A Summary of the Branchiobdellid (Annelida: Clitellata) Fauna of Mesoamerica

PERRY C. HOLT

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ABSTRACT

Holt, Perry C. A Summary of the Branchiobdellid (Annelida: Clitellata) Fauna of Mesoamerica. *Smithsonian Contributions to Zoology,* number 142, 40 pages, 19 figures, 1973.—The branchiobdellid fauna of Mesoamerica consists of sixteen species, assigned to four genera. Of these, all are endemic to the area except the widespread species, *Bdellodrilus illuminatus* and *Pterodrilus mexicanus.* The latter is considered to be a doubtful occupant of the region. Of the fourteen remaining species, three are assigned to the genus *Sathodrilus,* one newly described, and eleven to *Cambarincola,* ten of which are newly described. The names of thirteen species of the genus *Cambarincola* are emended to conform to the masculine gender of the generic name. The report of the presence in Mexico of *Cambarincola macrodontus* and *C. philadelphicus* (Rioja, 1943) is not accepted. A brief review of the pertinent literature is followed by discussions of methods and sources of materials, some remarks on taxonomic characters relevant to the Mesoamerican branchiobdellids, cross-referenced lists of species of branchiobdellids, their hosts and entocytherid ostracod associates, a short account of the ecology of the worms and an attempt to relate the distribution of Mesoamerican branchiobdellids with that of their hosts and associates. The conclusion is reached that representatives of all the main stocks of branchiobdellids reached southern Mexico in pre-Pliocene times and that there is no completely satisfactory way of differentiating between any subsequent invasions. The treatment of the species include keys, synonomies, bibliographic references, diagnoses, distribution and hosts, with all new species illustrated and fully described.

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Introduction

Brief references to, and more or less isolated descriptions of, new species of branchiobdellids, symbionts of freshwater crustaceans, from Mesoamerica have been published in the past. There is, however, no account of this fauna that treats together all of the known taxa. To record what is known of the Mesoamerican branchiobdellids is the objective of this paper.

The record must of necessity be incomplete and is likely to remain so. Earlier acquired material was collected incidentally by students of crayfishes and is in a generally poor state of preservation. Much of it has been lost in the curating of crayfish collections. My attempts to collect branchiobdellids by visiting many of the recorded localities for crayfish in Mexico during the summer of 1962 were usually unsuccessful, in spite of the devoted help of Professor Alejandro Villalobos of the Universidad Nacional Autónoma de México. The area is at the limits of the range of astacids in a land that is either semiarid with few streams or well watered but tropical and where the crayfishes must compete with freshwater crabs and shrimps. Some branchiobdellids have managed to take up a life on these hosts. More importantly, there is the apparent absence of crayfishes from many localities where Horton H. Hobbs, Jr., and Alejandro Villalobos once took them in relative abundance: an absence that I cannot explain.

So, with little hope that much additional material will be forthcoming, what is available, to my knowledge, is described and discussed herein.

ACKNOWLEDGMENTS.—I am deeply indebted to Dr. Alejandro Villalobos Figueroa, who first sent me Mexican branchiobdellids many years ago and who later went into the field with me. He has also most generously allowed me to remove all the branchiobdellids from the crayfish collections of the Instituto de Biología de la Universidad Nacional Autónoma de México. His hospitality and friendship is deeply appreciated. Dr. Horton H. Hobbs, Jr., made available to me several collections of Mexican branchiobdellids. He and Dr. Villalobos have identified the host animals for me and Dr. Hobbs and Dr. Marian H. Pettibone have read the manuscript. Dr. Hobbs, also, helped greatly in compiling crayfish and ostracod records and with discussions of distributional problems. My wife, Virgie F. Holt, my daughter, Susan E. H. West, and Señor Patricio Gonzáles Kipper, assisted me in field work in Mexico. Mrs. Susan S. Settle's assistance in preparing the manuscript is appreciated. My studies of branchiobdellid taxonomy, including my field work in Mexico, were supported for a number of years by National Science Foundation grants G–4439, G9828, and GB–372.

REVIEW OF THE LITERATURE.—The first reference to a branchiobdellid from Mesoamerica was by Ellis (1919:254), who described *Pterodrilus mexi-*

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canus from Mirador, Veracruz, Mexico. Rioja (1940) recorded the presence of *Bdellodrilus illuminatus* in Mexico and later (1943) that of *Cambarincola macrodontus* and *C. philadelphicus*. Goodnight (1940) had also reported *C. philadelphicus* in Mexico. (Since the name *Cambarincola* is masculine in gender, but traditionally has been treated as feminine, the emendation of several specific taxa of the genus is required.) Hobbs and Villalobos (1958) reported the presence of unidentified branchiobdellids on freshwater crabs in Mexico. Holt (1964) described *Cambarincola smalleyi* from Costa Rica and later (1968b) *Sathodrilus villalobosi* and *S. veracruzicus* from Mexico. Mesoamerican species from nonastacid hosts (Hobbs and Villalobos' records and *C. smalleyi*) were briefly referred to in a review paper (Holt, 1968a). Holt (1969:214) also discussed the geographical and phylogenetic relationships of these species and two Mexican members of the genus *Sathodrilus*. Much use is made, herein, of Hobbs' (1971) treatment of the entocytherid ostracods of Mexico and Cuba, animals that as epizoites share the same hosts.

If any other mention of branchiobdellids from Mesoamerica occurs in the primary literature on the order, it is either an incidental and passing reference or I am unaware of it.

METHODS AND DISPOSITION OF MATERIALS.—Materials collected by others than myself and field companions and used in this study were preserved in 70 percent ethyl alcohol. My collecting methods and procedures have been described elsewhere (Holt, 1960a:57), though it may be well to point out that I often turn my slides upside down in order to view a specimen from both sides, using for this purpose the flourite objective previously mentioned. Drawings, made with the aid of a camera lucida, often reflect this practice and are reversed in appearance from that of the specimen viewed from the cover slip side of the slide. In all cases, drawings are made so that the anterior of the animal and its illustrated parts are directed towards the reader's right and the reproductive systems are always presented in lateral view.

Keys to species presented herein apply only to the Mesoamerican members of the order and should not, therefore, be used in any attempt to identify branchiobdellids from north of the Rio Grande.

Except for some paratypes and a small number of specimens retained in my personal collections at Virginia Polytechnic Institute and State University, the materials are deposited in the National Museum of Natural History, Smithsonian Institution, and the collections of the Instituto de Biología, Universidad Nacional Autónoma de México. All holotypes are in the collections of the National Museum of Natural History whose catalog numbers (USNM: United States National Museum collections) and my personal catalog numbers (PCH) are listed with the locality data given for a species. Unless otherwise indicated, the collector of all materials was Dr. Alejandro Villalobos.

Fifty-six out of eighty-five collections of branchiobdellids contained material that was well enough preserved for use in this study. Only species represented in this material are included in the maps of distribution, though some of the previous records of other authors are accepted. Ostracod and branchiobdellid associates are not repeated in the treatments of species; they can be found in the lists.

TAXONOMIC CHARACTERISTICS.—The terminology used in branchiobdellid taxonomy and the taxonomic value of various characteristics have been discussed before (Holt, 1953, 1960a, 1965, 1968a, 1968b; Holt and Hoffman, 1959). Certain organ systems of the branchiobdellids appear invariant within the order, for instance, the location of ovaries and ovipores, the number and location of testes in the American members, features of the nervous system and, with minor exceptions, the digestive system. Among characters considered to be diagnostic of genera, the manner of discharge of the anterior nephridia—one or two dorsal nephridiopores opening on the third trunk segment—is constant among Mesoamerican members of the order: one nephridiopore opens middorsally on the dorsum of segment III. Parenthetically, the trunk segments are numbered separately from those, presumably four, which compose the head. Many features are intergenerically variable, among them, the number of denticles (teeth) borne by the pharyngeal placoids (jaws), though the overall facies of the jaws is usually characteristic of a genus; the lobation or tentaculation of the upper and lower lobes of the peristomium (upper and lower lips); the presence or absence of dorsal supernumerary longitudinal segmental muscles

(Holt, 1960b:171–172) which, in the contracted state, produce a greater diameter of the anterior (major) annulus of a segment and cause "dorsal ridges" upon all or some of the trunk segments, in the former case conferring a sawlike appearance to the animal in lateral view; and the presence or absence of fanlike or finger-like projections on dorsal ridges in some genera.

Secondary sexual organs, the male efferent apparatus and the spermatheca, furnish the most useful taxonomic characteristics. These organs have been described in detail for some species (Moore, 1895b; Holt, 1949, 1960a). An eversible penis (one that consists of a tube capable of being turned inside out) or a protrusible one (i.e., a conelike muscular mass that is capable of being projected through the gonopore surrounded by the partially everted atrial portion of the bursa) is considered a generic character and separates, for instance, the genus *Cambarincola* Ellis (1912) from *Bdellodrilus* Moore (1895b) and *Sathodrilus* Holt (1968b). The presence or absence of a prostate, or its rudimentary character, may be of generic value, as may other components of the male system and stable structures of the spermatheca; but in general a constellation of genitalic characteristics are used in the diagnosis of a genus (cf. Holt, 1960a, b, 1968b). Most of these structures are labeled in Figure 16.

A good deal of parallelism exists among the branchiobdellids, and a species of one genus may exhibit features that appear identical to those in members of otherwise very distinct genera. In general, important features for the characterization of these species are the shape and proportions of the jaws and the number and arrangement of the teeth they bear, the lobation of the lips, the proportions and structure of the male efferent apparatus (particularly the presence or absence of an ental bulb of the prostate which may or not be composed of histologically distinct cells—i.e., filled with large vacuoles of presumably secreted materials—from those of the spermiducal gland), and variations in the structure of the spermatheca.

For clarification of the zoogeographical relationships of Mesoamerican branchiobdellids a brief tabulation of some primitive features (characteristic of ancestral stocks as opposed to those considered to be advanced, more specialized, or characteristic of more recently evolved stocks) follows:

Primitive	*Advanced*
Eversible penis	Protrusible penis
Spermiducal gland without prostate	Prostate or "prostatic protuberance" present
Prostatic protuberance	Fully or partially separated prostate
Nondifferentiated prostate	Differentiated prostate
Spermiducal gland with deferent lobes	Spermiducal gland without deferent lobes
Deferent ducts enter ental end of spermiducal gland	Deferent ducts enter spermiducal gland ectad to ental end
Spermatheca with glandular ental process or thickened glandular wall of bulb	Spermatheca consisting of ectal duct and thin-walled bulb
Jaws subequal in size with several (5 or more) similar teeth	Jaws and teeth variously modified
No supernumerary segmental muscles	Supernumerary segmental muscles present

Lists Pertaining to Mesoamerican Branchiobdellida

Species List of Branchiobdellids

Numbers following each taxon refer to the number of the species' hosts indicated in the following list.

1. *Bdellodrilus illuminatus*, Mexico and United States: 9
2. *Cambarincola acudentatus*, Mexico: 1, 2
3. *Cambarincola carcinophilus*, Mexico: 16, 21
4. *Cambarincola ellisi*, Mexico: 17
5. *Cambarincola hoffmani*, Mexico: 7, 12
6. *Cambarincola jamapaensis*, Mexico: 5, 12, 14
7. *Cambarincola micradenus*, Mexico: 4
8. *Cambarincola nanognathus*, Mexico and Nicaragua: 18, 19, 21
9. *Cambarincola olmecus*, Mexico: 5, 6, 14
10. *Cambarincola smalleyi*, Costa Rica: 20
11. *Cambarincola susanae*, Mexico: 5, 11, 13, 17
12. *Cambarincola toltecus*, Mexico: 16, 21
13. *Pterodrilus mexicanus*, (?) Mexico and United States: 14
14. *Sathodrilus prostates*, Mexico: 5, 12, 16, 21
15. *Sathodrilus veracruzicus*, Mexico: 8, 12, 15
16. *Sathodrilus villalobosi*, Mexico: 4, 8, 10, 15

List of Hosts

Numbers following each taxon refer to the branchiobdellids in the list above.

ISOPODA: CIROLANIDAE

1. *Speocirolana bolivari* (Rioja, 1953) : 2
2. *Speocirolana pelaezi* (Bolivar y Pieltain, 1950): 2

DECAPODA: ASTACIDAE

3. *Cambarellus montezumae montezumae* (Saussure 1857) : 1
4. *Paracambarus paradoxus* (Ortmann, 1906) : 7, 16
5. *Procambarus acutus cuevachicae* (Hobbs, 1941) : 6, 9, 11, 14
6. *Procambarus aztecus* (Saussure, 1957) : 9
7. *Procambarus caballeroi* (Villalobos, 1944) : 5
8. *Procambarus contrerasi* (Creaser, 1931) : 15, 16
9. *Procambarus digueti* (Bouvier, 1897) : 1
10. *Procambarus erichsoni* Villalobos, 1958: 16
11. *Procambarus gonopodocristatus* Villalobos, 1958: 11
12. *Procambarus hoffmanni* (Villalobos, 1944) : 5, 6, 14, 15
13. *Procambarus llamasi* Villalobos, 1954: 11
14. *Procambarus mexicanus* (Erichson, 1946) : 6, 9, 13
15. *Procambarus riojai* (Villalobos, 1944) : 15, 16
16. *Procambarus ruthveni zapoapensis* Villalobos, 1954: 3, 12, 14
17. *Procambarus simulans regiomontanus* Villalobos, 1954: 4, 11
18. *Procambarus vazquezae* Villalobos, 1954: 8

DECAPODA: PSEUDOTHELPHUSIDAE

19. *Potamocarcinus nicaraguensis* Rathbun, 1893: 8
20. *Pseudothelphusa tumimanus* Rathbun, 1898: 10
21. *Pseudothelphusa (Tehuana) veracruzana* Rodriquez and Smalley, 1970: 3, 8, 12, 14

LIST OF KNOWN BRANCHIOBDELLID ASSOCIATES

Numbers following each taxon refer to the "Species List of Branchiobdellids."

1. *Bdellodrilus illuminatus*: none
2. *Cambarincola acudentatus*: none
3. *Cambarincola carcinophilus*: 12, 14
4. *Cambarincola ellisi*: none
5. *Cambarincola hoffmani*: none
6. *Cambarincola jamapaensis*: 14
7. *Cambarincola micradenus*: 16
8. *Cambarincola nanognatha*: 12, 14
9. *Cambarincola olmecus*: 11
10. *Cambarincola smalleyi*: none
11. *Cambarincola susanae*: 9, 16
12. *Cambarincola toltecus*: 3, 8, 14
13. *Pterodrilus mexicanus*: none
14. *Sathodrilus prostates*: 12
15. *Sathodrilus veracruzicus*: none
16. *Sathodrilus villalobosi*: 7

LIST OF ENTOCYTHERID ASSOCIATES

(See Hobbs, 1971:3)

Numbers following each entocytherid species refers to the "Species List of Branchiobdellids."

1. *Uncinocythere bicuspide* (Rioja, 1943) : 6, 7, 9,* 14, 15, 16
2. *Uncinocythere caudricuspide* (Rioja, 1945) : 6, 7, 16
3. *Uncinocythere dobbinae* (Rioja, 1943) : 5, 6, 7, 14, 15, 16
4. *Uncinocythere zaruri* Hobbs, 1971: 3, 8, 12, 14
5. *Ankylocythere bidentata* (Rioja, 1949) : 3, 9, 12, 14
6. *Ankylocythere heterodonta* (Rioja, 1940) : 1
7. *Ankylocythere sinuosa* (Rioja, 1942) : 4, 11
8. *Entocythere claytonhoffi* Rioja, 1942: 3, 9, 11, 12, 14
9. *Entocythere mexicana* Rioja, 1943: 5, 6, 14, 15
10. *Sphaeromicola cirolanae* Rioja, 1951: 2

* Questioned by Hobbs, 1971:22.

Ecological Notes

The ecology of the branchiobdellids, which was summarized by Holt (1968a), offers little help in considering the evolution of the Mesoamerican fauna; only five papers (Berry and Holt, 1959; McManus, 1960; Brown, 1961; Young, 1966; Bishop, 1968) have been devoted explicitly to the ecology of the branchiobdellids. It is known that some species occupy particular niches on their crustacean hosts, that some (*Bdellodrilus illuminatus* and *Cambarincola alienus* Holt, 1963) may be considered as true parasites, the former living in the gill chambers of crayfish, the latter in the brood pouches of isopods. More usually the worms occupy "preferred" areas on the exoskeleton of the host (Brown, 1961). Those branchiobdellids that live on protected parts of their hosts, such as those mentioned above, and in general, those that live on hosts other than astacids (e.g., *Cambarincola smalleyi* and *C. nanognathus* on crabs, *C. alienus* and *C. acudentatus* on isopods) seem more primitive than most of their congeners. It is as if these four species just mentioned early escaped the more rigorous competition offered by life on the exterior of astacid crayfishes. Consequently, other than showing some signs of specialization for a parasitic life, they have retained more primitive features than other members of the genus. But that this need not be so, is indicated by Blackford's (1966) finding of *Cambarincola vitreus* on the crab, *Callinectes sapidus* Rathbun, 1892, that has become acclimated to freshwater lagoons in Louisiana. In addition, Blackford (1966:6) showed that branchi-

obdellids are quite intolerant of salt water and I have never taken them from brackish water. Therefore, freshwater routes of invasion must be assumed for them.

The diet of the branchiobdellids seems to be any organic matter that they can find in their grazing on the host animals; the vast majority are not parasites, they are not species specific and, though it is known that some are intolerant of warm waters (Berry and Holt, 1959), essentially nothing is known of other aspects of their ecology or life cycles.

Zoogeographical Considerations

As previously emphasized, the knowledge of Mesoamerican branchiobdellids is too scanty to allow for anything but the most tentative theories of their history and origins. It is hoped that what little is known of their distribution and evolution will help in the evaluation of the theories proposed by Hobbs (1971). The lists above of hosts and associates are presented for this reason. Since his knowledge of the crayfishes and entocytherids of Mexico is based on a much greater body of knowledge than mine of the branchiobdellids, it is necessary to take his conclusions into careful account in formulating any theories of the origins of the Mesoamerican branchiobdellid fauna.

