicellular glands that open on its inner surface. The gut is filled with a coagulum, and since the worms inhabit the gill chambers of the host (Hobbs, Jr. personal communication), it may be assumed that this material is composed of the blood of the hosts.

Variation. – Other than a rather marked variation in size of mature animals (those with a well developed clitellum and maturing ova in segment VII), and the obvious presence of dorsal ridges in some specimens, a variation best accounted for by the use of different preservative fluids by the various collectors, there are no significant differences among the available specimens.

Affinities. – Obscure: the male reproductive system clearly places this species in the genus *Cambarincola*, but the jaws are reminiscent of those of *Bdellodrilus illuminatus* (Moore, 1894) and these, and the peculiarities of the spermiducal gland, remove *C. leoni* from a close relationship to any known member of the genus. The non-differentiated prostate places the species in Hoffman's (1963) Mesochoreus section of the genus and the affinities of *C. leoni* should perhaps be sought among the more primitive forms of this group. There is a Mexican branchiobdellid, *Cambarincola micradenus* Holt, 1973a, from La Cañada y Tetela de Ocampo, Pueblo, that has a peculiar spermiducal gland with a differentiated ental protion. *Cambarincola micradenus*, however, has jaws that are quite disparate in size, a prostate that actually lies almost free of the spermiducal gland beyond its origin from the latter and is much smaller in size. Other than that both are evolutionarily representative of old stocks (primitive) of the genus, they cannot be considered as closely related.

Hosts. *Procambarus orcinus*: an intergrade population of *P. (Ortmannicus) l. lucifugus* (Hobbs, 1940) and *P. l. alachua* (Hobbs, 1940); *Troglocambarus maclanei* Hobbs, 1942.

Distribution. – Known only from the type-locality, Indian Cave, Marion County, and Squirrel Cave, Alachua County, Florida. The Marion County record is near an area of Florida that may have been above sea level since Pliocene times; the Leon County and Alachua County records are from an area that was probably under marine waters in the early Pleistocene (Cooke, 1945). *Cambarincola leoni* appears to be a cavernicole and its presence in the limestone "sinks" of Florida to antedate the Pleistocene epoch.

Material examined. – The types and one specimen, PCH 2758, from the type-locality; two specimens, PCH 2360, on *Procambarus l. lucifugus* X *P. l. alachua* taken in Indian Cave, Marion County, Florida, by John E. and Martha R. Cooper, December 31, 1964.

Cambarincola sheltensis, new species (Fig. 4)

Type-specimens. – Holotype, USNM 49683, two paratypes (PCH 1846), taken on *Orconectes australis australis* (Rhoades, 1941) in Shelta Cave, Huntsville, Madison County, Alabama, by John E. and Martha R. Cooper, August 24, 1963; two paratypes, USNM 49684, and one paratype, PCH 1863, taken on *O. a. australis* in Shelta Cave, Huntsville, Madison County, Alabama, by James E. Laritner, 1965.

Diagnosis. – Medium sized branchiobdellids (holotype approximately 2.5 mm in length); upper lip with four blunt lobes; trunk segments with dorsal ridges; upper jaw slightly larger than lower, dental formula 5/5; bursa elongate oval, slightly less in length that 1/2 body diameter, often thin-walled, atrial fold present, both atrial and penial sheath with expanded cavities; spermiducal gland long, slender; prostate differentiated, only slightly shorter than spermiducal gland, about 1/3 diameter of latter, with prominent ental bulb; spermatheca with long muscular ectal duct, bulb subequal in length to latter, narrow spatulate, with thick, non-glandular wall.

Etymology. – For the type-locality, Shelta Cave.

Description. *Cambarincola sheltensis* is composed of moderate-sized worms. The holotype has the following dimensions: *total length* 2.5 mm; *greatest diameter*, 0.5 mm, *head length;* 0.5 mm; *head diameter*, 0.3 mm; *diameter, segment I*, 0.3 mm; *diameter, sucker*, 0.3 mm. The average dimensions of the type-series are as follows: *total length*, 2.8 mm (2.5-3.2 mm); *greatest diameter*, 0.5 mm (0.4-0.6 mm); *head length*, 0.5 mm (0.4-0.7 mm); *head diameter*, 0.4 mm (0.3-0.5 mm); *diameter, segment I*, 0.3 mm (0.3-0.4 mm); *diameter sucker*, 0.3 mm (0.2-0.4 mm).

The upper lip is shallowly divided into four blunt lobes; the lower into two; the lateral indentation between upper and lower lips is itself filled with a blunt lobe or is quite broad. An indeterminate number of oral papillae are present. Externally, only the peristomial sulcus is present; internally there is one prominent posterior internal pharyngeal sulcus. Supernumary muscles of the anterior (major) annuli of the trunk are not well developed, but the major annuli are slightly greater in diameter than the minor ones, producing low dorsal ridges. The anterior nephridiopore is not prominent.

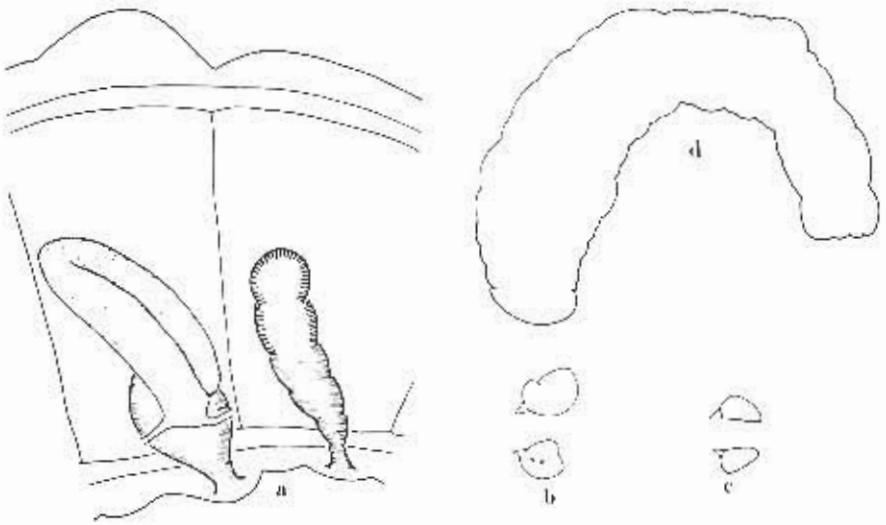

Fig. 4. *Cambarincola sheltensis*, new species. *a*, reproductive systems of holotype; *b*, same, oblique view of jaws of paratype; *c*, same, lateral view of jaws; *d*, same, outline of holotype.

The jaws are medium brown, well developed and the dental formula is 5/5. The upper jaw is only slightly larger in all dimensions than the lower.

The spermiducal gland is slender, somewhat greater in length than 1/2 the body diameter. Its diameter is about 1/7 of its length. There is a suggestion of an anterior deferent lobe in some specimens, but, though probably present, it is obscure in the holotype and in any case not prominent. The lumen of the gland, in spite of the gland's slenderness, is often expanded beyond the usual condition in other species.

The prostate is differentiated, about 1/3 the diameter of and only slightly less in length than the spermiducal gland. It ends in a large clear ental bulb. The bursa is distinguished by a thinner muscular wall and larger atrial and penial sheath cavities than is usual. Otherwise, in shape and size, it and the ejaculatory duct are not unusual.

The spermatheca, however, is distinctive and diagnostic when considered along with the characteristics of the male reproductive system. The muscular ectal duct widens gradually entally and passes imperceptibly into the thickwalled bulbular region which is only distinguished by its greater diameter and the presence within it of spermatozoa from the ectal duct.

Variation. – None, other than those differences in size and apparent differences in the male reproductive system mentioned above. The latter can readily be accounted for by the different aspects from which they are viewed.

Affinities. – *Cambarincola sheltensis* is known only from troglobitic crayfishes, and its closest relative, were it not for its peculiar spermatheca, would be

Cambarincola fallax Hoffman, 1963. These two species agree in jaw structure and dental formulae; dorsal ridges of the major annuli of the trunk segments (though these are much more pronounced in *C. fallax*); and in the general structure of the male reproductive system, except that the spermiducal gland and prostate of *C. sheltensis* are not so robust as those of *C. fallax*. They differ in the presence of peristomial tentacles in *C. fallax*, absent in *C. sheltensis*, and in the peculiar thick-walled spermatheca of *C. sheltensis*: that of *C. fallax* has a more usual thin-walled bulb without an ental process. Perhaps the simplest hypothesis is that *C. sheltensis* is the descendant of a primitive stock related to the Philadelphicus section (Hoffman, 1963) of which *C. fallax* is a member.

Host. – *Orconectes australis australis.*

Distribution. – Known with certainty only from the type-locality.

Material examined. – The type-series and seven other specimens, three of which are serially sectioned, from the same locality. In addition, several dubiously identified specimens taken on *Cambarus (Aviticambarus) hamulatus* (Cope, 1881) and *C. tenebrosus* Hay, 1902, in Salt River Cave, Jackson County, Alabama, by John E. Cooper, et al., August 7, 1967; others taken on *Cambarus (Aviticambarus) jonesi* Hobbs and Barr, 1960, and *Procambarus (Remoticambarus) pecki* Hobbs, 1967, in Key Cave, Lauderdale County, Alabama, by John E. and Martha R. Cooper, March 18, 1967; and possibly others (the collections were mixed with Shelta Cave material) taken on *O. a. australis* from Fern Cave, Madison County, Alabama, by John E. and Martha R. Cooper, (date unrecorded), have been studied and discarded. On the basis of jaw and general body characters, these animals were almost surely specimens of *C. sheltensis.*

Cambarincola leptadenus (Fig. 5)

Type-specimens. – Holotype, USNM 49678, one paratype, USNM 49679, two paratypes, PCH 2739, taken on *Cambarus (Erebicambarus) tenebrosus* Hay, 1902, in Bethel Cave, Perry County, Tennessee, by Horton H. Hobbs III, October 6, 1968.

Diagnosis. – Small branchiobdellids (about 2.2 mm in average length); body with dorsal ridges; jaws dark, subequal in size, dental formula 1/1 to 5/5; bursa small, ovoid, approximately 1/6 body diameter in length; spermiducal gland long, slender, about 1/3 body diameter in length, its diameter 1/4 or less its length, without deferent lobes; prostate non-differentiated, about 4/5 in length that of spermiducal gland, subequal to latter in diameter, with very large clear ental bulb; spermatheca with long ectal duct, elongate oval bulb, no ental process.

Etymology. – From the Greek, *leptos*, thin, and *adenos* gland; in reference to the slender spermiducal gland.

Description. Specimens of *Cambarincola leptadenus* are small to medium sized members of the genus. The holotype has the following dimensions: *total length*, 2.3 mm; *greatest diameter*, 0.4 mm; *head length*, 0.5 mm; *head diameter*, 0.4 mm; *diameter, segment 1*,0.3 mm; *diameter, sucker*, 0.4 mm. The type-series and one additional specimen, for a total of five, have the following average dimensions: *total length*, 2.2 mm (2.1-2.3 mm); *greatest diameter*, 0.4 mm (0.4-0.5 mm); *head length*,

0.5 mm (0.4-0.5 mm); *head diameter*, 0.4 mm (0.3-0.4 mm); *diameter, segment I*, 0.3 mm (0.2-0.3 mm); *diameter, sucker*, 0.4 mm (0.3-0.4 mm).

The peristomium is divided into upper and lower lips. The upper lips appear to be subdivided into four blunt lobes; the lower into two (all specimens are mounted entire in lateral aspect and most are partially macerated to the extent of a loosening of the cuticle from the body wall). An indeterminable number of oral papillae are present.

There are no external sulci of the head except for the peristomial one; a large posterior pharyngeal sulcus is present internally.

The jaws are not unusually large for epigean members of the genus, they are about 1/20 that of the head in length, and are dark brown. The dental formula seems to vary from 1/1 to 5/5, but the lateral teeth are relatively small, may wear away with age, and, in any case, are difficult to detect in lateral view. It is likely that the characteristic dental formula is 5/5.

There are low dorsal ridges present, particularly on the posterior segments, but the supernumerary muscles that produce them are thin and they are not prominent.

The spermiducal gland, as noted, is unusually slender; its diameter is about 1/4 or less its length. Oriented dorso-ventrally in the holotype, its more usual position is lying looped between the gut and ventral body wall. The prostate is somewhat shorter than the spermiducal gland, apparently non-differentiated (this point needs confirmation from better material, but there is no discernable histological difference between it and the spermiducal gland in the specimens available to me). The salient feature of the prostate is its remarkably large ental bulb.

The ejaculatory duct is a long, slender muscular tube, in keeping with the small size of the otherwise unremarkable bursa and the length of the spermiducal gland. The relative size of the bursa given above excludes its narrow outlet through the body wall.

The ectal duct of the spermatheca is approximately 1/2 the total length of the organ, but it is bent underneath the gut in its first lateral and then dorsal course to its junction with the spermathecal bulb. The latter is elongate oval in shape, thin-walled and without an ental process. The total length of the spermatheca approximates that of the bursa and spermiducal gland combined and is estimated at about 2/3 or more of the diameter of the segment in which it lies.

Variation. – Other than a possible difference in the number of teeth borne by the jaws, the only readily detectable variability is in the positions assumed by the relatively small components of the male reproductive system; they are often found lying looped and somewhat twisted underneath the gut. The ental bulb of the prostate often appears to compose the greater part of the organ, but this appearance is attributed to it so lying that it is viewed obliquely rather than laterally.

Affinities. – *Cambarincola leptadenus* resembles *C. demissus* Hoffman, 1963, in jaw structure and dental formula, in the small size of the reproductive organs and in the non-differentiated prostate with an ental bulb. The two species differ in the presence of dorsal ridges on the major annuli of *C. leptadenus*, absent in *C. demissus*; in the slender and long spermiducal gland and prostate of the former,

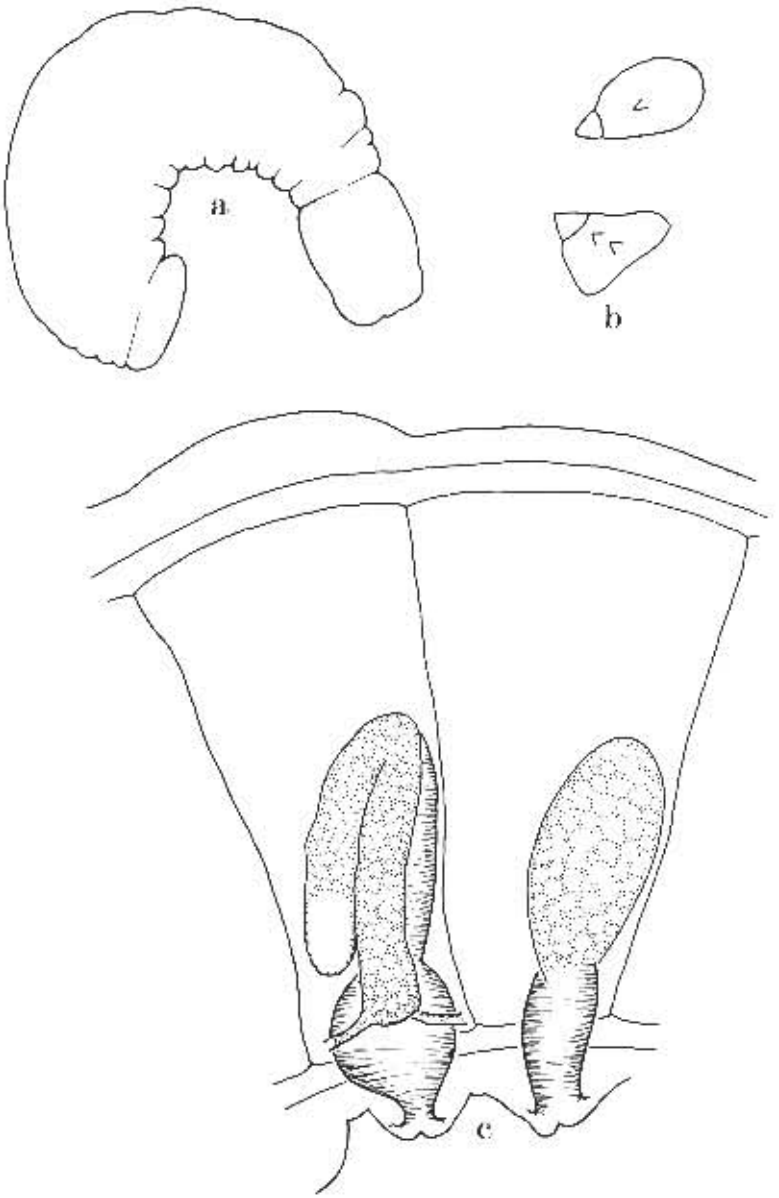

Fig. 5. *Cambarincola leptadenus*, new species. *a*, outline of holotype; *b*, same, lateral view of jaws; *c*, same, reproductive systems.

structures that are relatively much shorter and thicker in the latter; and in body shape: in *C. demissus* the posterior trunk segments are proportionately much greater in diameter. *Cambarincola marthae* differs from *C. leptadenus* in dental formula, 5/4 and 5/5 respectively, and the absence of dorsal ridges and the more normally proportioned, though still small, male reproductive organs of the former. Since we do not know the extent of convergence in these characters in the genus, it is inadvisable to designate either *C. demissus* or *C. marthae* as the closest relative of *C. leptadenus*. Indeed, some Mesoamerican species with a non-differentiated prostate may be the closest relative of *C. leptadenus*.

Host. – *Cambarincola tenebrosus*.

Distribution. – Known only from the type-locality.

Material examined. The type-series and eight other specimens from the type-locality.