The seemingly near total lack of host specificity on the part of both the entocytherids and the branchiobdellids (Hobbs, Holt, and Walton, 1967; Hart and Hart, 1969; Holt, 1969; Hobbs, 1971), except that both are confined to crustacean hosts, complicates any attempt to correlate the evolution of these symbionts and their hosts. In spite of their passive means of dispersal as obligate epizoites that can go only where their hosts do, the ability of both groups of commensals to move readily from one host to another produces distributional patterns that seem to be the results of three independent lines of evolution. Though Hobbs (1971: 7–18) has produced a plausible theory of the migration of entocytherid stocks into Mexico, I cannot do so in such detail for the branchiobdellids.

There are several reasons for this other than paucity of materials. The known hosts of branchiobdellids in Mesoamerica are twenty members of two orders and three families of crustaceans; on the other hand Hobbs (1917:3) lists forty hosts from the same orders and families for the entocytherids of Mexico and Cuba. The two species of branchiobdellids from Nicaragua (*Cambarincola nanognathus,* new species) and Costa Rica (*C. smalleyi*) are offset by three species of entocytherids on two hosts known from Cuba, so that there are twice as many hosts known for the entocytherids in Mexico as there are for the branchiobdellids, though there is one more (14 as opposed to 13) branchiobdellid species in Mexico than entocytherid ones. Nonetheless, I believe that I have only a minimal representation of the original Mexican branchiobdellid fauna before me. That the missing members of this fauna might well have contained species crucial to the reconstruction of the history of the order in Mesoamerica will, I hope, be assumed.

In my analysis of the zoogeography of the Mesoamerican branchiobdellid fauna. I have adopted Hobbs' (1971:7–18) faunal regions and accept the reality of the barrier imposed by the formation of the Cordillera Volcánico Transversal.

Bdellodrilus illuminatus is the only branchiobdellid of which I have seen a specimen from the Central Plateau region. Rioja (1940) reported it from "Xochimilco, Texcoco y de las Lagunas de Zempoala" on *Cambarellus montezumae montezumae* and *C. m. zempoalensis* for the latter locality. There is no reason to doubt these records. The species is distinctive and, though primitive (Holt, 1969:195–196), has been found at many widely separated localities on the continent. It must have reached the Central Plateau region on either the ancestor of the disjunct *Procambarus digueti* or the stock that gave rise to the Mexican members of the genus *Cambarellus* in pre-Pliocene times.

Ellis (1919) described *Pterodrilus mexicanus* on the basis of a single poorly preserved specimen presumably from Mirador, Veracruz, on *Procambarus mexicanus.* The genus *Pterodrilus* is common in the Appalachian and Ozarkian uplands of the United States, but I have not found any member of the genus in the Mexican collections and have been unable to locate Mirador with certainty. I suspect it is in the Southern Gulf Slope region and, hence, south of the Cordillera Volcánica Transversal. If so, and if Ellis' record is correct, then the genus *Pterodrilus* is of consider-

able antiquity. There are Ozarkian worms that I have assigned to *P. mexicanus,* which are indistinguishable in external features from the poorly preserved type. As stated earlier (Holt, 1968c:18), I doubt that Ellis' specimen was collected in Mexico. In any case, *P. mexicanus* must be disregarded in any consideration of the zoogeography of Mesoamerican branchiobdellids.

There are two species of *Sathodrilus* in the United States: *S. carolinensis,* the type-species from Anderson County, South Carolina, and *S. megadenus* from Haralson County, Georgia. Of the three Mexican species, *S. villalobosi* and *S. veracruzicus* occur north of the Cordillera Volcánico Transversal, but only *S. prostates,* newly described herein, is found on both sides of this barrier (Figure 19) in the Interjacent Gulf Slope and the upland area around Lake Catemaco in the Southern Gulf Slope. *Sathodrilus* is presumably the most primitive genus among the dominant group of North American branchiobdellids (Holt, 1969:196–197) and *S. veracruzicus* the most primitive species of the genus. *S. prostates* possesses characteristics which ally *Sathodrilus* with the genus *Tettodrilus* Holt, 1968b, and hence with *Cambarincola.* One possibility is that members of the genus *Sathodrilus* reached the Southern Gulf Slope with the first wave of pre-Pliocene crayfish invasions (Hobbs, 1971:11) and that the ancestors of the more primitive of the surviving members, *S. veracruzicus* and *S. villalobosi,* were left to the north by the formation of the Cordillera Volcánico while the somewhat more advanced *S. prostates* has survived on both sides of the barrier. On the other hand, Hobbs (pers. comm.) has suggested that the *Sathodrilus* stock, because of the similarities of its distribution to that of *Uncinocythere* (Hobbs, 1971:15, 17), represents, as does the latter, a Pliocene invasion into the Interjacent area. His *U. zaruri,* from the Southern Gulf Slope, may have reached there by sea with its crab host; *S. prostates,* occurring on the same crab species in the same area, could not have done so. Hobbs' suggestion (pers. comm.) that *S. prostates* crossed the divide with its host crab, which walked overland from stream to stream, is a possible but dubious explanation of the distribution of the species of *Sathodrilus.*

Tettodrilus friaufi Holt, 1968a, may have descended from the ancestors of *S. prostates*: *T. friaufi,* known only from streams of the Nashville basin in Middle Tennessee, is a relict species that can be derived from a somewhat advanced member of the *Sathodrilus* stock that survives today as *S. prostates.*

The genus *Cambarincola* is composed of 22 nominal species and 10 more are described below. It contains more species than any other known genus of the order, and I have in my collections a number of undescribed species from the southeastern, Ozarkian, and Pacific slope regions of the United States. Other than noting that the apparently primitive Mesoamerican species, e.g., *C. nanognathus,* new species, appears in the Southern Gulf Slope region and beyond into Nicaragua, there is little relationship between any phyletic lineages that might be proposed and their distribution. The only species with a differentiated prostate (*C. toltecus,* new species, and *C. smalleyi*) are known only from the Southern Gulf Slope and Costa Rica, respectively, and would appear, on the basis of the nature of their prostates, to be related to the more advanced Philadelphicus section of the genus (Hoffman, 1963:320). This may be an example of parallelism, and the overall impression conveyed by the Mesoamerican species of *Cambarincola* is that they are related to some element or elements of the more primitive cambarincoloid stock. One new species, *C. susanae,* ranges from the Northern Gulf Slope in the Rio Grande basin far south into Campeche. *Cambarincola susanae* resembles in some respects, *C. vitreus,* a widespread Central and Coastal Plains member of the Philadelphicus section, but differs from the latter in its undifferentiated prostate and perhaps specialized jaws. *Cambarincola susanae* resembles in its distribution *Entocythere claytonhoffi* (cf. Hobbs, 1971:15) and is without doubt a representative of the early pre-Pliocene invasion. *Cambarincola olmecus,* new species, known from the Northern Gulf Slope regions, in features of the jaws, the presence of dorsal ridges of the major annuli, and the thin-walled spermathecal bulb is perhaps an advanced member of the Mesochoreus section (Hoffman, 1963). Its ancestors, however, were present on both sides of the Cordillera Volcánico Transversal, so it, too, has a pre-Pliocene origin. *Cambarincola jamapaensis,* new species, found on both sides of the barrier, likewise is closer to the Mesochoreus

section. *Cambarincola ellisi,* new species, known only from the Rio Grande drainage of the Northern Gulf Slope, with its affinities with the Mesochoreus section, is the only species of the Mesoamerican fauna that may represent a Pleistocene or Recent invasion.

To summarize: The branchiobdellid fauna of Mesoamerica is ancient; many of its members reached the southern limits of the area in pre-Pliocene times. Although only 3 of the 13 known genera of American branchiobdellids are known from Mesoamerica, the three that are there, on the basis of any concept of the phylogenetic relationships of the branchiobdellid genera, indicate that in the evolution of the order many of the modern genera and some of the species are of pre-Pliocene origin. All evidence indicates that the Mesoamerican branchiobdellids are derived from stocks that arose in the uplands of the southern United States. Most or all members of the genus *Cambarincola* in Mesoamerica are derived from primitive stocks that today are represented by the Mesochoreus section. Members of this section are confined mostly to the Central Plains of the United States and areas immediately adjacent to the plains. If this be the case, however, such species as *C. toltecus,* new species, and *C. smalleyi,* with their similarities to the northern members of the genus with differentiated prostates, are examples of an amazing amount of parallelism in the evolution of the genus. Until all extant species of *Cambarincola* are studied in much more detail than they have been until now, these puzzles must remain unresolved.

The available data do not allow me to go beyond these speculations. I cannot correlate the migrations of any post-Miocene invaders with Hobbs' (1971: 10–14) postulated Pliocene and Pleistocene-Recent crayfish invasions. Nothing said, however, contradicts his theories of the sources, migration routes, and times of arrival in Mesoamerica of the crayfish hosts and the branchiobdellids' fellow travelers, the entocytherid ostracods. Certainly I concur enthusiastically with his approval of the statement by Martin and Harrell (1957:497) that "interpreting the eastern temperate (Arctotertiary) element in the Mexican montane biota exclusively in terms of Pleistocene dispersal raises more distributional problems than it solves." I might even go further and say, on the basis of my attempts to understand the distribution of the branchiobdellids, that this statement applies to the entire southeastern part of North America.

Faunal Regions of Mexican Branchiobdellids (as proposed by Hobbs, 1971:10)

Initials following the name of a species are those of another faunal region in which the species also occurs.

Southern Gulf Slope (SGS)

Cambarincola carcinophilus
Cambarincola jamapaensis (IGS)
Cambarincola nanognathus (Nicaragua)
Cambarincola olmecus (NGS)
Cambarincola smalleyi (only from Costa Rica)
Cambarincola susanae (IGS, NGS)
Cambarincola toltecus
Pterodrilus mexicanus
Sathodrilus prostates (IGS)

Interjacent Gulf Slope (IGS)

Cambarincola hoffmani
Cambarincola jamapaensis (SGS)
Cambarincola micradenus
Cambarincola susanae (SGS, NGS)
Sathodrilus prostates (SGS)
Sathodrilus veracruzicus
Sathodrilus villalobosi (NGS)

Northern Gulf Slope

Cambarincola acudentatus
Cambarincola ellisi
Cambarincola olmecus (SGS)
Cambarincola susanae (SGS, IGS)
Sathodrilus villalobosi (IGS)

Central Plateau

Bdellodrilus illuminatus

Order BRANCHIOBDELLIDA Holt, 1965

Discodrilidae Vejdovsky, 1884:38–40.—Pierantoni, 1912:1–17.—Ellis, 1912:481.

Branchiobdellidae Ludwig, 1886:782–783.—Hall, 1914:190.—Ellis [by implication], 1919:241.—Stephenson, 1930:795–802.—Goodnight, 1940:27.—Hoffman, 1963:271.

Branchiobdelloidea Hall, 1914:190.—Goodnight, 1940:27.

Branchiobdellida Holt, 1965:30–31.

Diagnosis (from Holt, 1965:30–31).—

Clitellate annelids with constant number of segments (15); without setae or prostomium; with the peristomium modi-

fied as an anterior sucker; with a posterior sucker; a pair of dental placoids (a dorsal and ventral one) in the pharynx; the body divided into a head of four segments and a trunk of eleven; anus dorsal and subterminal; two pairs of nephridia, an asymmetrical pair in segments 5 to 8 and a pair in segments 12 and 13; muscles non-syncytial, composed of cells with outer contractile and inner undifferentiated cytoplasm; testes in segments 9 and 10 or in segment 9 only; paired male funnels and ducts in each testicular segment, with the ducts uniting in each such segment to form an unpaired deferent duct, or if two such ducts they fuse in segment 10 and open in any case by means of an elaborate glandular and muscular apparatus through an unpaired pore on the venter of segment 10; a pair of ovaries and ovipores without free oviducts and funnels in segment 11; an unpaired spermatheca in segment 9; clitellum on segments 10 and 11; epizoites on freshwater crustaceans; holoarctic in distribution, extending into neotropical Central America.

The order has not yet been successfully divided into families. Goodnight (1940:27–28), accepting Hall's (1914:190) proposal that the group be considered a monotypic superfamily, proposed two subfamilies: the Branchiobdellinae, to be a monotypic group based on the Eurasian genus *Branchiobdella* Odier, 1823; and the Cambarincolinae, with the genus *Cambarincola* Ellis, 1912, as the type, to include the remainder of the family. *Branchiobdella*, with species from eastern Asia and Europe is distinctive in having lost a pair of testes and male funnels and ducts, but otherwise is too close in morphological characters to separate from a number of eastern Asian and North American genera. The order for the present is composed of the single family Branchiobdellidae.

Key to the Mesoamerican Genera of the Branchiobdellida

1. Penis protrusible 2
   Penis eversible 3
2. Without appendages borne on dorsal ridges ..... ***Cambarincola***
   With at least one dorsal ridge bearing appendages ..... ***Pterodrilus***
3. With bifid spermatheca, deferent ducts enter spermiducal gland ectally to its ental end ..... ***Bdellodrilus***
   Spermatheca never branched, deferent ducts always unite at ental end of spermatheca ..... ***Sathodrilus***

NOTE: This key is applicable only to the known Mesoamerican branchiobdellids and is not adequate to separate these genera from some of those of the United States.

Genus *Bdellodrilus* Moore, 1895

Bdellodrilus Moore, 1895b:497.

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 small 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 segments 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.

TYPE-SPECIES.—*Bdellodrilus illuminatus* (Moore, 1894), by subsequent designation (Goodnight, 1940:53).

Bdellodrilus illuminatus (Moore, 1894)

FIGURES 1, 19

Branchiobdella illuminata Moore, 1894:421–423.
Bdellodrilus illuminatus.—Moore, 1895b:497.

TYPE-SPECIMENS.—No longer extant, but taken at Philadelphia, Pennsylvania, and Watauga County, North Carolina, on *Cambarus bartonii* (Fabricius, 1798), by J. Percy Moore.

HOSTS.—UNITED STATES: *B. illuminatus* is known (Goodnight, 1940:54; Hobbs, Holt, and Walton, 1967:51) to occur on seven species of the genus *Cambarus* and there are several unpublished records in my collections. MEXICO: *Procambarus digueti, Cambarellus montezumae montezumae* (Rioja, 1940).

DISTRIBUTION.—*Bdellodrilus illuminatus* probably ranges over the continent wherever its astacid

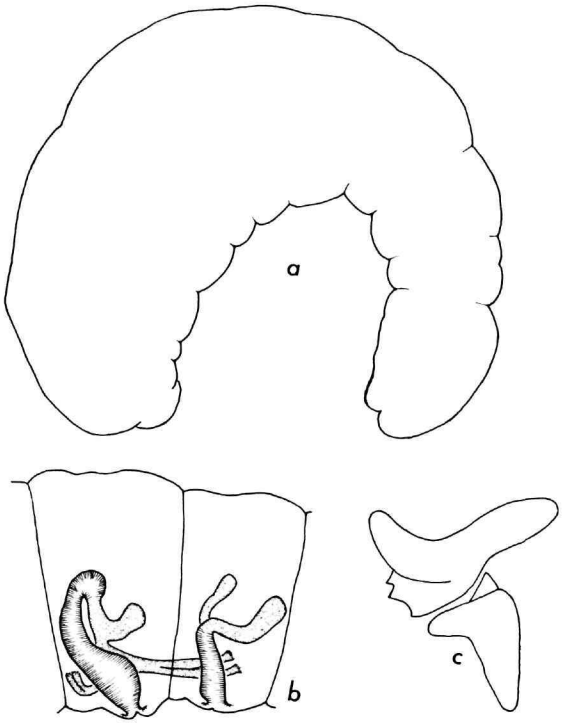

FIGURE 1.—*Bdellodrilus illuminatus*: *a*, animal from Giles County, Virginia; *b*, reproductive systems; *c*, jaws. (*a* and *c* from Hobbs, Holt, and Walton, 1967; *b*, redrawn from Moore, 1895b.)

hosts occur. Goodnight (1940:54) records it from Illinois; Hobbs, Holt, and Walton (1967:51–52) found it abundantly in their study of the Mountain Lake, Virginia, area; and I have scattered, unpublished records from many parts of the United States. It is an ancient and primitive species with specializations for a parasitic way of life in the gill chambers of its hosts. It probably reached the Central Plateau region of Mexico in pre-Pliocene times on either the ancestor of *Procambarus digueti* or the ancestors of the Mexican members of *Cambarellus* (Hobbs, 1917:12). Its apparent absence from the other faunistic regions of Mexico (and many parts of the United States) is probably an artifact of collecting. Most of the specimens of Mesoamerican branchiobdellids were removed from the sediments in museum jars containing crayfish collections; curators of such collections do not like to have their specimens damaged in a search for gill-inhabiting worms.

MATERIAL EXAMINED.—One specimen (PCH 1620) taken on *Procambarus digueti* at Jacona, Rancho Nueva Espana, km 470 carretera México-Guadalajara, Michoacán, by Dieter Enkerlin, 18 July 1950.

Genus *Cambarincola* Ellis, 1912

Astacobdella Leidy, 1851:206.
Branchiobdella.—Moore, 1894:427 [in part].
Bdellodrilus.—Pierantoni, 1912:24 [in part].
Cambarincola Ellis, 1912:481; 1919:263.—Hall, 1914:190.—Stephenson, 1930:801.—Yamaguchi, 1933:191; 1934:189.—Goodnight, 1940:30.—Holt and Hoffman, 1959:97.—Hoffman, 1963:271.—Hobbs, Holt, and Walton, 1967:52.—Holt, 1969:197.

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 noneversible; bursa subpyriform to obcordate; spermatheca never bifid."

TYPE-SPECIES.—*Cambarincola macrodonta* Ellis, 1912, by original designation.

RANGE.—North America. Species of the genus *Cambarincola* are the dominant components of the branchiobdellid fauna in all parts of North America where branchiobdellids occur (except from some streams of the Coastal Ranges and Cascade Mountains of the Pacific drainage), ranging from Ontario and Quebec to Costa Rica; and west to the Pacific coast of California, Oregon, Washington, and British Columbia.