Cambarincola dubius, new species (Fig. 6)

Type-specimens. – Holotype, USNM 49673, two paratypes, USNM 49674, four paratypes, PCH 2763, on *Cambarus (Erebicambarus) laevis* Faxon, 1914, and *Orconectes inermis testii* (Hay, 1891) taken from May's Cave, Monroe County, Indiana, by Horton H. Hobbs III, September 26, 1969; two paratypes, USNM 49675, two paratypes, PCH 2761, on *Cambarus laevis* taken from Mayfield's Cave, Monroe County, Indiana, by Horton H. Hobbs III, September 20, 1969.

Diagnosis. – Small to medium sized branchiobdellids (about 1.9 mm to 2.7 mm in length); dorsal ridges present; jaws dark brown, unequal in size (ratio of upper to lower approximately 4/3, anteroposterior dimension), dental formula 5/5; bursa elongate ovoid, about 1/3 body diameter in length; spermiducal gland reniform, thick, its diameter about 1/3 its length; prostate differentiated, slender, 1/6 or less in diameter that of spermiducal gland, its length about 2/3 that of latter, with prominent ental bulb; spermatheca with ovoid bulb, bulb subequal in length to ectal duct, total length approximately 1/2 diameter of body, without ental process.

Etymology. – Latin, *dubius*, uncertain, doubtful; in reference to the uncertainty as to whether the species is a troglobite and its close, and possibly confusing, resemblance to known epigean species.

Description. – Specimens of *Cambarincola dubius* are small to medium sized members of the genus. The holotype has the following dimensions: *total length*, 2.7 mm; *greatest diameter*, 0.4 mm; *head length*, 0.4 mm; *head diameter*, 0.2 mm; *diameter, segment I*, 0.2 mm; *diameter, sucker*, 0.2 mm. The average dimensions of the holotype and four paratypes are as folows: *total length*, 2.3 mm (1.9-2.7 mm); *greatest diameter*, 0.4 mm (0.4-0.4 mm); *head length*, 0.4 mm (0.3-0.4 mm); *head diameter*, 0.2 mm (0.2-0.2 mm); *diameter, segment I*, 0.2 mm (0.2-0.3 mm); *diameter, sucker*, 0.2 mm (0.2-0.3 mm).

The upper lip is subdivided into four low, blunt lobes that are difficult to see in my laterally mounted material. An indetermined number of oral papillae are present. The peristomial sulcus is not prominent; in the holotype, and some other specimens, there is a suggestion ventrally of another external sulcus of the head at

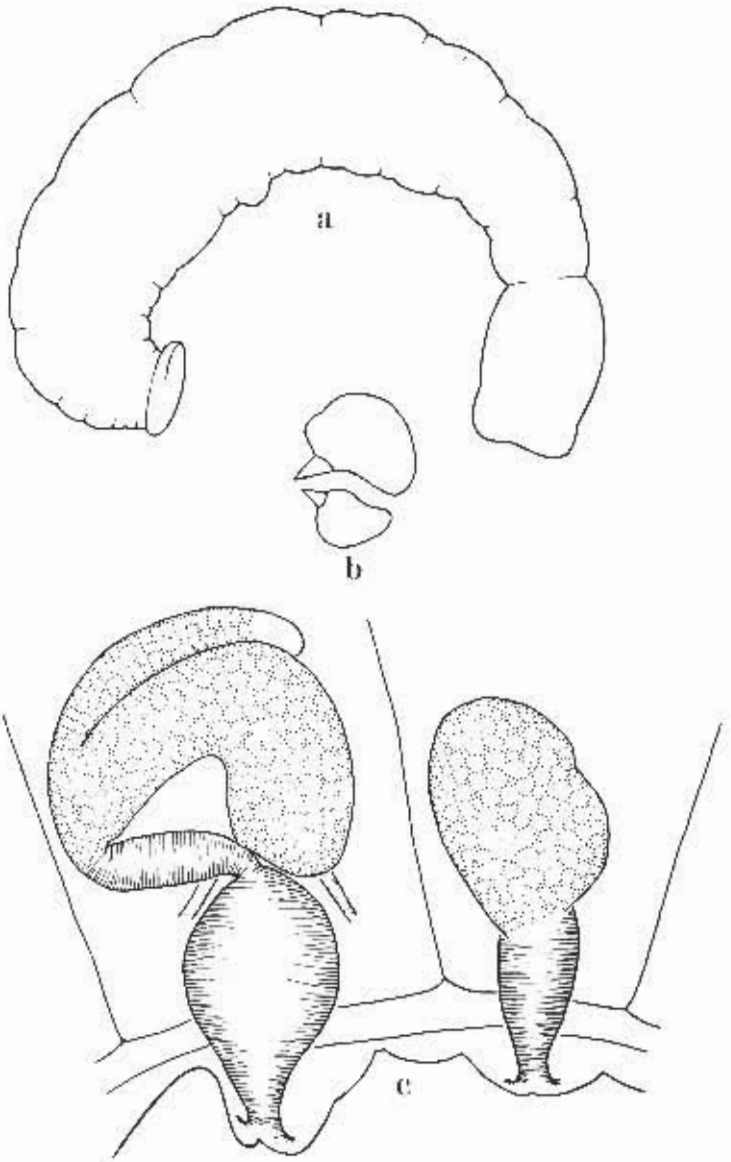

Fig. 6. *Cambarincola dubius*, new species. *a*, outline of holotype; *b*, same, lateral view of jaws, *c*, same reproductive systems.

the level of the prominent anterior internal pharyngeal sulcus. A second, much shallower, pharyngeal sulcus is present posteriorly.

Supernumerary muscles of the anterior annulus of the trunk segments are present, but the consequent raised dorsal ridges are not prominent. The anterior nephridiopore is not easily detected. The clitellum is well developed in fully mature specimens on segment VII, much less so on segment VI.

The jaws are disparate in size; the upper is distinctly larger than the lower. The dental formula is 5/5, but the lateral teeth are small and often not discernible in lateral view.

The spermiducal gland is relatively large and is bent at its mid-length, a flexure that produces a kidney-shaped appearance of the organ. It usually lies essentially horizontally in the coelom alongside the gut with its dorsal border at the level of that of the gut. There are no detectable deferent lobes.

The prostate is distinctly differentiated with a prominent clear ental bulb. It is rather slender, from 2/3 to 1/2 the length of the spermiducal gland and often lies medially between the latter and the gut so that it is difficult to see in many specimens. The ejaculatory duct is a prominent muscular tube, but presents no unusual features. Neither does the bursa, except for its somewhat elongated ovoid shape.

The spermatheca is almost equally divided into ectal duct and bulbular regions. There is no indication of an ental process. In the holotype the spermathecal bulb is distorted by a slight wrinkling of the body wall which has pressed it out of shape against the gut; the normal shape of the bulb is that of a broad oval.

Variation. – Other than the variability in features mentioned above which are attributed to the aspect from which the organs are viewed, there is only one variation of note in my material. In some specimens, otherwise apparently identical to the others, the spermathecal bulb is not distended, but it is a straight blindly ending tube similar in appearance to the ental process of the spermatheca as it has been described for a number of species (Holt, 1960a, *et. seq.*). This observation cannot cast doubt upon the reality of the spermathecal ental process in other species, but it does emphasize the need of care in the use of it as a taxonomic character. There is, in addition, the usual range in size among members of the species.

Affinities. The closest relative of *Cambarincola dubius* seems to be *Cambarincola fallax* Hoffman, 1963. The reproductive systems are broadly similar, though the prostate of *C. dubius* may be relatively a little shorter and the spermiducal gland more distinctly flexed than in *C. fallax*. The jaws of *C. fallax* are subequal in size and the peristomium is furnished with distinct, although unusually short and slender, tentacles, features absent in *C. dubius*. The dorsal ridges of *C. fallax* are more pronounced than those of *C. dubius*.

Hosts. – *Cambarus laevis, Orconectes inermis testii.*

Distribution. Known only from the two caves in Monroe County, Indiana, noted above.

Material examined. – Other than the types, seven additional specimens from the type-locality, two others from Mayfield's Cave and, uncertainly five specimens from Carmichael Cave, Monroe County, Indiana.

Cambarincola alienus Holt, 1963

Cambarincola alienus Holt, 1963: 97-100; Holt, 1969: 206, 208-210. *Cambarincola alienus* – Holt, 1973a.

Type-specimens. – Holotype, USNM 30415; seven paratypes, USNM 30416; seven paratypes, PCH 1325, on *Asellus alabamensis* taken from Wet Cave, Franklin County, Tennessee, by Harrison R. Steeves, Jr. (date unrecorded).

Diagnosis (from Holt, 1963). – "Medium-sized worms slightly less than 3.0 mm in average length (preserved material); minor segmental annulations obscure, body outline consequently smooth or often markedly constricted between segments; peristomium divided into dorsal and ventral lips without lobes or tentacles; dental formula, 5/4, jaws small and delicate; male reproductive organs small, rarely or never extending dorsad of the ventral border of the gut; spermiducal gland short and thick, without deferent lobes; prostate histologically similar to spermiducal gland, one-half to two-thirds the diameter and sub-equal in length to the latter; prostatic bulb absent; spermatheca elongate, with spermathecal duct, bulb and ental process present and of approximately equal length'."

Remarks. – No additional material of *Cambarincola alienus* has come to hand. The validity of the species is not in doubt, and, in effect, is confirmed by the discovery of the new species described above.

Cambarincola demissus Hoffman, 1963

Cambarincola demissa Hoffman, 1963: 365-367.
Cambarincola demissus – Holt, 1973a.

Type-specimens. – "Holotype and four paratypes, USNM 29948, from *Orconectes erichsonianus*, (Faxon, 1898) and *O.* species collected in a tributary to the Powell River at Big Stone Gap, Wise County, Virginia, by Horton H. Hobbs, Jr., and C. W. Hart on June 17, 1950" (Hoffman, 1963: 365).

Diagnosis (modified from Hoffman, 1963: 365-367). – Medium-sized worms, 2.8-3.2 mm in length; peristomium with lobes, long (1/3 of total head length); body outline smooth, body tapering markedly from segments VI, VII to anterior border of peristomium; jaws small, dorsal slightly larger than lower, dental formula 1/1 to 5/5, lateral teeth much smaller than median ones; male efferent apparatus small: bursa small, cordate, penial sheath 1/4 or less of organ's total size; spermiducal gland short, broad, at most only half again diameter in length, without deferent lobes; prostate slender, much shorter than spermiducal gland, non-differentiated, with clear distinct ental bulb; spermatheca short, extending dorsad less than 1/2 body diameter, without ental process.

Remarks. – Hoffman (1963: 365) speculated that this rare species might be an inhabitant of the gill chambers of the host. Its occurrence on a crayfish known only from caves has no special significance other than an extension of range: the host has no obvious troglobitic adaptations and there is no reason to think the branchiobdellid is a troglobite.

Additional locality records. In addition to the type locality, Hoffman (1963:

367) reported *Cambarincola demissus* from two unspecified species of *Cambarus*, taken in the Bluestone River, 11.2 miles east of Tazewell, on U.S. Highway 460, by Horton H. Hobbs, Jr., and C. W. Hart, Jr., June 18, 1950. (PCH 393).

Cave record. – The three specimens identified in the course of this study are from *Cambarus (Puncticambarus) nerterius* Hobbs, 1964, taken in Matt's Black Cave, 2.0 miles south of Renick, Greenbrier County, West Virginia, by J. A. Stellmack, January 21, 1965 (PCH 1840).

Cambarincola fallax Hoffman, 1963

Cambarincola fallax, Hoffman, 1963: 356-359 – Hobbs, Holt and Walton, 1967: 54, *et. seq*. – Holt, 1969: 207, *et. seq*., 1973a.

Type-specimens. – "Holotype and four paratypes, USNM 29945, from *Cambarus (Hiaticambarus longirostris* Faxon, 1885, collected in Maiden Spring Creek, about 1 mile east of Wardell, Tazewell County, Virginia, on June 19, 1959, by R. L. Hoffman. Additional paratypes from the same collection" (Hoffman: 1963: 356).

Diagnosis. – Medium sized branchiobdellids, up to 4.0 mm in length; body with prominent dorsal ridges; upper lip of peristomium with four distinct finger-like tentacles; jaws subequal in size, dental formula 3/3, 5/3, or 5/5; bursa elongate pyriform; spermiducal gland large, subreniform; prostate differentiated, slender, somewhat shorter than spermiducal gland, with distinct ental bulb; spermatheca with slender ectal duct, ovoid to fusiform bulb, extending dorsad hardly more than half body diameter, without ental process.

Remarks. – *Cambarincola fallax* is a common and widespread species as an epizoite of epigean crayfishes in the southern Appalachians: in caves (Table I) it has been taken only from hosts that, at best, must be regarded as trogloxenes.

Cave records. – Cantwell Valley Cave, Hancock County, Tennessee, taken on *Cambarus (Cambarus) bartonii bartonii* by Charles Maus and John R. Holsinger, October 28, 1966. (PCH 2416). Two specimens.

Fairmont School Cave, Hancock County, Tennessee, one mile west of Treadway, taken on *C. bartonii* by John R. Holsinger and David C. Culver, August 23, 1972. Six well preserved specimens.

McClung-Zenith Cave, Monroe County, West Virginia, taken on *C. b. bartonii* by John R. Holsinger, August 31, 1967. One poorly preserved specimen.

Cambarincola heterognathus Hoffman, 1963

Cambarincola heterognatha Hoffman, 1963: 362. – Hobbs, Holt and Walton, 1967: 55. Holt, 1969: 210.

Cambarincola heterognathus – Holt, 1973a.

Type-specimens. – "Holotype and paratype, USNM 29947, from *Cambarus* sp. collected in a tributary to Big Wilson Creek, 4 miles south of Mouth of Wilson on Va. Hy. 16, Grayson County, Virginia, by Horton H. Hobbs, Jr., and C. W. Hart, June 14, 1950" (Hoffman, 1963: 362).

Diagnosis. – Medium-sized branchiobdellids, length to about 3.0 mm; major annulations of body segments slightly or not at all greater in diameter than minor ones; jaws greatly disparate in size, upper at least twice lower in total size, dental formula 1/2; bursa, fusiform, length 1 1/2 times diameter; spermiducal gland subreniform, slightly greater in diameter entally, there subequal to bursa in diameter, somewhat greater than bursa in length; prostate small and slender, less than half as long as spermiducal gland, ental bulb present; spermatheca elongate, often constricted at midlength, obscure ental process present.

Remarks. – *Cambarincola heterognathus* is widely distributed in the mountainous regions of the Southeast. In this area the distinctive jaws alone are diagnostic. The recent discovery (Holt, 1973 b) of its presence in the "Panhandle" of Florida can only be interpreted as the survival of relic populations in a Pleistocene refugium.

Cave records. – McLaughlin-Unus Cave (part of the Culverson Creek Cave System), taken on *Cambarus b. bartonii* by Ed Bauer, May 5, 1967 (PCH 2413). Five specimens.

McClung-Zenith Cave, Greenbrier County, West Virginia, taken on *Cambarus b. bartonii* by John R. Holsinger, August 31, 1967. Three specimens.

Sinks of Gandy Cave, Randolph County, West Virginia, taken on *Cambarus b. bartonii* by John R. Holsinger, August 14, 1963. Four specimens.

Cambarincola philadelphicus (Leidy, 1851)

Astacobdella philadelphica Leidy, 1851: 209.
Branchiobdella philadelphica –Moore, 1894: 427.
Bdellodrilus philadelphicus – Moore, 1895: 498.
Cambarincola philadelphica – Ellis, 1912: 485.
Cambarincola philadelphicus – Holt, 1973a.

Type-specimens. – Collected from crayfish in and around Philadelphia by Joseph Leidy; probably not kept or deposited in the collections of the Philadelphia Academy of Natrural Sciences, since extensive efforts by Mr. C. W. Hart, Jr., to locate them failed.

Diagnosis (from Hoffman, 1963: 342). –"Peristomium divided into dorsal and ventral halves, the dorsal larger and with four low marginal lobations; jaws relatively large and subrectangular in lateral aspect, the dorsal jaw usually a little larger than the ventral, [dental formula 3/2 to 5/4]; male reproductive system moderate in size, filling from half to two-thirds of the coelom of one side of segment VI; bursa elongate, at least twice as long as broad, the penial sheath merging gradually into a fairly short ejaculatory duct; spermiducal gland slender and recurved ventrad, twice the diameter of prostate, latter [differentiated], long and slender, reaching to ental end of spermiducal gland."

Remarks. – *Cambarincola philadelphicus* is the most wide-ranging and common of the branchiobdellids of the eastern United States, absent in this area only from the more southern Coastal Plain, *i.e.*, from about the latitude of Washington, D.C., but extending northward into Canada and south and west throughout the uplands,

including the Interior Low Plateaus to roughly the Mississippi River. It is a variable species, not easily separated from its close relatives (see Hoffman, 1963: 343-348; Hobbs, Holt and Walton, 1967: 70) and, indeed may constitute a complex of closely related or sibling species. Its occurrence in caves is entirely with crayfishes that are primarily trogloxenes or, at best, troglophiles. There in no reason to think of *C. philadelphicus* as anything other than an accidental inhabitant of caves.

Cave records. – Carmichael Cave, Monroe County, Virginia taken on *Cambarus laevis* by Horton H. Hobbs III, October 4, 1969. (PCH 2764). Five specimens.

Fairmont School Cave, Hancock County, Tennessee, taken on *C. bartonii* by John R. Holsinger and David C. Culver, August 23, 1972. (PCH 2929). Twenty-two specimens.

Bowen Cave, Hardin County, Tennessee, host unknown, taken by Horton H. Hobbs III, October 5, 1968. (PCH 2738). Five specimens.

Wagoner's Cave, Tazewell County, Virginia, taken on *C. bartonii* by R. R. Holsinger, David C. Culver and Paul Starr, August 19, 1967. (PCH 2417). Five specimens.

Benedict's Cave, Greenbriar County, West Virginia, taken on *C. b. carinirostris* by West Virginia Association for Cave Studies, January 8, 1966. (PCH 1911). Discarded, specimens not counted.