NOMENCLATURAL EMENDATIONS.—The examples given under Article 30 (a), (i), (2) of the International Code of Zoological Nomenclature, adopted by the XV International Congress of Zoology, clearly prescribes that the generic name *Cambarincola* is masculine. Of the twenty-two validly published species names in the genus, the following 13, therefore, required emendation:

Cambarincola philadelphica (Leidy) (1851:209) to *C. philadelphicus*
Cambarincola macrodonta Ellis (1912:481) to *C. macrodontus*
Cambarincola vitrea Ellis (1918:49) to *C. vitreus*
Cambarincola chirocephala Ellis (1919:263) to *C. chirocephalus*

Cambarincola floridana Goodnight (1941:73) to *C. floridanus*

Cambarincola macrocephela Goodnight (1943:100) to *C. macrocephelus*

Cambarincola branchiophila Holt (1954:168) to *C. branchiophilus*

Cambarincola aliena Holt (1963:97) to *C. alienus*

Cambarincola mesochorea Hoffman (1963:307) to *C. mesochoreus*

Cambarincola virginica Hoffman (1963:322) to *C. virginicus*

Cambarincola holostoma Hoffman (1963:359) to *C. holostomus*

Cambarincola heterognatha Hoffman (1963:362) to *C. heterognathus*

Cambarincola demissa Hoffman (1963:365) to *C. demissus*

By provision of Article 31 (a) of the *International Code of Zoological Nomenclature,* the following emendation is required:

Cambarincola osceola Hoffman (1963:330) to *C. osceolai*

REMARKS.—Less than a decade ago, Hoffman (1963) accorded monographic treatment to the then known members of the genus, including within it 21 species of which 12 were newly described and 3 species formerly assigned to the genus were excluded. Since then two additional species (*C. alienus* Holt, 1963, and *C. smalleyi* Holt, 1964) have

Key to the Mesoamerican Species of the Genus *Cambarincola*

1. Prostate differentiated 2
   Prostate not differentiated 3
2. Spermatheca with thick-walled bulb; dental formula ¼; dorsal ridges present ..... ***C. tolectus,*** new species
   Spermatheca with thin-walled bulb, ental process; dental formula 6/6; dorsal ridges absent ..... ***C. smalleyi***
3. Dorsal ridges present 4
   Dorsal ridges absent, i.e., body outline smooth 5
4. Prostate equal to or exceeding spermiducal gland in length; prostatic bulb prominent ..... ***C. olmecus,*** new species
   Prostate shorter than spermiducal gland; prostatic bulb obscure . ***C. jamapaensis,*** new species
5. Spermiducal gland shorter than prostate, subequal to latter in diameter; middle segments of body not greatly exceeding head in diameter ..... ***C. micradenus,*** new species
   Spermiducal gland longer than prostate; or, if not, body corpulent, middle segments of body much exceeding head in diameter 6
6. Spermiducal gland with large deferent lobes; dental formula 7/6 ..... ***C. acudentatus,*** new species
   Spermiducal gland without large deferent lobes; dental formula less than 7/6 7
7. Spermiducal gland long, slender, bent back upon itself 8
   Spermiducal gland relatively short, never reflexed 9
8. Upper jaw noticeably larger than lower (ratio 5:3); prostate with obvious ental bulb; spermathecal bulb globular ..... ***C. susanae,*** new species
   Upper and lower jaws not so unequal in size (ratio 3:2); prostate without an ental bulb; spermathecal bulb elongate ovoid ..... ***C. ellisi,*** new species
9. Spermiducal gland shorter than prostate, less in diameter, body corpulent, diameter of midsegments much exceeding that of head ..... ***C. hoffmani,*** new species
   Spermiducal gland longer than prostate, latter arising some distance entad to junction with ejaculatory duct 10
10. Jaws thin, delicate, small; cells of ental portion of spermiducal gland finely granular; prostate approximately one-half diameter of spermiducal gland ..... ***C. nanognathus,*** new species
    Jaws of more nearly normal size, teeth prominent; spermiducal gland large, without two types of cells; prostate gland less than one-fourth of diameter of spermiducal gland ..... ***C. carcinophilus,*** new species

Note: *Cambarincola macrodontus* Ellis, recorded from Mexico by Rioja (1940) is not included, since the record is considered doubtful; the record of *C. philadelphicus* (Leidy) by Rioja (1940) is tentatively included under *C. jamapaensis.*

been placed in the genus. Despite the excellence of Hoffman's treatment, the genus is again badly in need of revision. In addition to the ten new species from Mesoamerica described below, I have in my collections an unknown, but large, number of unnamed ones from the southern Appalachians, the Ozarks, and the Pacific slope regions of the United States. The known existence of these undescribed forms renders futile any attempt to improve upon Hoffman's effort to divide the genus into "sections" and "groups." As will be shown, some of the criteria he used for these infrageneric groupings are no longer valid. It is still more futile, then, to speculate on the historical zoogeography of the genus, though I accept Hoffman's (1963:298) belief that the genus was widespread and speciose by late Miocene times and have briefly discussed above these ideas as applied to the Mesoamerican members of the genus.

Rioja (1943) recorded the presence in Mexico of *Cambarincola macrodontus* and *C. philadelphicus*. I have no animals remotely resembling *C macrodontus* in my materials, but consider the possibility that specimens of *C. jamapaensis*, new species, may have been the animals (which are no longer available) identified by Rioja as *C. philadelphicus*.

Cambarincola acudentatus, new species

FIGURES 2, 7

TYPE-SPECIMENS.—Holotype and one paratype (USNM 45435), six paratypes (PCH 489), four paratypes, Instituto de Biología, Universidad de México, taken on *Speocirolano bolivari* and *S. pelaezi*, from Grutas de Quintero, 11 km SW of Ciudad Mante, Tamaulipas, Mexico, 14 May 1950.

DIAGNOSIS.—M e d i u m - s i zed branchiobdellids (known specimens approximately 3.0 mm in

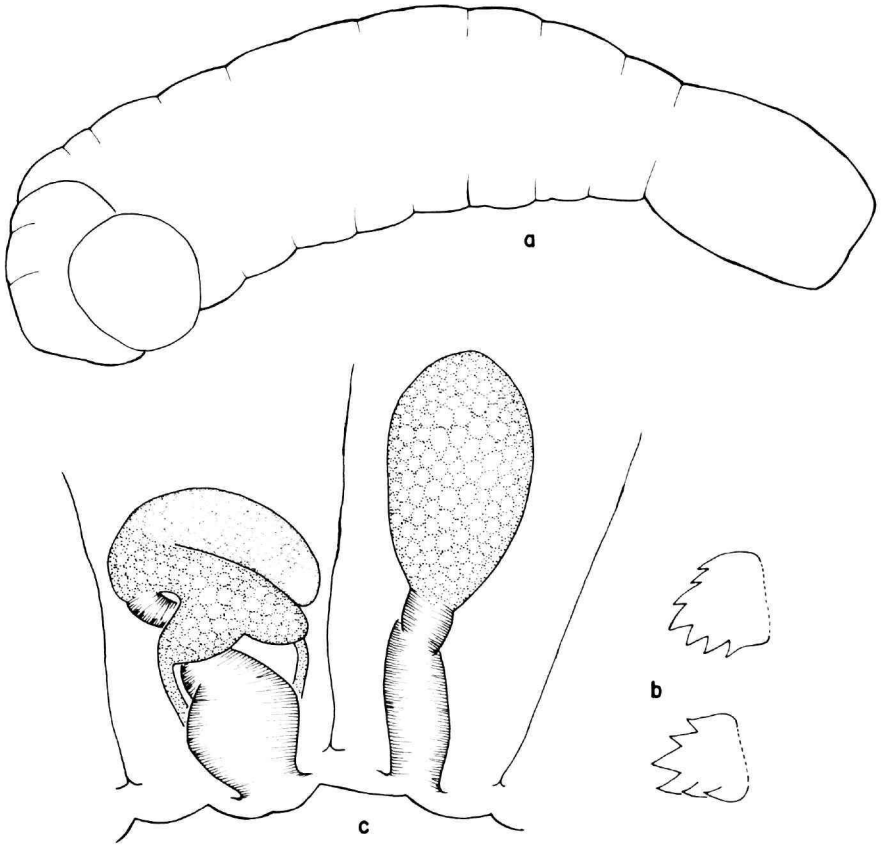

FIGURE 2.—*Cambarincola acudentatus*, new species: *a*, holotype; *b*, obliquely *en face* view of jaws; *c*, reproductive systems.

length); body outline smooth (no dorsal ridges); jaws light in color, delicate; dental formula 7/6, teeth sharp, prominent; bursa small, approximately 1/4 body diameter in length; spermiducal gland short, 3/4 length of bursa, with prominent deferent lobes; prostate subequal to spermiducal gland in length and diameter, its epithelial cells highly granular, different from those of spermiducal gland, with ental bulb; spermatheca with long ectal duct, expanded oval bulb, approximately 3/4 to 4/5 body diameter in total length.

ETYMOLOGY.—From Latin *acus* (needle) plus *dens* (tooth) in reference to the sharply pointed teeth.

DESCRIPTION.—*Cambarincola acundentatus* is a medium-sized worm of normal proportions. Only the holotype is unbroken or not too distorted to measure; posteriorly it is bent back upon itself. It has the following approximate dimensions: total length, 3.0 mm; greatest diameter (segment VII), 0.6 mm; head length, 0.7 mm; head diameter, 0.5 mm; diameter, segment I, 0.3 mm; diameter, sucker, 0.2 mm.

The lips are entire with the usual lateral indentations separating upper and lower ones. There is no evidence of oral papillae. The external furrow setting off the peristomium (lips) is not of unusual prominence. There is only one pharyngeal sulcus.

The body outline is smooth. The clitellar glands of segments VI and VII are only moderately developed. The sucker is somewhat less in diameter than segment I.

The jaws are distinctive. They are triangular in *en face* view, extremely light in color, delicate in appearance and approximately 40 by 40 microns in size. The dental formula is 7/6; the teeth are long and sharply pointed, the median tooth of the upper jaw and the paramedian ones of the lower jaw are larger than the others.

The spermiducal gland is provided with large deferent lobes and is short and of relatively small size, its length less than that of the bursa. The prostate is subequal to the spermiducal gland in both length and diameter, has a small ental bulb (i.e., the blind end is occupied by a noncellular, fluid-filled space) and is composed of cells that are not highly vacuolated but are granular, as is the case in some other Mesoamerican species. The ejaculatory duct is not unusual in its proportions or length. The bursa is disproportionately small and the penial sheath makes up approximately 3/7 of its total length, the bursal atrium the remainder. The penis is less clearly a protrusible cone of muscular tissue than in most species of the genus, but is not an obviously eversible tube.

The spermatheca is of ordinary shape and proportions: the ectal duct is a long muscular tube; the bulb is ovoid and thin-walled; there is no ental process; the total length approximates the diameter of segment V. Its only noteworthy feature is the disproportion between its size and the overall size of the male reproductive system; the spermatheca is not usually so much the larger.

VARIATION.—Other than subtle differences in size and appearance of the organs of the reproductive systems that are accounted for by differences in the aspects from which they are viewed, there are no detectable variations in my material.

AFFINITIES.—The closest relatives of *Cambarincola acudentatus* appear to be among the members of Hoffman's Mesochoreus section of *Cambarincola* and another isopod-inhabiting species, *C. alienus* Holt (1963).

All members of the Mesochoreus section have undifferentiated prostates without ental bulbs and spermiducal glands with variously developed deferent lobes. *Cambarincola acudentatus* differs from these species, exemplified by *C. mesochoreus,* in the apparent histological differences between its prostate and spermiducal gland; the prostate is granular, but the granules are smaller and apparently much more numerous than those of the spermiducal gland while, in *C. mesochoreus* and its relatives, the prostate is histologically indistinguishable from the spermiducal gland.

The ental bulb, present in *C. acudentatus,* is found in members of Hoffman's Philadelphicus section that have differentiated prostates, in *C. demissus* Hoffman (1963) with an undifferentiated prostate, and in several species newly described herein.

Cambarincola acudentatus, C. demissus, and *C. alienus* have remarkably small male reproductive systems. The prostate of *C. alienus* is undifferentiated without an ental bulb and there are no deferent lobes of its spermiducal gland. *Cambarincola smalleyi* Holt lacks the ental bulb of the prostate and deferent lobes of the spermiducal gland, but the

prostate is differentiated. Its dental formula is 6/6, close to that of *C. acudentatus,* but the jaws of *C. smalleyi* are subrectangular in form and the teeth are subequal in length.

The spermatheca varies within the species discussed: it possesses an ental process in *C. mesochoreus, C. alienus* and *C. smalleyi,* a structure that is absent in *C. acudentatus,* the other members of the Mesochoreus section, and in *C. demissus.*

The penis of *C. acudentatus* is somewhat puzzling and seems to be intermediate in some respects between that of *Tettodrilus friaufi,* a representative of the postulated ancestral stock of the genus *Cambarincola* (Holt, 1968b:314–317), and the presumably more advanced species of *Cambarincola.* In *T. friaufi* the penis is composed of an investing cuticle and a layer of epithelial cells that are not obviously muscular; in *C. acudentatus* the penis is muscular and differs from that of other species of *Cambarincola* in that it is proportionately longer. *Cambarincola acudentatus* further differs from *T. friaufi* in the nature of the prostate, which is incompletely separated from the spermiducal gland in the latter.

Nonetheless, it is difficult to find a near relative of *C. acudentatus.* Its affinities lie with a somewhat diverse group of species that, for one reason or another, have been considered as primitive members of the genus (Hoffman, 1963; Holt, 1963, 1964, 1968b, c). The jaws of *C. acudentatus,* with their large number of teeth, are diagnostic and clearly differentiate the species from any known others of the genus.

HOSTS.—*Speocirolana bolivari, S. pelaezi.* (*C. acudentatus* material came from a collection containing both of these isopods; therefore, I have no way of knowing whether it occurs on only one or both.)

MATERIAL EXAMINED.—The type-series.

Cambarincola carcinophilus, new species

FIGURES 3, 7

TYPE-SPECIMENS.—Holotype (USNM 45439), one paratype, Instituto de Biología, one paratype (PCH 698), taken on *Pseudothelphusa veracruzana* from Río Tapalapa, Santiago Tuxtla, Veracruz, Mexico by A. Villalobos and Horton H. Hobbs, Jr., 1957.

DIAGNOSIS.—Medium sized branchiobdellids (about 3.0 mm in length); body outline smooth; jaws subequal in size, small; dental formula 5/4; teeth prominent, sharp-pointed; bursa small (about 0.3 body diameter in length); spermiducal gland L-shaped, prominent, without deferent lobes; prostate undifferentiated, slender (its diameter 1/5–1/4 that of spermiducal gland), short reaching to about midlength of spermiducal gland, tapering entally; spermatheca spatulate, ectal duct expanded at juncture with bulb; latter thick-walled, small broad ental process present.

ETYMOLOGY.—From the Greek *karkinos* (a crab) plus *philos* (love) for this species' association with freshwater crabs.

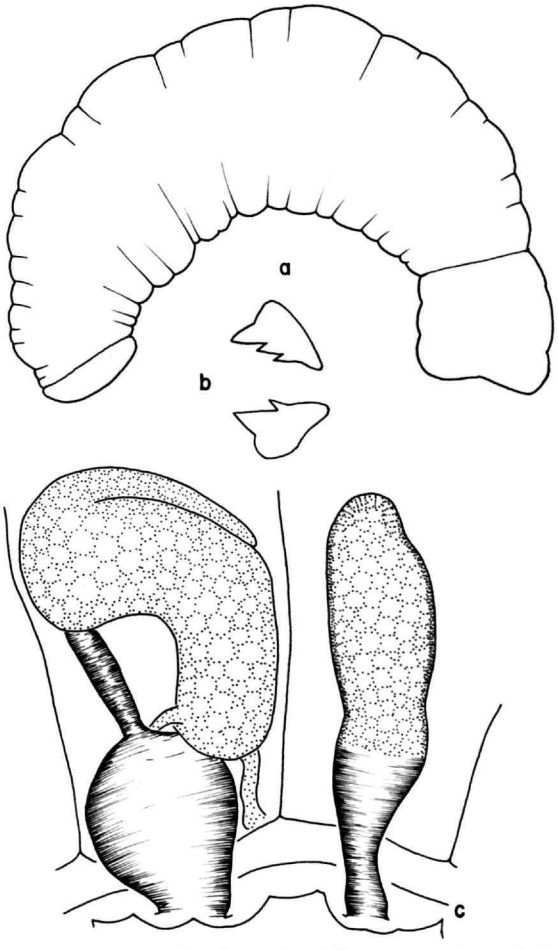

FIGURE 3.—*Cambarincola carcinophilus,* new species: *a,* holotype; *b,* lateral view of jaws, from paratype, PCH 698; *c,* reproductive systems.

DESCRIPTION.—*Cambarincola carcinophilus* is a medium-sized member of the genus. The holotype has the following dimensions: total length, 3.3 mm; greatest diameter, 0.6 mm; head length, 0.5 mm; head diameter, 0.4 mm; diameter, segment I, 0.4 mm; diameter, sucker, 0.3 mm. Only one other specimen from the type-series is fully mature; it is 3.0 mm in length. Other subadult specimens also designated as paratypes are about 2.0 mm long.

The lips each have a shallow median emargination. Oral papillae are absent. There is one prominent pharyngeal sulcus internally, externally the peristomial sulcus and one other at the level of the pharyngeal one are present, but not prominent.

Supernumerary longitudinal muscles of the body wall are absent or weakly developed. Consequently the major annulations of the body segments are only slightly, if at all, raised above the minor ones. The anterior nephridiopore presents no unusual features.

The jaws are small and approximately equal in size, their length somewhat less than 1/12 that of the head. In the larger specimens they are rather dark in color. The dental formula is 5/4 and the teeth, though the jaws appear hardly different in proportions from most members of the genus with a 5/4 dental formula, are large and distinct.