Benedict's Cave, Greenbrier County, West Virginia, taken on *C. b. bartonii* by J. E. Gravenmier, July 9, 1966. (PCH 2599). One specimen.

Buckeye Creek Cave, Greenbrier County, West Virginia, taken on *C. bartonii* by John E. Cooper, November 28, 1963. (PCH 1847). Five specimens.

Coffman Cave, Culverson Creek System, Greenbrier County, West Viriginia, taken on *Cambarus (Puncticambarus) nerterius* by John E. and Martha R. Cooper, May 9, 1964. (PCH 2370). Seven specimens.

Fuller's Cave, Culverson Creek System, Greenbrier County, West Virginia, taken on *C. b. bartonii* by David C. Culver, June 19, 1967. (PCH 2415). Two specimens.

Luddington's Cave, Greenbrier County, West Virginia, taken on *C. nerterius* by J. E. Gravenmier, October 29, 1966. (PCH 2601). One specimen.

Matt's Black Cave, Greenbrier County, West Virginia, taken on *C. nerterius* by J. A. Stellmack, July 4, 1964. (PCH 1840). Five specimens.

McLaughlin-Unus Cave, Culverson Creek System, Greenbrier County, West Virginia, taken on *C. b. bartonii* by Ed Bauer, May 5, 1967. (PCH 2413). Five specimens.

Wade's Cave, Greenbrier County, West Virginia, taken on *C. bartonii carinirostris* Hay, 1914, by West Virginia Association for Cave studies, April 23, 1966. (PCH 1910). Seven specimens.

Wade's Cave, Greenbrier County, West Virginia, host unknown, taken by H. Gentry, August 6, 1966. (PCH 2600). Nine specimens.

Ripley Cave, Monroe County, West Virginia, taken on *C. b. bartonii* by John R. Holsinger, August 21, 1964. (PCH 1841). Three specimens.

McClung-Zenith Cave, Monroe County, West Virginia, taken on *C. b. bartonii* by John R. Holsinger, August 31, 1967. (PCH 2418). One specimen.

Mystic Cave, Pendleton County, West Virginia, taken on *C. bartonii* by John R.

Holsinger, August 3, 1963. (PCH 1707). One specimen.

Linwood Cave, Pocahontas County, West Virginia, taken on *C. b. bartonii* by John R. Holsinger, and R. Baroody, September 3, 1967. (PCH 2420). Twelve specimens.

Sinks of Gandy Cave, Randolph County, West Virginia, taken on *C. bartonii* by John R. Holsinger, July 14, 1963. (PCH 1705). Sixteen specimens.

Cambarincola species A

In addition to unidentifiable material (Table 1), I have two collections, probably representing two separate species, of worms that are undoubtedly members of the genus *Cambarincola*. One is a menber of the *fallax-philadelphicus* complex and is alsmost surely representative of a common epigean, but undescribed species (it is known that there are several such species in the Tennessee and Cumberland drainages). The specimens are so badly macerated, however, that an adequate description is impossible.

The locality data: Bristol Caverns, Sullivan County, Tennessee, taken on *Cambarus bartonii cavatus* Hay, 1902, by John R. Holsinger, December 9, 1967. (PCH 2421). Fifteen specimens.

Cambarincola species B

Listed with *Cambarincola* species A under *Cambarincola* sp. nov. (Table 1) are specimens that apparently, but somewhat uncertainly, represent a new species of the genus. Again the material is too poor to describe, but the bursa is unusually large and muscular, proportionately greater so than in any known species of *Cambarincola*, and the jaws resemble those of *C. fallax*.

The locality data: Stream in Big Schacklett Cave, Meade County, Kentucky, 3.3 miles north of Big Spring, taken on *Cambarus tenebrosus* by Leslie Hubricht, September 28, 1957. (PCH 2532; USNM 18066). Six specimens.

Ankyrodrilus Holt, 1965

Type-species. – *Ankyrodrilus koronaeus*, by original designation.

Diagnosis (from Holt, 1965a: 10). – "Branchiobdellid worms with two pairs of testes; paired nephridipores on the dorsum of segment III; at least nine distinct segments visible in dorsal view; gut straight, with sacculations in segments II, III, IV, those of segments III and IV the larger; aggregations of gland cells present in lateral portions of segments VIII and IX; caudal sucker ventral; body depressed and tapering gradually from anterior end to its greatest width in segment VI, VII, or VIII; spermiducal gland large with blindly ending bifurcated proximal [ental] portion, vasa deferentia entering the median portion of the organ; bursa constricted between atrial and penial sheath portions, giving to the organ as a whole a reduplicated aspect; ejaculatory duct absent; spermeatheca composed of ectal duct, bulb, and ental process."

Remarks. – The genus *Ankyrodrilus* is composed of two species, mainly allopatric in range but overlapping in the southwestern tributaries of the New River in Virginia: a combined range that extends from the upper reaches of the Roanoke River in Virginia to streams of the Cumberland drainage in Tennessee. These species are known to ooccupy the exposed outer surfaces of the host crayfish and are in general facies typical epigean forms.

Ankyrodrilus legaeus Holt, 1965

Type-specimens. – Holotype, USNM 20872, four paratypes, USNM 30873, three paratypes, PCH 139, taken on *Cambarus bartoni cavatus* by J. T. Wheeler, four miles east of Ewing, Lee County, Virginia, August 18, 1948 (modified from Holt, 1965: 12).

Diagnosis (from Holt, 1965a:12). – "Upper jaw with five teeth; lower jaw with four-five teeth; teeth of upper jaw of unequal length, lateral teeth and median teeth shorter than others; lateral teeth of lower jaw longer than median teeth."

Remarks. – The two species of *Ankyrodrilus* differ in jaw structure: *A. koronaeus* has a 3/4 dental formula, with all the teeth of both jaws subequal in length. The specimens of *A. legaeus* from a cave can only be regarded as trogloxenes, as are those of the host crayfish.

Cave record. – Fairmont School Cave, Hancock County, Tennessee, taken on *Cambarus bartonii* by John R. Holsinger and David C. Culver, August 23, 1972, (PCH 2929). Eight specimens.

Bdellodrilus Moore, 1895

Type-species. – *Bdellodrilus illuminatus* (Moore, 1894) by monotypy.

Diagnosis (emended from Hobbs, Holt and Walton, 1967: 51). "Head elongated and less in diameter than anterior body segments: peristomium without lobes, body wall thin and glandular (parasitic facies); posterior sucker thin and weak; two pairs of testes, no prostate; [deferent ducts enter spermiducal gland ectally to its ental end]; penis eversible; spermatheca bifid; lateral glands present in trunk segements I through IX; anterior nephridia open by common pore; upper jaw longitudinal ridge bearing three teeth, lower jaw deep trough in which dorsal one fits, inhabitants of gill chambers, monotypic."

Remarks. –*Bdellodrilus* is a relatively primitive genus (Holt, 1969: 196, 200-201) with a continental distribution, that has survived as a parasite within the gill chambers of the host. There is no readily apparent reason why it should not be commonly associated with troglobitic crayfishes, but this is apparently not so.

Bdellodrilus illuminatus (Moore, 1894)

Branchiobdella illuminata Moore, 1894: 421.
Bdellodrilus illuminatus – Moore, 1895: 498.

Type-specimens. No longer extant; but taken at Philadelphia, Pennsylvania, and

in Watauga County, North Carolina, on *Cambarus b. bartonii* by J. Percy Moore.

Diagnosis. – As for the genus.

Cave records. Cantwell Valley Cave, Hancock County, Tennessee, taken on *Cambarus bartonii bartonii* by Charles Maus and John R. Holsinger, October 28, 1966. (PCH 2416). Two specimens.

Fuller's Cave, Culverson Creek Cave System, Greenbrier County, West Virginia, taken on *C. b. bartonii* by David C. Culver, June 19, 1967. (PCH 2415). One specimen.

Wade's Cave, Greenbrier County, West Virginia, taken on *C. b. carinirostris* by West Virginia Association for Cave Studies, April 23, 1966. (PCH 1910). Unknown number of specimens discarded.

Oedipodrilus Holt, 1967

Type-species. – *Oedipodrilus oedipus* Holt, 1967: 58, by original designation.

Diagnosis (emended from Holt 1967: 38). – Small to medium sized worms often with anterior segmental annulations greater in diameter than posterior ones; anterior nephridiopore on dorsum of segment III; jaws of variable size, shape, with unequal number of teeth; two pairs of testes; bursa large, with long penial sheath enclosing eversible penis provided with chitinous covering bearing recurved hooks; ejaculatory duct present; prostate usually incompletely divided from spermiducal gland, histologically similar to latter; spermatheca variously formed, but with expanded ectal duct, spermathecal bursa, ental process, or some combination thereof, in addition to spermathecal bulb.

Remarks. In addition to the type species, *Cambarincola macbaini* Holt, 1955, has been informally assigned to *Oedipodrilus* (Holt, 1969: 205) and is herein considered a member of the latter genus. Several species are known to occur in the United States, but Holt (1967: 60) was mistaken in believing that Mexican worms later assigned to *Sathodrilus* Holt, 1968b, belong to *Oedipodrilus*. Little else is known of the genus; it is badly in need of revision.