The ectal half of the spermiducal gland usually lies horizontally; the ental half vertically, i.e., the organ is bent so that it forms a right angle at its midlength. It is about 3/5 of the body diameter in length and about 1/4 of its own length in diameter. There are no deferent lobes. The prostate is short, ending entally at the midlength of the spermiducal gland in a narrowed, very obscure, ental bulb. Its diameter is at most 1/4 that of the spermiducal gland, an unusually small size of the organ among members of the genus, and it is undifferentiated, i.e., histologically indistinguishable from the spermiducal gland.

The ejaculatory duct is relatively long and the ovoid bursa correspondingly short: the latter is about 3/10 of the body diameter in length. The penial sheath region is not externally marked; the penis is of the typical cone-shaped, muscular protrusible type characteristic of the genus.

The spermatheca as a whole is spatulate in shape; the ectal duct widening entally to its juncture with the thick-walled bulb which ends entally in a short, broad and obscure ental process.

VARIATION.—Other than differences attributable to the age of the animals and degree of extension of the body at death, there are no detectable variations among my limited number of specimens. The unusually large diameter of the type-specimens may be due to an artifact of fixation and, if so, the relative sizes of the reproductive organs as given above would not be representative of the species.

AFFINITIES.—*Cambarincola carcinophilus* cannot be readily associated with any of the species of the genus that have an undifferentiated prostate. Its affinities are to be sought among the Mesoamerican species discussed herein. Among these it is perhaps closest to *C. nanognathus,* from which it differs in the larger jaws with more prominent teeth; in the larger spermiducal gland that is not narrowed ectally, regionally differentiated, or provided with deferent lobes; and in the relatively smaller prostate that is more completely separated, i.e., arises nearer the junction of the spermiducal gland and the ejaculatory duct.

HOSTS.—*Pseudothelphusa veracruzana, Procambarus ruthveni zapoapensis.*

DISTRIBUTION.—*Cambarincola carcinophilus* is only known from two localities in the lowlands of southern Veracruz in the Southern Gulf Slope region.

MATERIAL EXAMINED.—The type-series; three specimens (PCH 700) taken on *Pseudothelphusa veracruzana* and *Procambarus ruthveni zapoapensis* from Arroyo de Zapoapan de Cabaña, Verucruz, by A. Villalobos and H. H. Hobbs, Jr., 1957. Temnocephalids were associated with the branchiobdellids at the latter locality.

Cambarincola ellisi, new species

FIGURES 4, 7

TYPE-SPECIMENS.—Holotype (USNM 45443), taken on *Procambarus simulans regiomontanus* from Río San Juan, San Juan, Nuevo Leon, by Salvador Contreras, 18 April 1964. Paratype (PCH 1844), taken on *P. s. regiomontanus* from Arroyo de la Cruz, km 245 de la carretera México-Monterrey, 14 February 1964.

DIAGNOSIS.—Small branchiobdellids (holotype, 1.8 mm in length); body outline smooth; jaws

small, dark, upper jaw larger than lower (ratio 3:2), dental formula 5/4; bursa small, spherical, diameter approximately 1/5 that of body; spermiducal gland long, slender, subequal in length to body diameter, bent completely back upon itself, without deferent lobes; prostate undifferentiated, slender, entally ending at bend of spermiducal gland, without prostatic bulb; spermatheca with long ectal duct (exceeding 1/2 body diameter in length), bulb cylindrical to subovate.

ETYMOLOGY.—Named in honor of the late Max M. Ellis, who first defined the genus *Cambarincola*.

DESCRIPTION.—Only the types of *C. ellisi* are known. The holotype has the following dimensions: total length 1.8 mm; greatest diameter, 0.26 mm; head length, 0.3 mm; head diameter, 0.16 mm; diameter, segment I, 0.16 mm; diameter, sucker 0.16 mm. The paratype is of closely comparable dimensions.

The lips are entire; oral papillae are questionably present; the peristomium is well delimited by an external sulcus. The head shows one other very shallow external furrow, and there is only one internal pharyngeal sulcus.

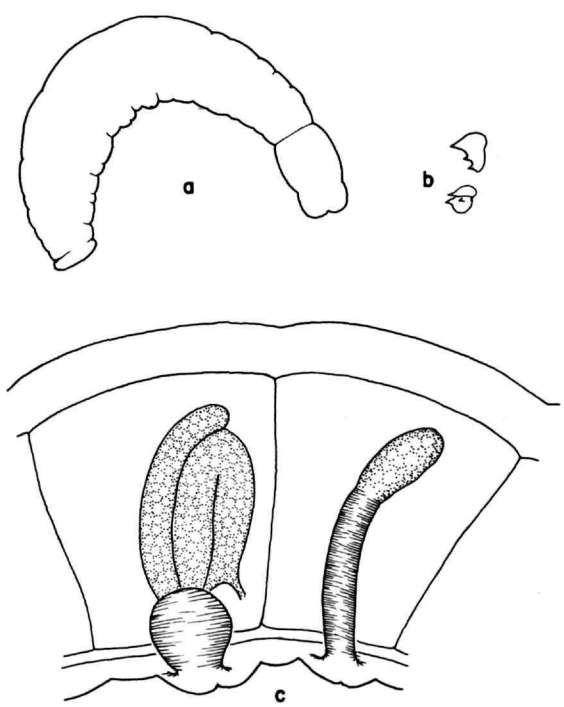

FIGURE 4.—*Cambarincola ellisi*, new species: *a*, holotype; *b*, obliquely lateral view of jaws; *c*, reproductive systems.

The body outline is remarkably smooth with very shallow intersegmental furrows and secondary furrows, which demarcate the minor annulations. *C. ellisi* is a small gracile worm.

The jaws are darker than is usual for such small animals, otherwise, with their 5/4 dental formula, they are similar to those of most, but by no means all, members of the genus.

The spermiducal gland is extremely long and slender, without deferent lobes. The gland runs dorsad from the junction of the deferent ducts to the dorsal border of the gut, where it is sharply reflexed in the holotype so that the two portions actually are in contact, but a small space separates the ental and ectal portions of the gland in the paratype. In total length the gland is subequal to the body diameter. The prostate is undifferentiated, subequal in diameter to the spermiducal gland, lacks an ental bulb and ends entally at the point of flexure of the spermiducal gland.

The bursa is small, scarcely extending inward beyond the inner face of the body wall, spherical, about 65 microns in diameter (between 1/4 and 1/5 of the body diameter). The ejaculatory duct is correspondingly short, but not mensurable in my specimens and distinctly dilated along its midlength.

The ectal duct of the spermatheca is only slightly less than 1/2 the body diameter in length and composes 0.6 of the total length of the spermatheca. The spermathecal bulb is subcylindrical in the holotype and apparently the wall is thickened, but in the paratype it is globose and thin-walled, as is usually the case when full of sperm, and there is no evidence of an ental process.

VARIATION.—Since only the two types are known and both are described above, nothing can be said of variability in the species.

AFFINITIES.—*Cambarincola ellisi* differs in no important respect from *C. vitreus* Ellis, 1918, except for the undifferentiated prostate without an ental bulb, the apparently smaller size of the entire worm and the more nearly spherical shape and smaller size of the bursa (Hoffman, 1963:326). The histological features of the prostate and the presence or absence of an ental prostatic bulb have proven to be reliable taxonomic characters in the past and

can usually be detected in poorly preserved material. The types of *C. ellisi* are not well preserved and I do not entirely discount the possibility that subsequent collecting will reduce *C. ellisi* to synonymy with *C. vitreus*. Among Mesoamerican members of the genus, *C. ellisi* is closest to *C. susanae* from which it differs in the shapes and proportions of the jaws, in its proportionately much longer spermiducal gland and prostate, and in the absence of deferent lobes of the spermiducal gland.

HOST.—*Procambarus simulans regiomontanus.*

DISTRIBUTION.—The basin of the Río San Juan, which is a tributary to the Río Grande. *C. ellisi* is, therefore, geographically the closest of the Mesoamerican branchiobdellids to those of the United States.

MATERIAL EXAMINED.—The type-series.

Cambarincola hoffmani, new species

FIGURES 5, 7

TYPE-SPECIMENS.—Holotype (USNM 45447), taken on *Procambarus hoffmanni* at Los Estajos, 6 km NE of Zihuateutla, Arroyo de Tlatentiloyan, Puebla, Mexico, 11 November 1949; two paratypes (PCH 1622), taken on *Procambarus caballeroi* at Villa Juárez, Puebla, Mexico, May 1944.

DIAGNOSIS.—Small, corpulent branchiobdellids (holotype, 2.3 mm in length), body outline smooth; upper jaw much larger than lower, dental formula 1/2; bursa about 0.3 body diameter in length, pyriform, atrial fold prominent; spermiducal gland short, about 2/3 length of bursa, without deferent lobes; prostate undifferentiated, slightly longer and greater in diameter than spermiducal gland, rudimentary prostatic bulb present; spermatheca with long ectal duct, ovoid bulb.

ETYMOLOGY.—It is a pleasure to name this species in honor of the eminent diplopodologist, Professor Richard L. Hoffman, in recognition of his contribution to our knowledge of the genus *Cambarincola*.

DESCRIPTION.—*Cambarincola hoffmani* is a small worm. The holotype has the following dimensions: total length, 2.3 mm; greatest diameter, segment VII, 0.7 mm; head length 0.4 mm; head diameter, 0.3 mm; diameter, segment I, 0.3 mm; diameter, sucker, 0.4 mm. The two paratypes from a different locality are of comparable size, but, since they have suffered some distortion in preservation, were not measured.

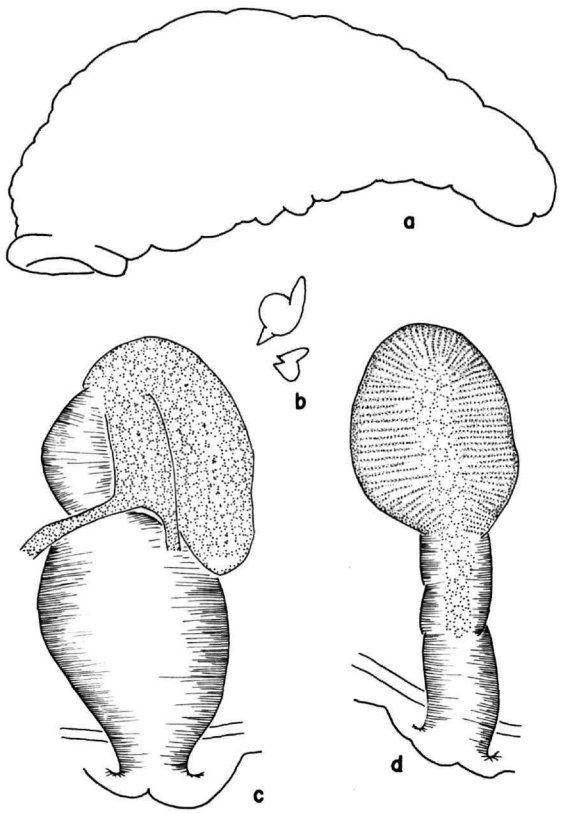

FIGURE 5.—*Cambarincola hoffmani*, new species: *a*, holotype; *b*, obliquely lateral view of jaws; *c*, male reproductive system; *d*, spermatheca.

The peristomium, except for the usual lateral emarginations, appear to be undivided into lobes, but this point is not firmly determinable in my material. A number of oral papillae are present. The body is smooth in outline, i.e., there are no or very weak supernumerary muscles, but is distinctive in its proportions. The reproductive segments are much greater in diameter than usual, although the reproductive systems themselves are not of unusual proportional size. The anterior nephridiopore, in its usual position, is clearly visible.

The jaws are distinctive. The upper jaw bears a single large median tooth and is produced anteriorly and laterally in large wing-like extensions. The lower jaw is roughly rectangular and bears

two paramedian teeth. The upper jaw is almost three times the lower in size. The ratio of the greatest measurable dimensions of the upper to the lower jaw is 5:2. Both jaws are dark brown in color, but the teeth are almost colorless.

The spermiducal gland lacks deferent lobes and is short and thick with a definite lumen in the holotype that appears to be filled with a granular material. The prostate is both longer and greater in diameter than the spermiducal gland and indistinguishable from the latter in appearance, except that entally there is a clear space that seems comparable to the prostatic bulb of some other species.

The ejaculatory duct is relatively short and thick. Although the pyriform bursa is relatively small, there is a distinct atrial fold present and the muscular penis fills the inner penial sheath portion and extends, in the holotype, into the atrial portion through the opening in the atrial fold.

The spermatheca is provided with a long ectal duct that is bent laterad and then dorsad, ending at the ventral border of the gut in an ovoid "bulb." (In the holotype, the spermatheca is pressed backward against septum 5/6 so that it actually lies lateral to and at the same level as the spermiducal gland.) The bulb, except that its rather small lumen contains spermatozoa, has the appearance of the ental processes of the spermathecae of some other branchiobdellids, with a remarkably thick and apparently nonglandular wall. More unusual, yet, spermatozoa are present in the ental portion of the ectal duct, whose wall is clearly muscular, so that it is possible that the "bulb" of the spermatheca of *C. hoffmani* is homologous to the ental process of other species and that the ental portion of the ectal duct represents the true spermathecal bulb.

VARIATION.—None in the material examined.

AFFINITIES.—Body shape, size, and the proportionally small reproductive organs are similar to those of *C. demissus* Hoffman, 1963, but *C. hoffmani* differs in the much larger prostate and details of the spermatheca, bursa, and jaws. The undifferentiated prostate may indicate a primitive status for both species, the other similarities are more likely paralellisms associated with similar habits or habitats (Hoffman, 1963:365, postulated, on the basis of appearance, that *C. demissus* inhabits the gill chambers of the host, and without any real evidence, I concur in this guess for both species). Most, not all Mesoamerican members of the genus lack differentiated prostates (but cf. *C. smalleyi* Holt, 1964, and *C. toltecus,* new species, described herein). *Cambarincola micradenus,* new species, in the thickened wall of its spermatheca and similar jaws, may well be closest to *C. hoffmani,* but the differences in body proportions—those of *C. micradenus* are more typical of the genus—and those of the male reproductive systems clearly separate the two species.

HOSTS.—*Procambarus hoffmanni, P. caballeroi.*

DISTRIBUTION.—The Interjacent Gulf Slope in Puebla, Mexico.

MATERIAL EXAMINED.—The type-series.

Cambarincola jamapaensis, new species

FIGURES 6, 7

TYPE-SPECIMENS.—Holotype and five immature paratypes (USNM 45438); one paratype (PCH 1592), taken on *Procambarus mexicanus* from the Río Jamapa at 7 km NE of Coscomatepec, Veracruz, Mexico, by P. C. and V. F. Holt, 9 July 1962.

DIAGNOSIS.—Small branchiobdellids, about 2.0 mm in length; major annulations of body segments greater in diameter than minor ones; jaws dark, triangular; dental formula 5/4; bursa ovate, approximately 1/3 body diameter in length, penial sheath portion short; spermiducal gland slightly longer than bursa, without prominent deferent lobes; prostate only slightly shorter than spermiducal gland, its cells more densely granular than those of latter, with small ental bulb; spermatheca with long ectal duct, expanded ovoid bulb.

ETYMOLOGY.—This species is named for the type-locality, the Río Jamapa.

DESCRIPTION.—*Cambarincola jamapaensis* is a small branchiobdellid, approximately 2.0 mm in length. The holotype and paratype are the only mature animals among the type-material and they are of approximately the same size. The holotype has the following dimensions: total length, 2.0 mm; greatest diameter, segment VII, 0.3 mm; head length, 0.45 mm; head diameter, 0.3 mm; diameter, segment I, 0.3 mm; diameter, sucker, 0.3 mm.

The upper lip bears four blunt lobes, often obscured by the extension of the animal or fixation while attached by the mouth; the lower lip is di-

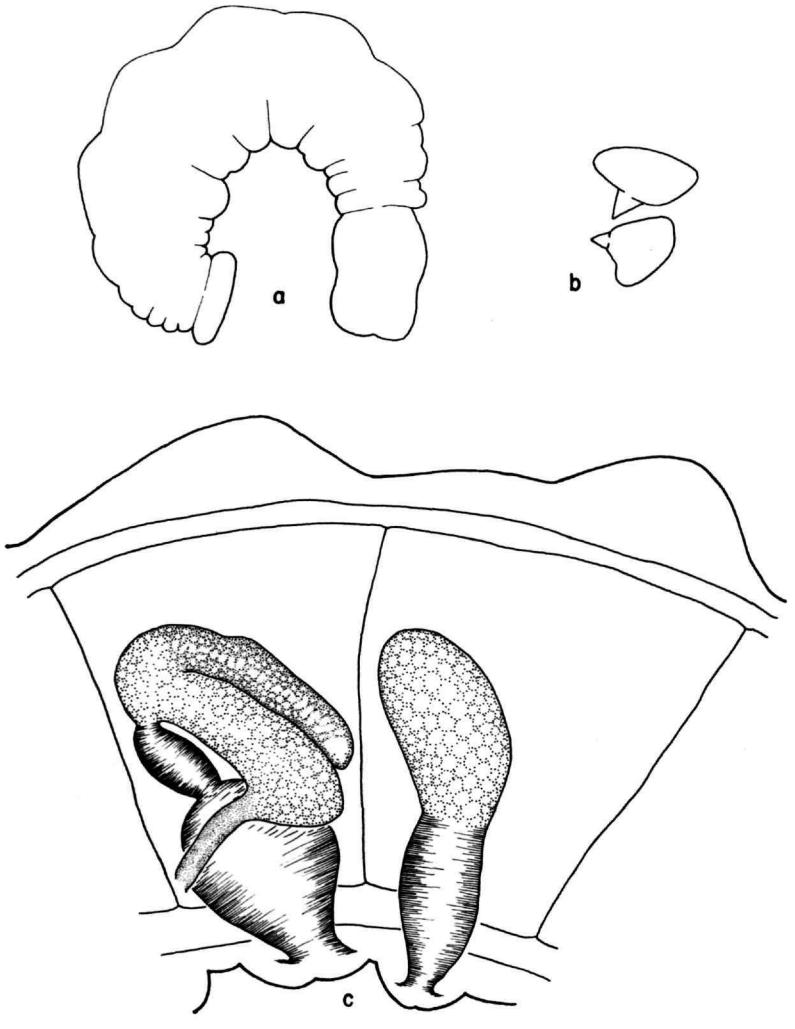

FIGURE 6.—*Cambarincola jamapaensis*, new species: *a*, holotype; *b*, lateral view of jaws; *c*, reproductive systems.

vided into two lobes by a slight median emargination; laterally, in the indentation between upper and lower lips on each side there are two much smaller lobes. Oral papillae are absent. The peristomial sulcus is not unusually prominent and internally there is only one prominent pharyngeal sulcus that is marked externally by a shallow furrow that encircles the head.

The major annulations of the body segments are greater in diameter than the minor ones. The anterior nephridiopore is prominent in the holotype, the "nephridial vesicle" (Moore, 1897) is large and surrounded by glandular cells, but is obscured by the orientation of the animal on the slide in the paratype. The clitellum, as usual in species with raised ridges on the dorsa of major annulations, is not noticeably well developed.

The jaws are triangular in both *en face* and lateral aspects, dark brown in color and approximately 1/6 of the head diameter in width. The dental formula is 5/4; the median teeth are strong, somewhat blunt; the much smaller lateral ones are obscure in lateral view.

The spermiducal gland is between 1/3 and 1/2

of the body diameter in length, straight (not bent back upon itself), without deferent lobes. The prostate is approximately 4/5 the length of the spermiducal gland and 3/5 its diameter. Its cells are more densely granular than those of the spermiducal gland, but not differentiated. An ental prostatic bulb is present. The bursa is ovoid in length with a short, externally nondelimited penial sheath region. The penis is an almost spherical muscular mass.

The spermatheca has a long ectal duct portion and an oval thin-walled spermathecal bulb (not expanded nor filled with spermatozoa in the holotype).

VARIATION.—Only two of my specimens are sexually mature and, except for the difference in the

FIGURE 7.—Distribution of five Mexican members of the genus *Cambarincola*.

degree of expansion of the spermathecal bulb, there are no detectable differences between them that cannot be accounted for by the usual differences in position and degree of contraction of the bodies at death.

AFFINITIES.—*Cambarincola jamapaensis* is very similar in appearance to the Appalachian members of the Philadelphicus section. Indeed Rioja (1943) has recorded *C. philadelphicus* from localities in Puebla (Hauchinango, Necaxa, and Villa Juárez). It is extremely unlikely that *C. philadelphicus* occurs in Mexico and if Rioja was dealing with *C. jamapaensis* (one of the more likely possibilities), the mistake is understandable. Most students of the branchiobdellids of that time would have unhesitatingly assigned my specimens to *C. philadelphicus* on the basis of peristomial and jaw characters, body form and an overall resemblance of the reproductive systems. Yet the animals are not so large, and the lobes of the upper lip and the raised major annulations of *C. jamapaensis* are not so prominent as they are in *C. philadelphicus* and the prostate is markedly different in the two species. The prostate is composed of vacuolated cells in *C. philadelphicus* and densely granular ones in *C. jamapaensis,* a difference earlier considered to be of fundamental importance and one upon which Hoffman (1963) based his subgeneric sections. Although this grouping of species, with the addition to our knowledge of the Mesoamerican branchiobdellids, may no longer be tenable, the histological characteristics of the prostate are constant within a species and clearly justify according species status to the animals from the Río Jamapa.

Among Mesoamerican congeners of *C. jamapaensis, C. olmecus* and *C. toltecus* have dorsal ridges. *Cambarincola olmecus* has a much longer prostate with a larger ental bulb than does *C. jamapaensis; C. toltecus* has a differentiated prostate and a thick walled spermatheca, neither of which are present in *C. jamapaensis.*

HOSTS.—*Procambarus mexicanus, P. hoffmanni, P. acutus cuevachicae.*

DISTRIBUTION.—*Cambarincola jamapaensis* is known with certainty only from the type-locality in the Southern Gulf Slope. With some hesitation I have assigned specimens (see below) from north of the Cordillera Volcánico in the Interjacent Gulf Slope to the species. It is likely that these worms, if this assignment is correct, are conspecific with those from Puebla identified as *C. philadelphicus* by Rioja (1943).

MATERIAL EXAMINED.—The type-series; three specimens (PCH 702), on *Procambarus hoffmanni* at Mi Ranchito, Villa Juárez, Puebla, Mexico, by A. Villalobos and H. H. Hobbs, Jr., 4 April 1957; one (PCH 703), taken on *P. acutus cuevachicae* at El Ajenjibre, Mesa de San Diego, km 262 de la carretera México-Tuxpan, Puebla, Mexico, by A. Villalobos and H. H. Hobbs, Jr., 12 April 1957.

Cambarincola micradenus, new species

FIGURES 8, 14

TYPE-SPECIMENS.—Holotype and two paratypes (USNM 45448), one paratype (PCH 1615), taken on *Paracambarus paradoxus* at La Cañada y Tetela de Ocampo, Puebla, Mexico, May 1944.

DIAGNOSIS.—Small branchiobdellids (known specimens approximately 2.5 mm in length); body outline smooth (no raised dorsal ridges); dental formula 1/2; upper lip with four, lower lip with two, low indistinct lobes; bursa small, about 3/7 body diameter in length; spermiducal gland very small, hardly more than 1/3 length of bursa, without deferent lobes; prostate slender, subequal to spermiducal gland in diameter, twice latter in length, undifferentiated; with ental bulb; spermatheca club-shaped with long ectal duct, short thick-walled bulb, approximately 1/2 diameter of body in length.

ETYMOLOGY.—From Greek *mikros* (little) plus *adenus* (gland) in reference to the remarkably small spermiducal gland.

DESCRIPTION.—*Cambarincola micradenus,* as is true of most Mesoamerican branchiobdellids, is a small worm. The holotype has the following dimensions: total length, 2.7 mm; greatest diameter, 0.5 mm; head length, 0.4 mm; head diameter, 0.3 mm; diameter, segment I, 0.3 mm; diameter, sucker, 0.4 mm. The other known specimens are smaller; the smallest is 1.8 mm in total length.

The peristomium is rather weakly lobed and there are no oral papillae.

The body wall is thin and there are no, or very weak, supernumerary muscles, hence the body outline is smooth and the major annulations are only very slightly greater in diameter than the minor

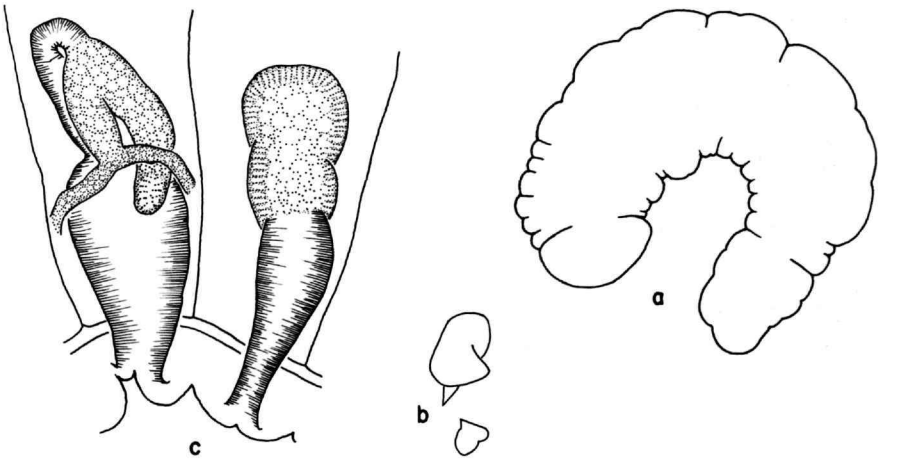

FIGURE 8.—*Cambarincola micradenus*, new species: *a*, holotype; *b*, lateral view of jaws; *c*, reproductive systems.

ones, even in strongly contracted specimens. The single anterior nephridiopore is clearly visible on the dorsum of segment III. The posterior segments are provided with a large number of glands (apparently more, or more prominently, than is common) that appear to empty to the outside through the sucker.

The jaws are prominent and distinctive. The upper is more than twice the lower in its greatest dimension and bears a single large tooth; the lower bears two much smaller teeth.

The gut of some of the specimens is filled with a coagulum that may be the blood of the host.

The spermiducal gland is remarkably small in proportion to the relatively small male reproductive system as a whole. It is about 1/3 the length of the bursa and lacks deferent lobes. The prostate exceeds by approximately 1/3 its length that of the spermiducal gland and is undifferentiated, although its cells appear slightly more granular than those of the spermiducal gland. It ends entally in a thick-walled bulb that is quite different in appearance from the usual thin-walled prostatic bulbs of other branchiobdellids with such a feature.

The ejaculatory duct is relatively long, exceeding slightly the spermiducal gland in length, with an expanded lumen and a relatively thin muscular wall. The penis is difficult to interpret in the available material, but appears to consist of the protrusible muscular cone characteristic of the genus. If so, it is rather thin-walled, but there is no observable evidence of an eversible cuticular lining. The bursa is elongate pyriform in shape, about 3/7, or less, the body diameter in length, and is marked internally by a well-developed atrial fold.

Any accurate estimation of the length of the spermatheca is not possible, since it is normally bent to the side, but in side view its ental end barely reaches the ventral border of the gut. The ectal duct, however, approximates half the total length of the organ and the bulb is lined with a glandular epithelium which confers upon the entire spermathecal bulb the appearance of the ental process of the spermatheca known from some other species. The clitellum, in the better preserved specimens, is unusually well developed, particularly on segment VII.

VARIATION.—Other than in size and quality of preservation, there are no detectable differences among the available material.

AFFINITIES.—The spermiducal gland and prostate of *Cambarincola micradenus* are peculiar and reminiscent of those of *Tettodrilus friaufi* (cf. Holt, 1968b:313, 315). The jaws, however, are specialized and the animal has the general facies of a gill-inhabiting species, although nothing is known of its microhabitat. The most that can be said of the relationships of *C. micradenus* is that it is a primitive member of the genus, apparently close to *Tettodrilus friaufi*, which has been postulated to represent the group from which *Cambarincola* arose (Holt, 1968b:313–314). Indeed, at first, I was

inclined to place *micradenus* in *Tettodrilus,* but the protrusible penis of *micradenus* as opposed to the eversible one of the latter and, to a much lesser extent, the specialized features of the jaws seem to argue for retaining it among the members of *Cambarincola.* Its closest relative within the genus is *C. hoffmani,* new species, primarily because of the nature of the spermiducal gland and prostate, the thick-walled spermathecal bulb and the similar jaws. The addition of this species and that of the others herein assigned to the genus *Cambarincola* will require a revision of the groupings proposed by Hoffman (1963:300–301).

HOSTS.—*Paracambarus paradoxus.*

DISTRIBUTION.—*Cambarincola micradenus* is known only from the type-locality in the Interjacent Gulf Slope.

MATERIAL EXAMINED.—The type-series.

Cambarincola nanognathus, new species

FIGURES 9, 14

TYPE-SPECIMENS.—Holotype (USNM 45444); one paratype (PCH 1830); one paratype, Instituto de Biología, Universidad de México, on *Potamocarcinus nicaraguensis* taken at Isleta de Granada, Lago de Nicaragua, Nicaragua, by G. Alviléz, 13 July 1964.

DIAGNOSIS.—Small branchiobdellids (known specimens approximately 2.0 mm in length); body outline smooth (no dorsal ridges); jaws light in color, small, dental formula 5/4; bursa small, approximately 1/4 or less body diameter in length; spermiducal gland slender, approximately 1.8 times bursal length, cells of ental half finely granular, without prominent deferent lobes; prostate incompletely divided from spermiducal gland, approximately 1/2 as long as latter, undifferentiated, with ental bulb; spermatheca approximately 2/3 body diameter in length, ectal duct and bulb subequal in length, ental portion of bulb thick-walled.

ETYMOLOGY.—From Greek *nanos* (dwarf) plus *gnathos* (jaw) in reference to the small size of the jaws.

DESCRIPTION.—*Cambarincola nanognathus* is a small member of the genus. The holotype has the following dimensions: total length, 2.1 mm; greatest diameter, segment VII, 0.4 mm; head length, 0.3 mm; head diameter, 0.25 mm; diameter, segment I, 0.3 mm; diameter, sucker, 0.2 mm. (Many specimens of the series are poorly preserved, partially macerated and grossly extended; none of these were measured.) The average dimensions of the holotype and four paratypes, with ranges given in parentheses, are as follows: total length, 1.9 mm (1.6–2.1 mm); greatest diameter, segment VII, 0.4 mm (0.3–0.5 mm); head length, 0.3 mm (0.25–0.5 mm); head diameter, 0.2 mm (0.2–0.3 mm); diameter, segment I, 0.3 (0.2–0.3 mm); diameter, sucker, 0.2 (0.2–0.2 mm). The undistorted specimens studied are of rather uniform size and proportions.

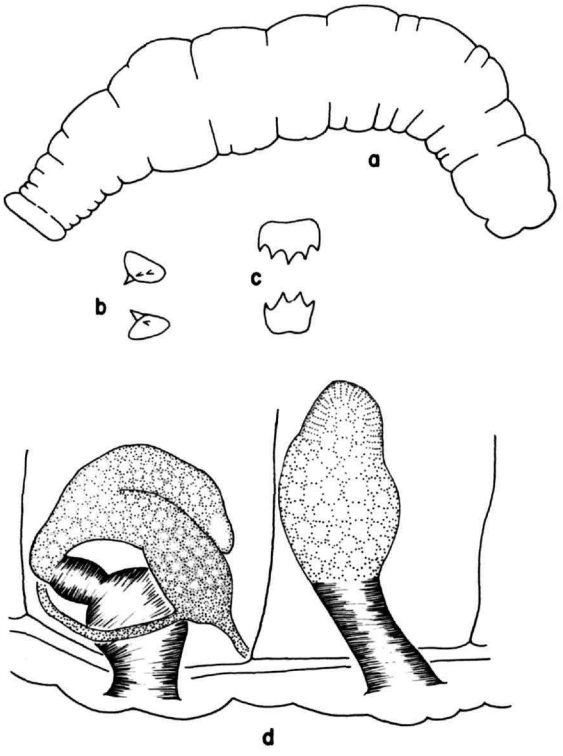

FIGURE 9.—*Cambarincola nanognathus,* new species: *a,* holotype; *b,* lateral view of jaws; *c, en face* view of jaws; *d,* reproductive systems.

The lips are entire without median indentations. There are no oral papillae. The peristomium is set off by a deep sulcus. Internally, there is only one prominent pharyngeal sulcus.

The body outline is smooth, although intersegmental grooves are prominent. The anterior nephridiopore, usually difficult to detect in entire animals, is obvious in almost all specimens. The

clitellum, especially on segment VII, is well developed.

The jaws are of the usual form for members of the genus. They are triangular in lateral view and subrectangular in *en face* view. They are lightly, though distinctly colored. But their small size is notable. The upper jaw illustrated (from a poorly preserved specimen) measures 26 by 15 microns; the lower (from the same specimen), 22 by 15 microns. The dental formula is 5/4 and the median teeth of each jaw are longer than the lateral ones.

The spermiducal gland is relatively long and slender and without obvious deferent lobes. The glandular cells of its ental portion are filled with small granules; ectally they lack such granules. The prostate is undifferentiated, noticeably less in diameter than the spermiducal gland, about 1/2 its length and incompletely separated, i.e., it unites with the spermiducal gland about 1/3 the length of the latter entad to its union with the ejaculatory duct. A distinct ental prostatic bulb is present. The ejaculatory duct is not remarkable in any way, nor is the bursa except for its small size (about 100 microns in length).

The spermatheca, about 2/3 of the body diameter in total length, has a relatively long ectal duct. The middle portion, the spermathecal bulb, is of usual appearance, but the ental part, somewhat less in diameter than the bulb in many specimens, has a wall composed of a taller columnar epithelium than the bulb proper—a condition suggestive of the ental process of the spermatheca in some species (Holt, 1960a:64).

VARIATION.—Some apparent variation in the number of teeth borne by the jaws occurs, but most likely this is due to the breaking of lateral teeth. In any case, it is difficult in such small animals to determine the number and arrangement of the teeth, but there is little doubt that the normal dental formula of the species is 5/4.

AFFINITIES.—*Cambarincola nanognathus* appears to be closely related to *C. acudentatus*, new species, and *C. smalleyi*. It differs from *C. acudentatus* in the smaller size of its jaws and its dental formula, in the absence of deferent lobes and in the finely granular ental portion of its spermiducal gland (unique among known members of the genus), in the incompletely separated prostate and in the ental process (if the thicker wall of the ental portion of the spermatheca may be called an ental process) of its spermatheca. It differs from *C. smalleyi* in dental formula (6/6 in the latter), in its undifferentiated prostate and prostatic bulb (the prostate of *C. smalleyi* is differentiated but lacks the ental bulb) and perhaps, most uncertainly, in the ental process of the spermatheca (distinct in *C. smalleyi*). *Cambarincola nanognathus* is a primitive member of the genus on the basis of the prostate, differentiated ental part of the spermatheca, and, perhaps, in its small size, delicate jaws, and lack of dorsal ridges. The histological differences along the course of the spermiducal gland canot be accounted for now. Such differences are characteristic of some branchiobdellids without a prostate, e.g., species of *Xironogiton* Ellis (Holt, 1949), but were unknown among species of *Cambarincola* and those of related genera with prostates. In the small size of the animal itself, the jaws and the male reproductive system, in the incompletely separated and undifferentiated prostate with an ental bulb and in the thick-walled ental part of the spermatheca, *C. nanognathus* resembles putatively primitive species of *Pterodrilus* Moore (Holt, 1968c), but lacks any dorsal ridges, of which at least one is present in all known species of *Pterodrilus*. Perhaps it stands near the point of divergence of the two closely related genera. But the combination of characters discussed above, particularly the spermiducal gland, clearly differentiates it from any species of these two genera.

HOSTS.—*Potamocarcinus nicaraguensis, Pseudothelphusa veracruzana, Procambarus vazquezae.*

DISTRIBUTION.—*Cambarincola nanognathus* ranges from the Río Tapalapa and Laguna de Catemaco in southern Veracruz, Mexico, to the type-locality in Nicaragua, which is the second southernmost locality from which a branchiobdellid has been recorded. It, thus, partially fills the gap between its closest relatives, *C. acudentatus* and *C. smalleyi*, the southernmost known branchiobdellid.