Oedipodrilus macbaini (Holt, 1955)

Cambarincola macbaini Holt, 1955: 27.

Type-specimens. – Holotype, USNM 25952, taken on an unkown host from Charles Creek, Boyd County, Kentucky, by Rodney MacBain, 1948.

Diagnosis (emended from Holt, 1955: 27). – Lips entire; anterior annulations not greatly greater in diameter than posterior ones, body outline consequently rather "smooth"; jaws small and delicate, dental formula 5/4; bursa longer than body diameter, usually bent caudad at dorsal border of gut, penial sheath enclosing long eversible penis with chitinous hooks; spermatheca with long, expanded ectal duct which reaches dorsal border of coelom, spermathecal bulb long, extending anteriorad, without ental process or spermathecal bursa.

Cave record. Bristol Caverns, Sullivan County, Tennessee, on *Cambarus bartonii cavatus* taken by John R. Holsinger, December 9, 1967. (PCH 2421). Four specimens.

Xironodrilus Ellis, 1918

Type-species. – *Xironodrilus formosus* by original designation (Ellis, 1919:244).

Diagnosis (from Hobbs, Holt and Walton, 1967: 62). – "Body depressed, widening gradually from segment I to segment VII; deferent ducts entering ental end of spermiducal gland; prostate absent; bursa spherical."

Remarks. – Members of the genus range from the upland regions of the southern Appalachians west to the Ozarkian uplands, northward to the shores of Lake Superior. All are epizoites of the exposed surfaces of the carapace of cambarine hosts and are unlikely to be found, other than adventitiously, in caves.

Xironodrilus formosus Ellis, 1918

Type-specimens. – "Holotype, USNM 17626, taken on *Cambarus rusticus* Girard (det. Faxon) from the White River, Irondale, near Anderson, Indiana, by Max M. Ellis, August, 1915" (Ellis, 1919: 244).

Diagnosis (from Hobbs, Holt and Walton, 1967: 62). – "Dental formula 4/3 to 6/5, teeth subequal in size with lateral teeth somewhat shorter than median ones; spermathecal duct distinct, bulb of spermatheca globose or cylindrical; spermiducal gland simple U-shaped tube, less than twice diameter of vasa deferentia; ejaculatory duct absent."

Cave locality. – Briston Caverns, Sullivan County, Tennessee, on *Cambarus bartonii cavatus* taken by John R. Holsinger, December 9, 1967. (PCH 2421). Six specimens.

Xironogiton Ellis, 1919

Type-species. – *Xironogiton oregonensis* by original designation. *X. oregonensis* has recently been reduced to synonomy with *X. instabilis* (Moore, 1894) (Holt, in press).

Diagnosis (from Holt, in press). – "Medium to large branchiobdellids (known species from approximately 1.4 to 7.5 mm, preserved specimens, in length); body terete anteriorly, depressed posteriorly, without peristomial tentacles or dorsal projections on trunk segments, posterior sucker directed ventrad; jaws subrectangular; paired nephridiopores on dorsum of segment III; with two pairs of testes; spermiducal gland with vasa deferentia entering ectally; prostate or prostatic protuberance absent; ejaculatory duct present; penis protrusible, noneversible; bursa large, heavily muscular, spherical, ellipsoid or asymmetrically subpyriform; spermatheca disproportionately small."

Remarks. – The genus *Xironogiton* has been revised recently (Holt, in press). The center of speciation of the genus is in the drainage of the Pacific Northwest, but *X. instabilis*, common in the west, is also a common inhabitat of cold moutain streams from North Carolina and Tennessee northward to northern New York. All members of the genus occupy the exposed chelipeds of their astacid hosts (both astacines and cambarines) and none are likely candidates for any continued existence in caves.

Xironogiton instabilis (Moore, 1894)

Branchiobdella instabilia Moore 1894: 425-427. – Smallwood, 1906: 100-111. Ellis, 1912: 484.
Bdellodrilus instabilis, – Pierantoni, 1912: 22. – Hall, 1914: 190, 192.
Xironogiton oregonensis oregonensis Ellis, 1919: 249-251. (in part).
Xironogiton oregonensis pectinatus Ellis, 1919: 251. (in part).
Xironogiton instabilius. – Ellis, 1919: 252-253. (in part).
Xironogiton instabilius instabilius Goodnight, 1940: 45-47. – Holt 1949: 536. – McManus, 1960: 421-427. (in part).
Xironogiton instabilius oregonensis. Goodnight, 1940: 47-48. (in part).
Xironogiton instabilius. – Berry and Holt, 1959: 5-11. – Hobbs, Holt and Walton, 1967: 64. – Holt, 1968a: 82-84, 86, 88, 91; 1969: 194, 196-197, 201-202, 213.
Xironogiton instabilia. Franzén, 1962: 369-383.
Xironogiton instabilis. Holt (in press).

Type-specimens. – Moore's original material has been lost, but in any case, the types are those of Ellis' *X. oregonensis* by subsequent designation (Holt, in press). Holotype, USNM 17639, taken on *Astacus* [=*Pacifastacus leniusculus*] *klamathensis* (Stimpson [1857]) (det. Faxon) at Eugene, Oregon, by J. E. Guthberlet, October, 1914 (Ellis, 1919: 249).

Diagnosis (from Holt, in press). – "Medium sized branchiobdellids (length about 2.0-2.7 mm); segments I-IV terete, segments V-VIII broadly flattened, often indistinguishable externally; jaws subrectangular, dental formulae from about 4/4 to 11/11, teeth often but not always of unequal length; bursa subspherical to pyriform; spermiducal gland extending dorsad, bending mesad over bursa, never extending to opposite body wall; spermatheca clavate, very small."

Cave records. – Wagoner's Cave, Tazewell County, Virginia, on *Cambarus hartonii cavatus* taken by John R. Holsinger, David C. Culver and Paul Starr, August 19, 1967. (PCH 2417). Five specimens.

Mystic Cave, Pendleton County, West Virginia, on *Cambarus hartonii hartonii* John R. Holsinger, August 3, 1963. (PCH 1707). No specimens kept.

UNIDENTIFIED MATERIAL

As noted in the introduction to this paper, much of the material I have received from speleologists was too badly preserved for identification. Although some identifications of both hosts and branchiobdellids are questioned (Table 1), there is relatively little doubt in my mind of the correctness of these identifications. In order, however, to alert future collectors to the occurrence therein of branchiobdellids, the caves from which this unidentified material came, with the abbreviations for the host species are recorded in the following table along with the more certainly identified material. A list of host species, with appropriate abbreviations, is presented first so that the branchiobdellid identifications, host species and caves may be presented in tabular form.

HOSTS OF CAVE BRANCHIOBDELLIDS

Initials preceding names are used to identify hosts in the following table of eastern cave branchiobdellids and their localities. Initials in roman type identifies normally epigean hosts taken in caves; those in italic type, hosts that are normally both epigean and troglophilic; those in boldface type, hosts regarded as true troglobites. Authors and dates of host cambarine species are taken from Hobbs, 1972. Authors and dates of asellid species were furnished by Fleming.

Decapoda, Astacidae: Cambarinae

1. (Cb). *Cambarus (Cambarus) bartonii* (Fabricius, 1798).
2. (Cbb). *C. (C.) b. bartonii* (Fabricius, 1798).
3. (Cbr). *C. (C.) b. carinirostris* Hay, 1914.
4. (Cbv). *C. (C.) b. cavatus* Hay, 1902.
5. (Cc). *C. (Jugicambarus) cryptodytes* Hobbs, 1941.
6. (Ch). *C. (Aviticambarus) hamulutus* (Cope, 1881).
7. (Cj). *C. (A.) jonesi* Hobbs & Barr, 1960.
8. (CD). *C. (Depressicambarus) latimanus* (LeConte, 1856).
9. (*Cl*). *C. (Erebicambarus) laevis* Faxon, 1914.
10. (Cn). *C. (Puncticambarus) nerterius* Hobbs, 1964.
11. (*Ct*). *C. (Erebicambarus) tenebrosus* Hay, 1902.
12. (Csp). *C.* species.
13. (Oa). *Orconectes australis australis* (Rhoades, 1941).
14. (Oi). *O. inermis testii* (Hay, 1891).
15. (Os). *Orconectes* species – Shelta Cave, Madison Co., Ala.
16. (Ps). *Procambarus* species – Simm's Sink, Suwannee Co., Fla.
17. (Ph). *P. (Ortmannicus) horsti* Hobbs and Means, 1972.
18. (Pl). *P. (O.) lucifugus lucifugus* (Hobbs, 1940).
19. (Pa). *P. (O.) l. alachua* (Hobbs, 1940).
20. (Po). *P. (O.) orcinus* Hobbs and Means, 1972.
21. (Pp). *P. (Remoticambarus) pecki* Hobbs, 1967.
22. (Tm). *Troglocambarus maclanei* (Hobbs, 1942.
23. (Un). Unidentified, epigean, cambarine crayfish.

Isopoda: Asellidae

24. (*Aa*). *Asellus alabamensis* (Stafford, 1911).
25. (*As*). *A. Stygius* (Packard, 1871).
26. (*Asp*). *A.* species.

TABLE 1. Caves, Branchiobdellids and Hosts

Branchiobdellid names with asterisks are those of new species described herein. The preceding list of hosts gives not only the abbreviations, in parenthesis, for each host species, but by the use of different letter type an indication of the usual habitat of the host. Question marks before the name of an animal, branchiobdellid or host, indicates some residual doubt as to its correct identification. All materias studied, whether identifiable or not are included.

CAVES	BRANCHIOBDELLIDS	HOSTS
Region 1: Tennessee, Hancock Co., Cantwell Valley Cave	*Bdellodrilus illuminatus* *Cambarincola fallax*	Cbb
Hancock Co., Fairmont School Cave	*Ankyrodrilus legaeus*: *C. fallax*; *C. philadelphicus*	Cb
Sullivan Co., Bristol Caverns	*Cambarincola* sp. A; *Oedipodrilus machaini*, *Xironodrilus formosus*	Cbv
Virginia, Tazewell Co., Wagoner's Cave	*C. philadelphicus* *Xironogiton instabilis*	Cbs
West Virginia, Greenbrier Co., Benedict's Cave	*C. philadelphicus* unidentified	Cbb
Greenbrier Co., Buckeye Creek Cave	*C. philadelphicus*	Cbs
Greenbrier Co., Coffman Cave (Culverson Creek System)	? *C. philadelphicus*	? Cn
Greenbrier Co., Fuller's Cave (Culverson Creek System)	? *B. illuminatus*; ? *C. philadelphicus*	Cbb
Greenbrier Co., General Davis Cave	Unidentifiable	Csp
Greenbrier Co., Luddington's Cave	*C. philadelphicus*	Cn
Greenbrier Co., Matt's Black Cave	? *C. demissus*; ? *C. philadelphicus*	Cn
Greenbrier Co., McLaughlin-Unus Cave (Culverson Creek System)	*C. heterognathus*; ? *C. philadelphicus*	Cbb
Greenbrier Co., Wade's Cave	*B. illuminatus*; ? *C. philadelphicus*; Unidentifiable	Cbb Cbr
Monroe Co., Ripley Cave	*C. philadelphicus*	Cbb
Monroe Co., McClung-Zenith Cave	? *C. fallax*; *C. heterognathus*, ? *C. philadelphicus*	Cbb

CAVES	BRANCHIOBDELLIDS	HOSTS
Pendleton Co., Mystic Cave	*C. philadelphicus*; *X. instabilis*	Cbs
Pocohontas Co., Blue Spring Cave	Unifidentifiable	Cbb
Pocohontas Co., Linwood Cave	*C. philadelphicus*	Cbb
Randolph Co., Sinks of Gandy Cave	*C. heterognathus* *C. philadelphicus*	Cb Cbs
Region 2: Florida, Alachua Co., Goat Sink	*C. leoni**	Pa
Alachua Co., Squirrel Chimney	? *C. leoni**	Tm
Gilchist Co., The Bat Hole	? *C. leoni**	Pa
Jefferson Co., Big Blue Spring	Unidentifiable	Ph
Jackson Co., Girard's Cave	Unidentifiable	Cc
Leon Co., Oak Ridge Blue Sink (=Gopher Sink)	*C. leoni**	Po
Marion Co., Indian Cave	*C. leoni**	Pt X Pa
Suwanee Co., Simm's Sink	? *C. leoni**; Unidentifiable	Ps
Georgia, Decatur Co., Climax Cave	Unidentifiable	Cc
Region 3: Kentucky, Meade Co., Big Shacklet Cave	? *Cambarincola sp. B.*	*Ct*
Indiana, Monroe Co., Carmichael Cave	? *C. dubius** ? *C. philadelphicus*	*Cl*
Monroe Co., Mayfield's Cave	*C. dubius**	Cl
Monroe Co., May's Cave	*C. dubius**	*Cl* Oi
Region 4: Alabama, Jackson Co., Salt River Cave	? *C. sheltensis**	Ch *Ct*
Lauderdale Co., Key Cave	? *C. sheltensis**	Cj Pp
Madison Co., Shelta & Fern Caves	Uncertain (collections mixed) ? *C. sheltensis**	Oa
Madison Co., Shelta Cave	? *C. sheltensis**	Os Oa
Georgia, Walker Co., Blowing Springs Cave	Unidentifiable	CD

CAVES	BRANCHIOBDELLIDS	HOSTS
Kentucky, Barren Co., Cole Cave	Unidentifiable	Asp
Barren Co., Brown Cave	*C. steevesi**	Aa
Green Co., Newt Cave	Unidentifiable	As
Todd Co., Glover's Cave	*C. steevesi**	Aa
Trigg Co., Taylor Cave	*C. steevesi**	Aa
Tennessee, Franklin Co., Wet Cave	*C. alienus*	Aa
Hardin Co., Bowen Cave	*C. philadelphicus*	un
Jackson Co., Carter Cave	*C. marthae**	Aa
Perry Co., Bethel Cave	*C. leptadenus**	Cl

EVOLUTIONARY AND ZOÖGEOGRAPHICAL CONSIDERATIONS

It would be presumptious to attempt to add to the zoögeographical and evolutionary hypotheses advanced by Thomas C. Barr, Jr., his students and colleagues, to explain the distribution of cavernicolous animals in eastern North America. An insuperable difficulty, in my case, is the inability, with the data at hand, to formulate any plausible scheme of evolutionary relationships within the genus *Cambarincola*, the only one of any interest among the branchiobdellids reported herein from caves. There are two obvious reasons that I can advance in my defense: the mixture of characters that are used to define species of the group are such that a great deal of parallelism is suspected and I know of the existence of a large number of undescribed species within the genus. Indeed, our paucity of knowledge of the genus is such that with the exception of three species, I cannot be sure that any branchiobdellid is truly troglobitic.

Those that are parasitic in the broad pouches of female troglobitic isopods (*Cambarincola alienus, C. marthae, C. steevesi* and probably the Mexican *C. acudentatus*) may be considered as host specific and, hence, as troglobites. *Cambarincola leoni*, as a parasite in the gill chambers of a troglobitic crayfish, may or may not be confined to its troglobitic host: there is no reason why it may not occur in the gill chambers of epigean hosts of the region. The only factor that would prevent any branchiobdellid from taking up a cave-dwelling existence is the lack of food on the exterior surfaces of the available crayfish hosts.

The data from the branchiobdellids, nonetheless, may be of some interest and help to the evolutionarily inclined biospeleogists. In order to discuss these data

concisely, I have divided the area into four regions (Figure 7). Region 1 is composed of the upper reaches of the Tennessee River drainage in Virginia, the Greenbrier River system and part of the Monongahela drainage in West Virginia. Region 2 consists of the upper part of the peninsula of Florida, part of the Florida panhandle and adjacent southern Georgia. Region 3 encircles, but does not include, the Nashville Basin (northwestern Georgia, northern Alabama, eastern and western portions of the Highland Rim in Tennessee, a portion of south-central Kentucky) and is composed of some of the cavernous areas in the Tennessee River, Cumberland River and Green River drainages. Region 4 includes four caves: one in the Ohio River drainage in Meade County, Kentucky, and three in the White River drainage in Monroe County, Indiana.

Region 1 is of little interest. Though one crayfish *(Cambarus (Puncticambarus) nerterius)* is endemic to the Greenbrier drainage (Hobbs, 1972) and is known only from caves, it is at best a troglophile, and all the identifiable branchiobdellids are well known epigean forms and can be considered only as trogloxenes. It may, perhaps, support what has been said above about the "preadaptations" of branchiobdellids, that the most common species of eastern branchiobdellids, *Cambarincola philadelphicus*, is found associated with three of the four records I have of *C. (P.) nerterius*. The other record of a branchiobdellid taken on this crayfish is the rare, and perhaps gill inhabitant, *Cambarincola demissus*. The other crayfish and all of the identifiable branchiobdellids of Region 1 are known epigean species and must be regarded as trogloxenes (Table 1).

Region 2 is inhabited by at least five endemic troglobitic crayfishes. One branchiobdellid, *Cambarincola leoni*, is associated with four of these hosts (Table 1). The questionable identifications of *C. leoni* are based on the distinctive jaw structures of this species and may be provisionally accepted as correct. Unfortunately, there is at least one other species of branchiobdellids found on Floridian troglobitic crayfishes and at this time there is no way of determining whether it represents one of the recently treated epigean species of Florida (Holt, in press b) or indeed whether there is more than one species involved.