MATERIAL EXAMINED.—The type-series; 39 others from the type-locality (PCH 1830); 25 specimens (PCH 696) taken on *Procambarus vazquezae* from Laguna de Catemaco, Playa Azul, Veracruz, Mexico by A. Villalobos and H. H. Hobbs, Jr., 15 April 1957; 22 (PCH 697) taken on *Pseudothelphusa veracruzana*, from the Río Tapalapa, Santiago Tuxtla, Veracruz, Mexico by A. Villalobos and H. H. Hobbs, Jr., 9 April 1957.

Cambarincola olmecus, new species

FIGURES 10, 14

TYPE-SPECIMENS.—Holotype (USNM 45445), one paratype (USNM 45446), one paratype (PCH 201), and one paratype, Instituto de Biología, Universidad de México; taken on *Procambarus aztecus* at Tomatlán, Veracruz, Mexico, 3 November 1948.

DIAGNOSIS.—Medium-sized branchiobdellids (2–3 mm in length); major annulations of body segments greater in diameter than minor ones; jaws triangular, dark; dental formula 5/4; bursa pyriform, approximately 1/3 body diameter in length; spermiducal gland slender, curved, with small deferent lobes; prostate with finely granular cells (nondifferentiated), equal to or exceeding spermiducal gland in length, with prominent expanded ental bulb, often curved away from spermiducal gland; spermatheca with large, approximately ovoid, bulb, without ental process.

ETYMOLOGY.—This species is named for the Olmecs, one of the early peoples of Mexico.

DESCRIPTION.—*Cambarincola olmecus* ranges from about 2.0 to 3.0 mm in length, somewhat larger than most Mesoamerican members of the genus but moderately small for the genus as a whole. The holotype has the following dimensions: total length, 2.9 mm; greatest diameter; 0.46 mm; head length, 0.5 mm; head diameter, 0.3 mm; diameter, segment I, 0.26 mm; diameter, sucker, 0.3 mm. The average dimensions, with ranges given in parentheses, of five specimens from Ciudad Men-

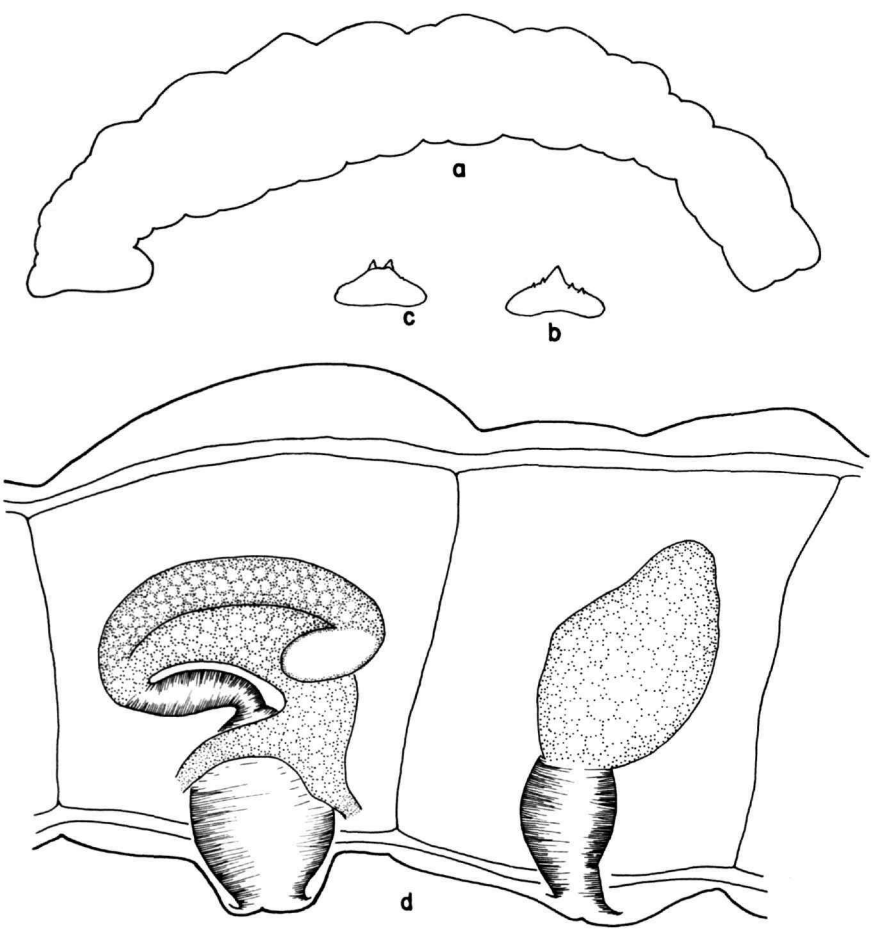

FIGURE 10.—*Cambarincola olmecus*, new species: *a*, holotype; *b*, *en face* view of upper jaw; *c*, *en face* view of lower jaw; *d*, reproductive systems.

doza, Veracruz, are as follows: total length, 2.3 mm (1.9–2.5 mm); greatest diameter, 0.4 mm (0.35–0.5 mm); head length, 0.4 mm (0.4–0.5 mm); head diameter, 0.3 mm (0.3–0.3 mm); diameter, segment I, 0.3 mm (0.3–0.3 mm); diameter, sucker, 0.3 mm (0.2–0.3 mm).

The dorsal lip is divided into four short, blunt lobes by very shallow indentations and the lower lip into two. Between the upper and lower lips there are small medial lobes, each of which may appear subdivided in some specimens. There are no oral papillae. Internally, there is only one prominent pharyngeal sulcus. Externally, the peristomial sulcus is prominent in dorsal view and another shallow furrow encircles the head at the level of the pharyngeal sulcus.

The major annulations are marked dorsally by raised ridges which are not usually prominent. The anterior nephridiopore is not easily seen.

The brown jaws are triangular in both *en face* and lateral views. The dental formula is 5/4, but the lateral teeth of both jaws in larger (? older) animals are often obscure or worn away so that the dental formula may appear to be 1/2.

The spermiducal gland, approximately 1/2 the body diameter in length and slightly curved, is provided with deferent lobes of which the anterior is the larger. The prostate frequently exceeds and always appears to be at least subequal in length and is about 1/2 the diameter of the spermiducal gland. Its ental end is often bent back upon itself or away from the spermiducal gland. It is always provided with a large, often expanded, ental bulb formed by a reduction of the prostatic epithelium to a thin layer of nonglandular cells, which enclose an expansion of its lumen. The glandular cells of the prostate are not markedly vacuolated as in the differentiated type of a prostate, but often appear to be more finely granular than those of the spermiducal gland.

The ejaculatory duct, penis, and bursa present no significant features. The bursa is about 1/3 the body diameter in length and the penial sheath portion, approximately 1/2 of the total length, is somewhat reduced in diameter; the organ is, therefore, pyriform.

The ectal duct of the spermatheca is somewhat thick and about 1/3 the total length of the organ; the bulb is subovoid with a suggestion of an ental process produced by the lesser diameter of its ental end, but the wall of this narrowed portion of the bulb is not histologically distinct from that of its middle portion and contains spermatozoa.

VARIATION.—The dental formula of *C. olmecus,* as mentioned above, appears to vary from 5/4 to 1/2. Apparently in older animals the lateral teeth, always relatively small, wear away with age. The prostate is always as long as the spermiducal gland and in many specimens appears to be longer, but its ental end is not closely bound by its peritoneal investment to the latter and is often bent in various directions away from it. The ental bulb of the prostate may be expanded to differing degrees, although it is always unusually prominent. Likewise, though not rare among the branchiobdellids, the bulb of the spermatheca, and particularly its ental part, may be distended to a greater or lesser extent so that in some, presumably younger animals, the spermatheca may appear to have an ental process. None of these variations seem to be correlated with the geographical distributions of the populations from which they come. No other variations were noted, except the usual differences in size and proportions that are dependent upon age and differing concentrations of fixatives.

AFFINITIES.—*Cambarincola olmecus,* as is true of *C. jamapaensis,* new species, is in many respects similar to species previously assigned to the Philadelphicus section of the genus; *C. jamapaensis,* then, may be its closest relative. *Cambarincola olmecus* is slightly larger; the prostate is longer and its ental bulb much more prominent; the bursa is pyriform rather than ovoid; and the spermathecal bulb is less obviously ovoid with a suggestion of an ental process. These two species are closely related and if further collecting were possible, it is conceivable that they could be shown to be local variants of the same species, yet, for now, the length of the prostate serves to sharply separate the two. *Cambarincola ingens* Hoffman, 1963, is similarly separated from *C. philadelphicus* (Leidy, 1851), and there is no doubt that they are distinct, though largely sympatric, species.

HOSTS.—*Procambarus aztecus, P. mexicanus, P. acutus cuevachicae.*

DISTRIBUTION.—*Cambarincola olmecus,* though not, apparently, a primitive member of the genus, at least among the Mesoamerican ones, is found

on both sides of the Cordillera Volcánica Transversal in the Northern Gulf Slope in San Luis Potosí and in the Southern Gulf Slope in Veracruz. It probably occurs, or has occurred, in the Interjacent Gulf Slope.

MATERIAL EXAMINED.—The type-series; over seventy specimens (PCH 1601) taken on *Procambarus mexicanus* at Ricon de la Doncella, Ciudad Mendoza, Veracruz, 18 May 1956; seven (PCH 1621, 1625) taken on *P. acutus cuevachicae* at Aquismón, km 419 de la carretera México-Valles, San Luis Potosí, 6, 7 April 1956.

Cambarincola smalleyi Holt, 1964

FIGURES 7, 11

Cambarincola smalleyi Holt, 1964:1.

TYPE-SPECIMENS.—Holotype (USNM 30940); one paratype (USNM 30941); one paratype in the collections of Tulane University (Dr. A. E. Smalley); one paratype (PCH 1702) taken on *Pseudothelphusa tumimanus* from Río Hondura, eight miles north of San Jeronimo de Moravia, San José Province, Costa Rica, by A. E. Smalley, 9 July 1962.

DIAGNOSIS (from Holt, 1964:1).—

Medium-sized members of the genus; head approximately equal in diameter to that of segment I and the sucker, showing external evidence of being composed of four segments; prosomites of body segments not appreciably greater in diameter than metasomites; jaws homodont and isomorphic, dental formula 6/6. Male reproductive system: the prostate about two-thirds the size of the spermiducal gland in length and diameter and histologically different [differentiated, with large vacuolated cells] from the latter, the prostate lacking an ental bulb; the spermiducal gland without deferent lobes; the bursa elongate pyriform in shape. Female reproductive system: spermatheca with a long ectal duct and an ental process.

AFFINITIES.—*Cambarincola smalleyi* and *C. toltecus,* new species, are the only Mesoamerican members of the genus with differentiated prostates, otherwise they differ in the raised dorsal ridges and the unusual spermatheca of the latter. The jaws are unusual and are most like those of *C. acudentatus,* new species. The latter, however, differs from *C. smalleyi* in the lack of an ental process of the spermatheca, in its nondifferentiated prostate and the presence of large deferent lobes of its spermatheca. Perhaps *C. nanognathus,* new species, the next southernmost branchiobdellid, is closest to *C.*

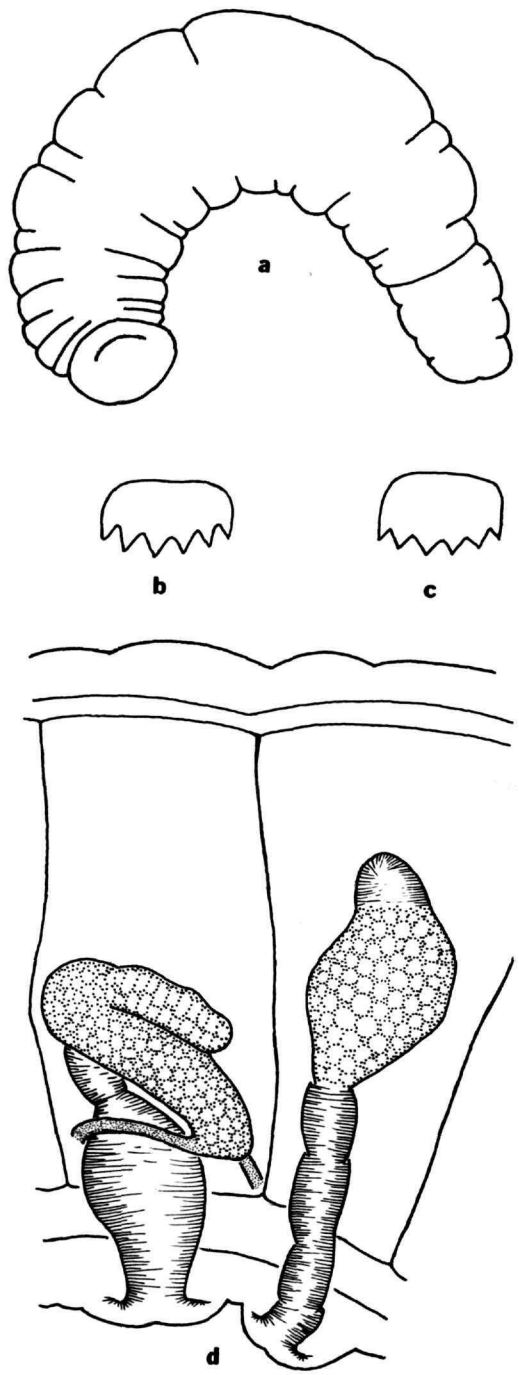

FIGURE 11.—*Cambarincola smalleyi: a,* holotype; *b,* dorsal jaw, paratype; *c,* ventral jaw, paratype; *d,* reproductive systems. (From Holt, 1964.)

smalleyi, but they differ in dental formulae and the nature of the prostate.

HOST.—*Pseudothelphusa tumimanus.*

DISTRIBUTION.—Known only from the type-locality.

REMARKS.—With the discovery of several other branchiobdellids, including *C. nanognathus,* new species, which has been taken from both crabs and crayfish in southern Mexico and Nicaragua, I cannot be as sure as I was when I said of *C. smalleyi* (Holt, 1964:3): "Yet cambarine crawfishes must have carried them to Costa Rica, lost in competition with tropical crabs, and passed their commensals to their conquerors." It is possible that the transferral of branchiobdellids to crabs occurred much farther north in Mexico, and that they were then carried (by crabs) in Mexico to Nicaragua and Costa Rica—beyond the southernmost regions ever reached by crayfish.

Cambarincola susanae, new species

FIGURES 12, 14

TYPE-SPECIMENS.—Holotype and two paratypes (USNM 45441), ten paratypes (PCH 1629), three paratypes, Instituto de Biología, Universidad de México, taken on *Procambarus acutus cuevachicae* at Cueva Chica, El Pujal, 3 km northeast of Valles, San Luis Potosí, Mexico, 9 May 1950.

DIAGNOSIS.—Small branchiobdellids (known

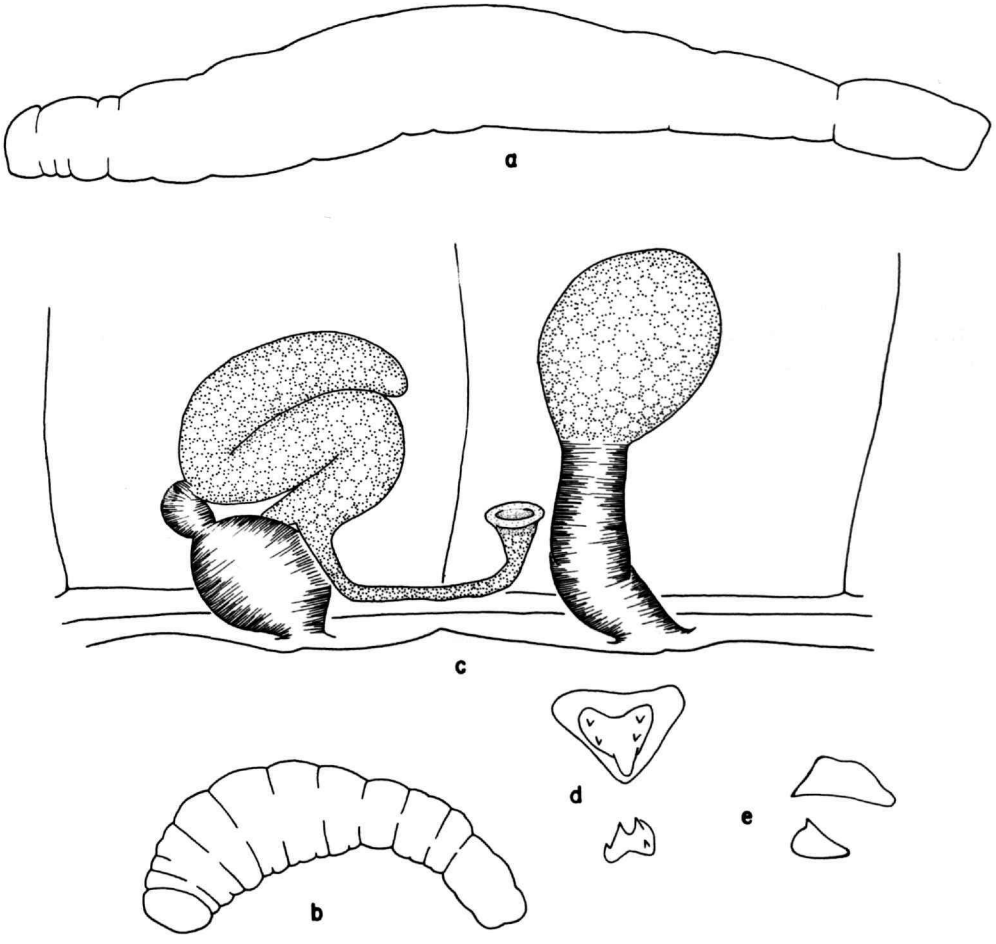

FIGURE 12.—*Cambarincola susanae,* new species: *a,* holotype; *b,* paratype (contracted); *c,* reproductive systems; *d,* obliquely *en face* view of jaws; *e,* lateral view of jaws.

specimens approximately 2 mm in length); body outline smooth (no raised dorsal ridges); upper jaw larger than lower (ratio of length to width in both upper and lower jaw approximately 5:3), dental formula 5/4; bursa small, spermiducal gland long, bent back upon itself, with small deferent lobes, prostate undifferentiated, ental end extending to bend of spermiducal gland, with small ental bulb; spermatheca with expanded bulb, no ental process.

ETYMOLOGY.—This species is named in honor of my daughter, Mrs. Susan E. H. West, who in her childhood was assiduous and courageous in assisting me in collecting branchiobdellids.

DESCRIPTION.—*Cambarincola susanae* is a small branchiobdellid. The holotype, greatly extended and selected for clarity with which its internal structures may be seen rather than for its typical proportions, has the following dimensions: total length, 3.2 mm; greatest diameter, segment VII, 0.4 mm; head length, 0.5 mm; head diameter, 0.25 mm; diameter, segment I, 0.2 mm; diameter, sucker, 0.25 mm. The average dimensions of the holotype and four other specimens, each from a different locality, with ranges given in parentheses, are as follows: total length, 2.3 mm (1.6–3.2 mm); greatest diameter, segment VII, 0.4 mm (0.3–0.5 mm); head length, 0.35 mm (0.25–0.5 mm); head diameter, 0.2 mm (0.2–0.3 mm); diameter, segment I, 0.2 mm (0.2–0.3 mm); diameter, sucker, 0.2 mm (0.2–0.3 mm). The usual proportions of the animals in a contracted state, as it would normally be collected, are illustrated in Figure 12*b*.

The dorsal lip is divided into four very short and broad lobes by shallow indentations; the lower lip is entire. There are no oral papillae. The peristomial sulcus is shallow. The body, smooth in outline, presents no unusual features.

The jaws are distinctive. The upper jaw, almost twice the length and width of the lower one, consists of a triangular tooth-bearing ridge set upon a larger base. The lower jaw is deeply concave on its free (internally facing) surface with a deep indentation or sulcus between the median teeth. Both jaws are distinctly brown, though not extremely dark. The dental formula is 5/4.

The deferent ducts expand slightly to form rather small deferent lobes before they unite to produce the spermiducal gland. The latter is long and bent back upon itself at its midlength. The prostate is approximately half the length of the spermiducal gland and ends entally in a small, often narrowed, ental bulb at the flexure of the spermiducal gland. It is not histologically distinct from the spermiducal gland; the cells of the glandular epithelium of both are finely granular throughout the length of both organs.

The ejaculatory duct is not remarkable. The bursa is short, almost spherical in shape, and approximately 1/4 the body diameter in length (0.1 mm).

The ectal duct of the spermatheca, curved around the gut in the holotype, is approximately 2/3 the body diameter in length. The bulb of the spermatheca is expanded, subspherical in shape, and lacks an ental process.

VARIATION.—There is considerable variability in size and proportions among the specimens that compose my material, ascribed to the various concentrations of the alcohol used in the collection and storage of the host crayfish. Many specimens are greatly extended and often badly macerated. No significant differences in the reproductive systems occur, except that the spermathecal bulb is cylindrical and unexpanded in some animals. There is some variability in the relative size of the jaws and among the specimens of a collection from the Río San Juan, Nuevo Leon (PCH 1606), the ratio of the anteroposterior length of the upper to the lower jaw varies from approximately 2:1 to 6:5.

AFFINITIES.—The jaws of *C. susanae* are most nearly like those of *C. heterognathus* Hoffman, but the latter is an Appalachian member of the Philadelphicus section of the genus with a short spermiducal gland and a very short and differentiated prostate; it is not likely that the two are closely related. *C. vitreus* Ellis has a long spermiducal gland that is bent back upon itself, as is that of *C. susanae,* but this inhabitant of the Mississippi Valley and the Coastal Plains of the United States is likewise a member of a group of species with a differentiated prostate and otherwise is unlike *C. susanae.* The relationships of *C. susanae* would appear, therefore, to lie with other members of the genus from Mesoamerica, from all of which, except for *C. ellisi,* new species, it is easily distinguished by the marked dissimilarity in the size of the upper and lower jaws and the length of the spermiducal gland.

HOSTS.—*Procambarus gonopodcristatus, P. acutus cuevachicae, P. simulans regiomontanus, P. llamasi.*

DISTRIBUTION.—*Cambarincola susanae* occurs in five states in Mexico, ranging from the Rio Grande drainage in Nuevo Leon (Río San Juan) to western Campeche in the Yucatan Peninsula and hence, in all of Hobbs' faunistic regions except the Central Plateau.

MATERIAL EXAMINED.—The type-series and 17 others (PCH 1629); one specimen (PCH 1627) taken on *Procambarus llamasi* at 10 km S of Escarcega, Campeche, 14 January 1953; 8 (PCH 1606) taken on *P. simulans regiomontanus* at San Juan, Río San Juan, Nuevo Leon, by Laura Treviño Rodríguez, 22 May 1960; 3 (PCH 1628) taken on *P. acutus cuevachicae* at El Ajenjibre, Mesa de San Diego, km 262 de la carretera México-Tuxpan, Puebla, 9 May 1950; 18 (PCH 1621) taken on *P. acutus cuevachicae* at Aquismón, km 419 de la carretera México-Valles, San Luis Potosí, 6 April 1956; 7 (PCH 1625) taken on *P. acutus cuevachicae* at 4 kms E Aquismón, San Luis Potosí, 7 April 1950; 16 (PCH 1604) taken on *P. gonopodocristatus* at Mana de Casse, Veracruz, 18 July 1957.

REMARKS.—*Cambarincola susanae* may be an inhabitant of the gill chamber of the hosts (the host animals were museum material and I did not examine the branchial chambers of any of them). The body wall is thin and delicate as in known inhabitants of the gill chambers and unlike, in this respect, most other branchiobdellids; the gut is often, though not always, filled with a homogeneous material that may be the blood of the host. Most gill-dwelling branchiobdellids probably are ectoparasites, feeding on the host's blood.

Cambarincola toltecus, new species

FIGURES 13, 14

TYPE-SPECIMENS.—Holotype (USNM 45436); two paratypes (USNM 45437); two paratypes, Instituto de Biología, Universidad National Autónoma de México; two paratypes (PCH 697); taken on *Pseudothelphusa veracruzana* from Río Tapalapa, Santiago, Tuxtla, Veracruz, Mexico, by A. Villalobos and H. H. Hobbs, Jr., 17 April 1957.

DIAGNOSIS.—Small to medium-sized branchiobdellids; major annulations of body segments greater in diameter than minor ones; jaws dark, dental formula 1/4, lateral teeth of lower jaws minute, obscure; bursa globose, small, approximately 1/7 body diameter in length, penial sheath approximately 1/2 bursal length; spermiducal gland without deferent lobes, approximately 1½ times bursa in length; prostate differentiated, subequal to spermiducal gland in diameter, 2/3 latter in length, with rudimentary prostatic bulb; spermathecal bulb with thickened wall, irregularly spatulate in shape.

ETYMOLOGY.—This species is named for the Toltecs, a people of presumably northern origin who invaded Mexico in earlier times.

DESCRIPTION.—*Cambarincola toltecus* is perhaps a little larger than most Mesoamerican members of the genus, but is small for the genus as a whole. The holotype has the following dimensions: total

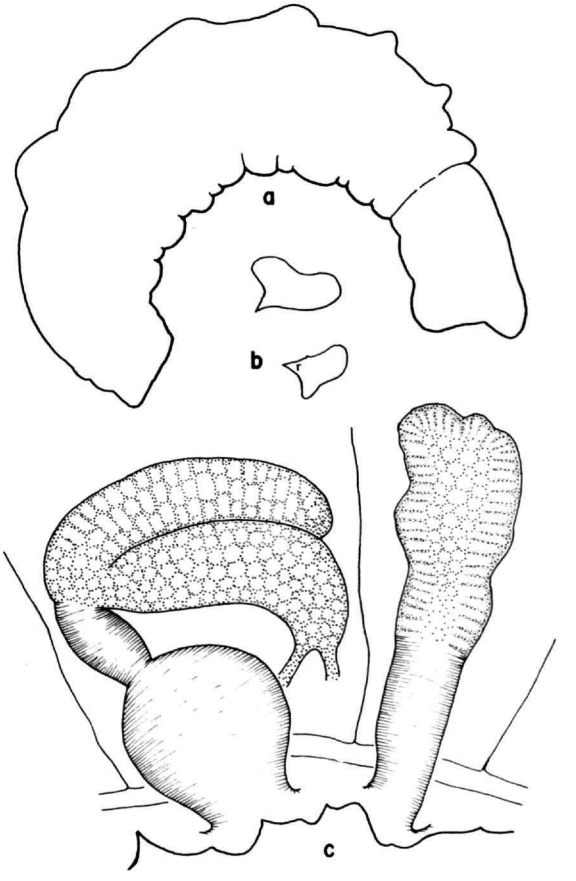

FIGURE 13.—*Cambarincola toltecus*, new species: *a*, holotype; *b*, lateral view of jaws; *c*, reproductive systems.

length, 2.7 mm; greatest diameter, 0.5 mm; head length, 0.5 mm; head diameter, 0.3 mm; diameter, segment I, 0.3 mm; diameter, sucker, 0.25 mm. The average dimensions of five specimens (the holotype and four paratypes), with ranges given in parentheses, are as follows: total length, 2.4 mm (2.1–2.7 mm); greatest diameter, 0.4 mm (0.4–0.5 mm); head length, 0.5 mm (0.4–0.5 mm); head diameter, 0.3 mm (0.25–0.3 mm); diameter, segment I, 0.3 mm (0.3–0.3 mm); diameter, sucker, 0.25 mm (0.2–0.25).

The dorsal lip always projects beyond the lower one and bears four blunt lobes; the lower lip has a shallow median emargination; the lateral emargination, which divides the peristomium into upper and lower lips, is broad and deep and often appears to contain a small lateral lobe. An indeterminate number of oral papillae are present. As usual, there is only one prominent internal pharyngeal sulcus, but externally the head shows no signs of segmentation.

The major annulations of most body segments are markedly greater in diameter than the minor ones which are indistinct. The anterior nephridiopore is difficult to detect in available material.

The jaws are subrectangular in lateral view. The upper is slightly the larger: the ratio of the length of the upper to the lower jaw is 5:4 in the holotype (54 to 43 microns). The upper jaw bears a single large tooth; the lower, two paramedian ones and often two minute indistinct lateral denticles. Both jaws are distinctly brown in color, but not unusually dark.

There are no deferent lobes of the spermiducal gland, which is about 1½ times the bursa in length and L-shaped with the short arm of the "L" ental and directed ventrad. The histology of the gland is indistinguishable from that of more northern and better known species of the Philadelphicus section of the genus. The same is true of the differentiated prostate which is about 2/3 the length of the spermiducal gland and subequal to it in length. There is apparently a rudimentary or small prostatic bulb present, which appears to be filled with a granular material in the holotype.

There are no notable features of the ejaculatory duct and bursa. The former is rather short and the later globose in shape with the penial sheath portion composing approximately half the organ.

The irregularly spatulate spermatheca extends almost to the dorsal border of the gut. The ectal duct composes about 1/3 of the organ; the bulb has a thickened wall that histologically resembles the ental processes of species which have them, but spermatozoa are present within the rather narrow lumen of the bulb to its ental end.

VARIATION.—There is some question about the presence of oral papillae; they can be seen in the holotype with difficulty, but not distinctly enough to count. In some other specimens they cannot be detected. My material is poorly preserved, though adequate for the diagnosis of the species. It is not macerated, but, rather, it has the appearance of having been preserved in methanol. The lower jaw often seems to bear minute lateral teeth, but these minute denticles can easily be overlooked and it is not at all certain that they occur in all specimens.

AFFINITIES.—*Cambarincola toltecus* has a closer relationship to members of the Philadelphicus section of the genus than do the other Mesoamerican members. Except for the structure of the prostatic bulb, the male reproductive system is much like that of *C. philadelphicus* (Leidy, 1851), as is the lobation of the peristomium. The raised annulations approach in their distinctness those of *C. fallax* Hoffman, 1963, and several other more northern species. *Cambarincola toltecus,* however, differs from these species in its dental formula and particularly in the peculiarities of its spermatheca. None of the known members of the Philadelphicus section have spermathecae with thickened bulbular walls or spermathecal ental processes. Among the Mesoamerican species of the genus, *C. smalleyi* Holt has a differentiated prostate, but lacks the raised major annulations, while *C. olmecus,* new species, and *C. jamapaensis,* new species, have them; all differ in details of the spermatheca and jaws. *Cambarincola toltecus,* along with *C. olmecus* and *C. jamapaensis,* appear to form a group of southern, and presumably more primitive, relatives of the northern Philadelphicus section.

HOSTS.—*Procambarus ruthveni zapoapensis, Pseudothelphusa veracruzana.*

DISTRIBUTION.—The type-locality and Arroyo de Zapoapan de Cabaña, Veracruz, Mexico. Both localities are in the Southern Gulf Slope region in the tropical lowlands of Veracruz.

MATERIAL EXAMINED.—The type-series and four-

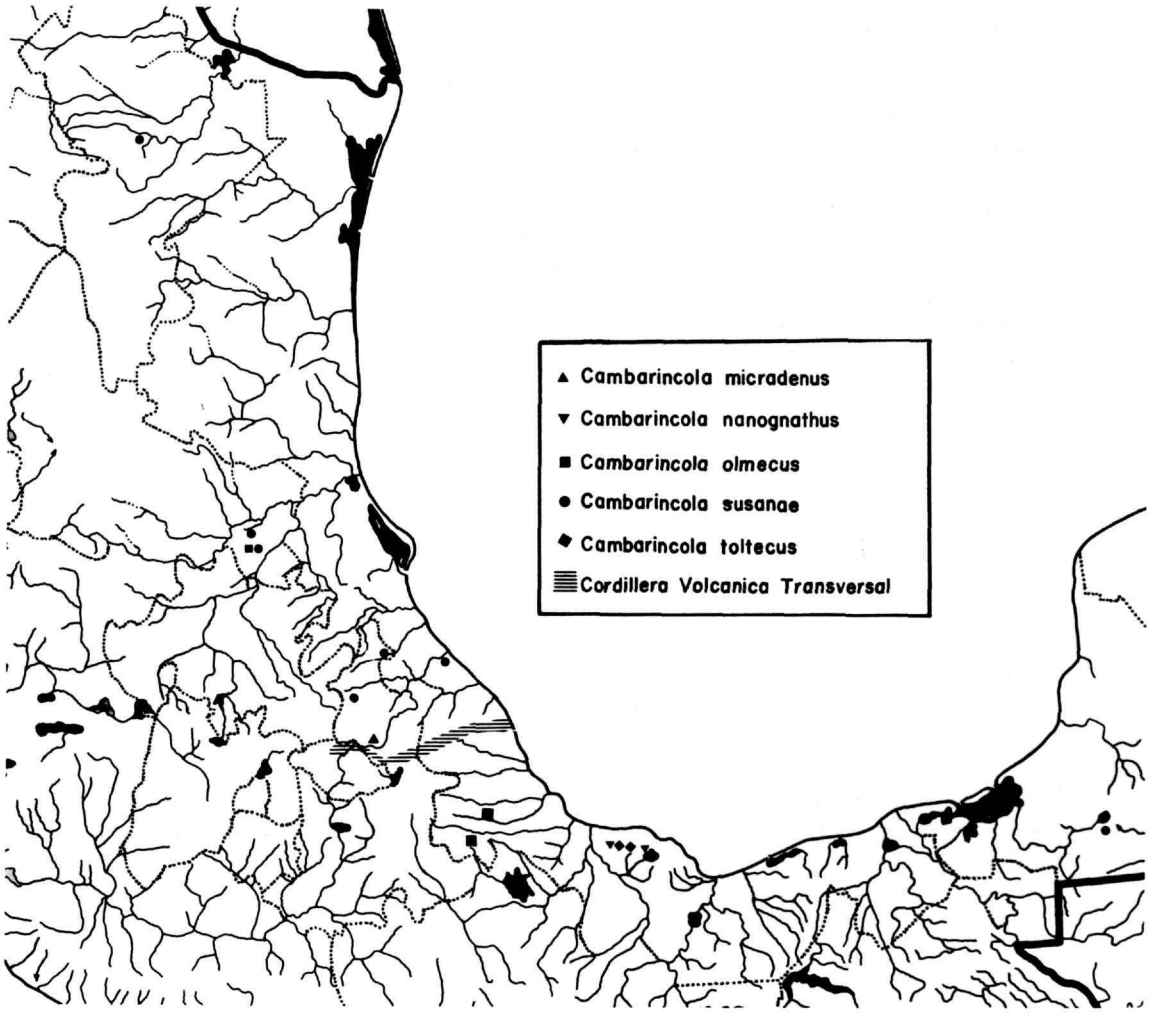

FIGURE 14.—Distribution of five Mexican members of the genus *Cambarincola*.

teen others (PCH 697); fifteen specimens (PCH 700); taken on *Procambarus ruthveni zapoapensis* and *Pseudothelphusa veracruzana* from Arroyo de Cabaña, Veracruz, Mexico.

Genus *Pterodrilus* Moore, 1895

Pterodrilus Moore, 1895a:449.—Holt, 1968c:1

DIAGNOSIS (from Holt, 1968c:3).—

Small branchiobdellids (known forms less than 2.0 mm in length) of delicate appearance; cylindrical; prosomite of segment VIII always with elevated dorsal ridge, those of other segments often so, dorsal ridges often bearing fan- or finger-like projections; jaws delicate, light in color or colorless, triangular in shape, dental formula 5/4; prostate present, incompletely divided from spermiducal gland; bursa ovoid to pyriform, penis sheath short, penis non-eversible; spermatheca with long ectal duct, bulb clavate or spatulate; anterior nephridia open by common dorsal pore on segment III.

TYPE-SPECIES.—*Pterodrilus alcicornus* Moore, 1895a:449–450, by subsequent designation (Goodnight, 1940:58).