In reality, Region 3 should be confined to the three caves in Monroe County, Indiana, from which I have material, but the Meade County, Kentucky, record is of an unidentifiable worm which is probably a member of the epigean fauna of the region and the same may be true of *Cambarincola dubius* and is certainly so of the presence of *C. philadelphicus*, or a very closely related species, or variant, of the latter, in Carmichael Cave. One of the hosts, *Orconectes inermis testii*, is troglobitic; the other, *Cambarus laevi* is a troglophile found also in epigean waters. The non-specificity of branchiobdellids in their choice of hosts is emphasized again by the occurrence of *C. dubius* on both of these crayfishes (Horton H. Hobbs III kept his collections of crayfish separated by species, so this statement cannot be questioned). The closest relative of *C. dubius*, appears to be *C. fallax* (see above).

I can make only one point in reference to Regions 1 and 3: they both, though inhabited by troglobitic crayfishes, have no branchiobdellids that can be considered unambiguously as such. *C. dubius* may be, but its general facies is of an epigean, non-gill inhabiting worm and there are no identifiable species from Region 1 that

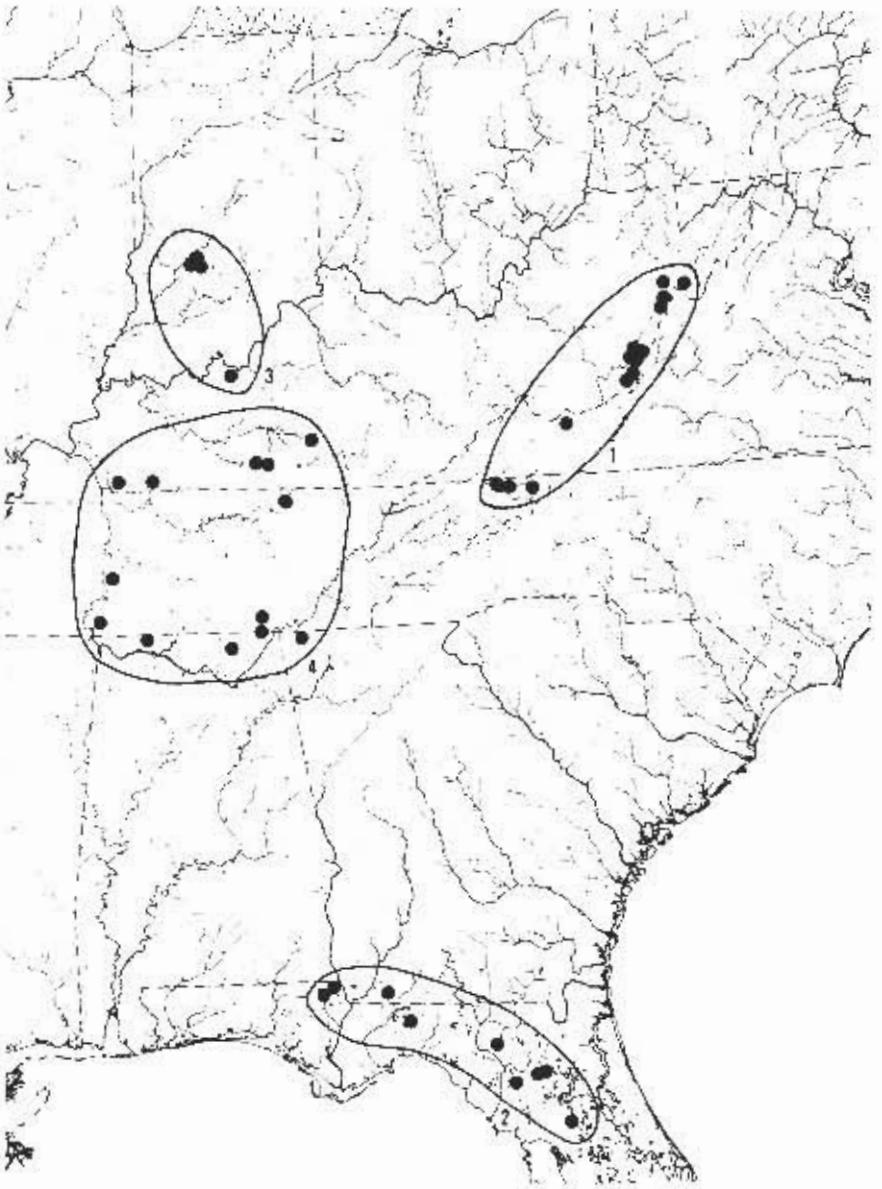

Fig. 7. Distribution of eastern North American caves in which branchiobdellids have been found.

are not known as epigean forms. The unidentified material is most likely, on the basis of appearance, composed of the same species as those which can be identified. The basis for this pattern of distribution, I would suggest, lies in the effects of the Pleistocene glaciations (Region 3 was possibly covered by ice one or more times during the Pleistocene and Region 1 lies so close to the southern border of the Wisconsin glaciation and is at such an elevation that one can reasonably assume the Pleistocene extirpation of its epigean branchiobdellid fauna and a subsequent reinvasion of the area) and a slower rate of evolution, at least an apparently slower rate as determined by detectable morphological changes, of the branchiobdellids than that of their hosts. There may be other reasons, *e.g.*, the influence of the times of origin of the caves concerned, and the preadaptations of branchiobdellids to life in caves, but I must leave the matter with these speculations.

Region 4, however, presents a different story. The branchiobdellids from the brood pouches of troglobitic isopods, *Cambarincola aliena, C. marthae* and *C. steevesi*, are almost surely true troglobites confined to their special microhabitat on their hosts. One possibly new member of this group is an unidentified worm from *Asellus stygius* (Packard, 1871) from the Newt Cave, Green County, Kentucky. The others, ranging from southcentral Tennessee to southcentral Kentucky are from *Asellus alabamensis*. The students of evolutionary biospeleology may wish to consider this. But, though these branchiobdellids are superficially similar, I would suggest that they are derived from relatively primitive separate epigean ancestors (see the discussion of the affinities of these species above).

Two new species from troglobitic and troglophilic crayfish hosts occurs in this region. *Cambarincola sheltensis* is known with certainty only from the type locality, but it, or a species now indistinguishable from it, occurs in at least two other caves on possibly as many as five troglobitic or troglophilic hosts (Table 1). *C. sheltensis* is superficially much like the isopod inhabiting species, but there is no good reason to believe that it is descended from the ancestral stock of any of the latter species. The possibilities of convergence in adaptation to what must be rather similar ecological niches and the difficulties of formulating phylogenetic hypotheses for the members of the genus *Cambarincola* (see above) negate the postulation of any such phylogenetic relation.

The other new cave dwelling branchiobdellid, *Cambarincola leptadenus*, whose host is the troglophilic *Cambarus tenebrosus*, though a distinctive species, may have as its closest relatives geographically distant species, *C. demissus*, from the Valley and Ridge Province of the Appalachians, or a Mesoamerican species (see above). It is quite likely a troglophile, perhaps only a troglexene, and the possibility that the single known locality, Bethel Cave, Perry County, Tennessee, for it represents one of a few populations of a mostly epigean localized and primitive species is quite real. One cannot know at this time.

There are probably two true troglobitic branchiobdellids known from obligate cave crayfishes, *Cambarincola leoni* and *C. sheltensis*, and possibly, but much less likely, two others *C. leptadenus* and *C. dubius*, both known primarily from troglophilic hosts. Three branchiobdellids are almost certainly obligate inhabitants of the brood pouches of troglobitic isopods. All seven are members of a single

genus; all appear to be in one way or another primitive within this genus; no consistent scheme of evolutionary or zoögeographical relationships can be proposed for them.

SUMMARY

Branchiobdellids are found as epizoites on crustaceans of the orders Isopoda and Decapoda (cambarine crayfishes) in caves of eastern North America. Species that may be considered as troglobites, since they are not known from epigean waters, appear to be confirmed to truly troglobitic isopods and possibly a few troglobitic crayfishes from Florida and the Tennessee-Kentucky Highland Rim cave belt. The majority of the records of branchiobdellids from caves are of representatives of common epigean forms epizoötic on crayfishes. Cross-referenced lists of branchiobdellids, their hosts and cave localities are presented. Some of the new species described are apparently troglobitic or troglophilic, but they present no consistent phylogenetic or geographical pattern and separate origins for them from primitive stocks of the genus *Cambarincola* are postulated.

RESUME

Dans des grottes de l'Est de l'Amérique du nord, on trouve des Branchiobdellides épizoïtes de Crustacés appartenant aux orders des Isopodes et des Décapodes (Ecrevisses Cambarines). Espèces qui, pouvant être considérées comme troglobies puisqu'inconnues des eaux épigées, semblent être limitées aux Isopodes véritablement troglobies et peut-être à quelques écrevisses hypogées de Floride et de la ceinture de grottes de la bordure montagneuse du Tennessee et du Kentucky. La plupart des observations sur les Branchiobdelles sont faites sur des représentants de formes épigées communes épizoïtes d'écrevisse. Des listes annotées de ces Branchiobdelles sont présentées, avec indication de leurs hôtes et de l'emplacement des grottes. Toutes, ou du moins la plupart, des nouvelled espèces décrites sont apparemment troglobies ou troglophiles, mais elles ne présentent aucune unité phylogénétique ou géographique; ausi faut-il envisager pour elles des origines distinctes à partir de lignées primitives du genre *Cambarincola*.

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