Pterodrilus mexicanus Ellis, 1919

FIGURE 15

Pterodrilus mexicanus Ellis, 1919:254.—Goodnight, 1940:63.—Causey, 1955:44.—Holt, 1968c:15.

TYPE-SPECIMEN.—Holotype (USNM 17654), taken on *Procambarus mexicanus* at Mirador, Mexico, by Nelson and Goldman (date unknown).

DIAGNOSIS (from Holt, 1968c:15).—"Dorsal ridge on segment VIII, typically bearing four conical projections, remainder of segments without ridges; bursa large, elongate, length exceeding 1/2 body diameter; ejaculatory duct short; prostate about 1/2 diameter of and subequal in length to spermiducal gland, undifferentiated; spermatheca shorter than body diameter, bulb thick-walled."

HOSTS.—*Procambarus mexicanus* in Mexico (Ellis, 1919) and eight species of *Orconectes* Cope, 1872, in the Ozark plateau region of Arkansas, Oklahoma and Missouri (Holt, 1968c:16).

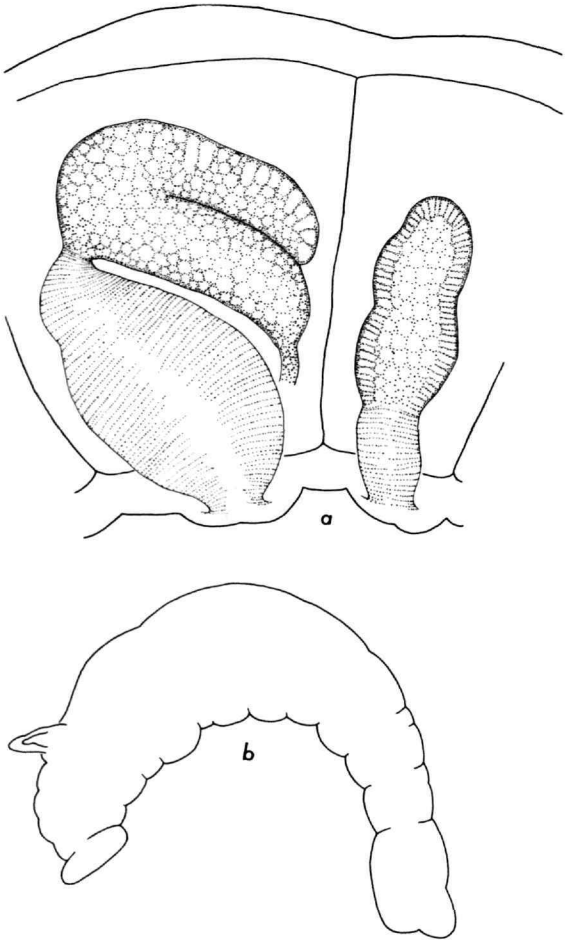

FIGURE 15.—*Pterodrilus mexicanus*: *a*, reproductive systems; *b*, animal from Wayne County, Missouri. (From Holt, 1968c.)

REMARKS.—The genus *Pterodrilus* has been revised recently (Holt, 1968c). The status of *P. mexicanus*, based upon a unique specimen, was discussed in this revision and approximately 100 specimens from Arkansas, Missouri, and Oklahoma were assigned to it (Holt, 1968c:15–18). The holotype has four prongs borne on a single dorsal ridge on segment VIII, as do the Ozarkian animals. I could not locate Mirador while in Mexico; all attempts to collect near the suspected locality from which Ellis' specimen came failed. Of the hundreds of specimens from Mexico that I have seen, not any could possibly be considered as a member of the genus *Pterodrilus*. Whether or not *P. mexicanus*, or a very similar species (since the number and arrangement of the "dorsal appendages" of *Pterodrilus* show little intraspecific variability), exists or once existed in Mexico probably may never be known. If *P. mexicanus* or a similar form did or does exist in Mexico, the probability is great that it was there in pre-Pliocene times (cf Hobbs, 1971: 10–12). The genus *Pterodrilus* is believed to be derived from some early cambarincoloid stock (Holt, 1968c:4–5) and there are relatively advanced species of *Cambarincola* south of the Cordillera Volcánico Transversal.

Genus *Sathodrilus* Holt, 1968

Sathodrilus Holt, 1968b:294.

DIAGNOSIS (emended from Holt, 1968b:294).—Medium-sized worms (known species 1.6–4.6 mm in length) with two pairs of testes; unpaired nephridiopore on dorsum of segment III; body terete, without peristomial tentacles or dorsal projections on trunk segments, though dorsal ridges may be present; spermiducal gland with vasa deferentia entering entally; prostate ranging from absent through bulb-like prostatic protuberance to large one that arises considerably entally to junction of spermiducal gland with ejaculatory duct; ejaculatory duct present; penis eversible, but attached by cytoplasmic strands to inner wall of penial sheath, without cuticular hooks; spermatheca with or without ental process.

TYPE-SPECIES.—*Sathodrilus carolinensis* by original designation (Holt, 1968b:294).

RANGE.—From the southeastern borders of the Appalachian uplift in South Carolina and Georgia

Key to the Mesoamerican Species of the Genus *Sathodrilus*

1. Spermiducal gland with prostatic protuberance or prostate 2
   Spermiducal gland without prostatic protuberance or prostate ..... *S. veracruzicus*
2. Spermiducal gland with prostatic protuberance ..... *S. villalobosi*
   Prostate present ..... *S. prostates*, new species

to the Interjacent and Southern Slope faunistic regions of Mexico. This range is discontinuous; representatives of the genus are not known to occur between northwestern Georgia and northern San Luis Potosí.

Sathodrilus prostates, new species

FIGURES 16, 19

TYPE-SPECIMENS.—Holotype (USNM 4532), on *Procambarus acutus cuevachicae* taken at El Ajenjibre, Messa de San Diego, km 262 de la carretera México–Tuxpan, Puebla, Mexico, by A. Villalobos and H. H. Hobbs, Jr., 12 April 1957; two paratypes (USNM 45432), on *Pseudothelphusa veracruzana* taken at Rio Tapalapa, Veracruz, Mexico, by A. Villalobos and H. H. Hobbs, Jr.; one paratype (USNM 45433), on *Procambarus ruthveni zapoapensis* at Arroyo de Zapoapan de Cabaña, Veracruz, Mexico; one paratype, Instituto de Biología, Universidad de México, from the latter locality; seven paratypes (PCH 700), from the latter locality.

DIAGNOSIS.—Small branchiobdellids, average length about 1.8 mm; body outline smooth except for raised major annulation of segment VIII; jaws small, light in color, dental formula 5/4; bursa large, somewhat more than 1/2 body diameter in length, penial sheath about 2/5 bursal length, penis eversible; spermiducal gland subequal to bursa in length, 3/10 its length in diameter, with prominent anterior deferent lobe; prostate present, arising approximately at junction of ectal and median thirds of spermiducal gland, subequal in diameter to latter, undifferentiated, with small prostatic bulb; spermatheca with ectal spermathecal bursa, short ectal duct, wall of spermathecal bulb glandular, ental process prominent and glandular.

ETYMOLOGY.—From Greek *prostates* (one who stands before) in reference both to the presence of a prostate gland in this species and its possible phylogenetic position as a remnant of the sathodriloid stock that gave rise to the genus *Cambarincola* and its relatives.

DESCRIPTION.—*Sathodrilus prostates* is a small worm, exceeded in size by all known members of the genus except *S. veracruzicus*. The holotype has the following dimensions: total length, 2.0 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 of the paratypes chosen randomly, with ranges given in parentheses, are as follows: total length, 1.8 mm (1.1–2.0 mm); greatest diameter, 0.3 mm (0.25–0.4 mm); head length, 0.3 mm (0.25–0.4 mm); head diameter, 0.2 mm (0.15–0.2 mm); diameter, segment I, 0.2 mm (0.2–0.2 mm); diameter, sucker, 0.2 mm (0.15–0.2 mm).

Lobes, if present, of the lips are obscurely delimited. Oral papillae are present. The peristomial sulcus is present, but there is no other external sign of segmentation of the head and internally only one pharyngeal sulcus. The body is smooth in outline, except in some specimens where the intersegmental furrows are strongly marked and a prominently raised ridge is present on the major annulation of segment VIII.

The jaws, light brown in color and with a dental formula of 5/4, are unremarkable.

The anterior deferent duct enters the spermiducal gland ventral to and at some distance from the point of entry of the posterior deferent duct producing an anterior deferent lobe (Hoffman, 1963:287). The spermiducal gland is approximately 1/2 the body diameter in length and about 2/5 its own length in diameter. A large prostate arises from the spermiducal gland near the ectal 1/3 of the latter and terminates in a small narrowed bulb near the ectal part of the anterior deferent lobe. It is histologically similar to the spermiducal gland.

The ejaculatory duct is relatively long and frequently curves dorsally over the gut in its course from the spermiducal gland to the bursa, but otherwise presents no unusual features.

The bursa, which is large (more than 1/2 the

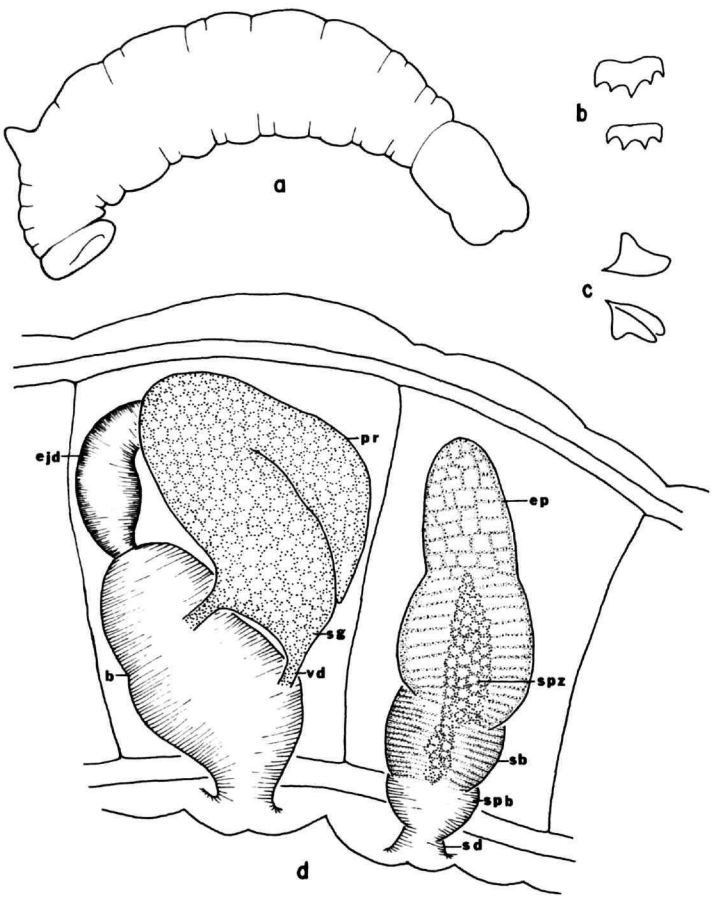

FIGURE 16.—*Sathodrilus prostates*, new species: *a*, holotype; *b*, *en face* view of jaws (from PCH 700 = USNM 45433); *c*, lateral view of jaws; *d*, reproductive systems [b=bursa; ejd=ejaculatory duct; ep=ental process of spermatheca; pr=prostate; sb=bulb of spermatheca; sd=spermathecal duct; spb=spermathecal bursa; spz=spermatozoa; sg=spermiducal gland; vd=vas deferens].

body diameter in length and usually inclined posteriorad in the segment) is composed of a large penial sheath region which encloses what appears (in the limited available material) to be an eversible penis connected along its length by strands of muscle to the muscular wall of the penial sheath. An atrial fold is present at the inner portion of the bursal atrium.

The spermatheca is composed of four distinct regions. Ectally a very short duct leads into a muscular walled enlargement of a type previously designated as a spermathecal bursa (Holt, 1960a:64), which is lined with cuticle and is essentially spherical in shape. The spermathecal bursa leads entally into another subspherical portion, which is not lined with cuticle, but which has strands of presumably glandular cells projecting inward from its walls. This appears to be the main sperm storage portion of the organ and is, hence, the spermathecal bulb. A large portion of the spermatheca follows entally with glandular cells projecting into its lumen and, in some specimens, with a few (?)

spermatozoa stored within. The ental end of the spermatheca consists of a narrowed ental process, composed of large granulated glandular cells, but lacks an obvious lumen.

VARIATION.—All my specimens are mounted entire. Apparent differences among them are best accounted for by the degree of extension and contraction of the animals at death, their overall sizes, and the relative positions of the reproductive organs. After several false starts, it became obvious that they all conform, except for differences in size and stage of maturity, to the description of the holotype. In addition, though always present, the distinctness of the raised annulation on segment VIII may be obscured in greatly extended and younger specimens; also, the lateral teeth of the jaws may be difficult to see. In only a few specimens have spermatozoa been detected in the third (unnamed, but presumably outer part of the ental process) portion of the spermatheca. Therefore, although I am not sure of their presence in the holotype, they are indicated in that position in Figure 16*d*. There can be no doubt as to the conspecificity of the material I have assigned to this somewhat unusual species.

AFFINITIES.—It is with considerable reluctance that I assign this species, with its obvious similarities to members of several other genera, to the genus *Sathodrilus*. I have discussed the relationships of these genera previously (Holt, 1968b:294–295) and herein I need only refer to some of the peculiarities of *S. prostates*. In body form, particularly in the raised major annulation of segment VIII, *S. prostates* resembles certain species of *Pterodrilus*, notably *P. choritonamus* Holt (1968c:26–28). The only reason for not including *prostates* in *Pterodrilus* as a close relative of *P. choritonamus* is the eversible penis of the former. They differ otherwise chiefly in the more elaborate differentiations of the spermatheca of *S. prostates*. The genera *Sathodrilus, Magmatodrilus,* and *Ceratodrilus* form a remarkably similar group of animals and now (with the discovery of *S. prostates*) are most clearly separated by features of body ornamentation, jaw structure, and geographical isolation (cf. Holt, 1960a, b, 1967, 1968b, 1969:197–198). Figure 2 (in Holt, 1969:196) illustrating the relationships of branchiobdellid genera reflects greater phyletic distances between these genera and the others of the *Sathodrilus* lineage than objectively exists. The problem is confounded by the apparent parallelism in such structures as peristomial projections, raised annulations of body segments, some of which bear finger- or fan-like projections, the degree of development of the prostate, and wide ranges in body size. *Sathodrilus prostates* must, therefore, on the basis of our present knowledge be considered as close to, or representative of the stock that, perhaps almost simultaneously, gave rise to the genera *Ceratodrilus, Magmatodrilus, Tettodrilus, Pterodrilus,* and *Cambarincola,* with *Oedipodrilus* and *Ellisodrilus* regarded as composed of more specialized groups of derivative species.

Within the genus *Sathodrilus, S. prostates* is closer to *S. carolinensis* in features of the bursa, penis, and rudimentary prostatic bulb, but in the differentiated nature of the spermatheca *S. prostates* is closer to *S. megadenus*. Both *S. carolinensis* and *S. megadenus* are from the piedmont regions at or near the southern borders of the Appalachians. Among the apparently more distantly related Mexican members of the genus, *S. villalobosi* possesses a prostatic protuberance, but the penis has evolved towards the condition found among the species of *Oedipodrilus,* as has that of *S. veracruzicus* which, however, entirely lacks any rudiment of a prostate. None of the other species of *Sathodrilus* have prominently raised major annulations of the body segments (the first three segments of *S. megadenus* have slightly raised major annulations), so the raised annulation of segment VIII of *S. prostates* is distinctive. Except for *S. villalobosi*, which has heavy and dark jaws and presumably a dental formula of 1/4, the jaws and dental formulae of the species of *Sathodrilus* are remarkably similar to each other and to those of *Pterodrilus* and many species of *Cambarincola*.

HOSTS.—*Procambarus acutus cuevachicae, P. hoffmanni, P. ruthveni zapoapensis, Pseudothelphusa veracruzana.*

DISTRIBUTION.—From the lower slopes of the Sierra Madre Oriental in Puebla, the Interjacent Gulf Slope, to the lowlands of Veracruz south of the Cordillera Volcánica Transversal, the Southern Gulf Slope. *S. prostates* is one of the species that is found on both sides of the barrier produced by the Cordillera Volcánica Transversal, though so far to the south of the barrier only in streams

that drain the flanks of the volcanic mountain, San Martin, which stands on the coastal plain.

MATERIAL EXAMINED.—The type-series; several specimens (PCH 702) taken on *Procambarus hoffmanni* at Mi Ranchito, Villa Juárez, Puebla, Mexico, 4 April 1957.

Sathodrilus veracruzicus Holt, 1968

FIGURES 17, 19

Sathodrilus veracruzicus Holt, 1968b:305.

TYPE-SPECIMENS.—Holotype (USNM 37105); six paratypes (USNM 37106 and 45440), taken on *Procambarus hoffmanni* at Coyutla, Veracruz, Mexico, 16 April 1949.

DIAGNOSIS (from Holt, 1968b:305).—

Small, slender, terete worms; lips entire; dental formula 5/4; bursa long, exceeding body diameter in length, penial sheath about 3/4 total length, less in diameter than bursal atrium; eversible penis with thickened wall attached by few strands to penial sheath; ejaculatory duct short, about 1/3 length of spermiducal gland; spermiducal gland small, about 1/3 as long as bursa; no prostatic protuberance; spermatheca long, spermathecal duct subequal to body diameter in length, bulb cylindrical, long, no ental process.

AFFINITIES.—See *Sathodrilus prostates*.

HOSTS.—*Procambarus contrerasi, P. hoffmanni, P. riojai*.

DISTRIBUTION.—*Sathodrilus veracruzicus* is known from the states of Puebla and Veracruz in the Interjacent Gulf Slope region.

Sathodrilus villalobosi Holt, 1968

FIGURES 18, 19

Sathodrilus villalobosi Holt, 1968b:299.

TYPE-SPECIMENS.—Holotype (USNM 37101), four paratypes (USNM 37102), and four paratypes (PCH 208), taken on *Paracambarus paradoxus* at Tetela de Ocampo, 35 km NE of Zacapoaxtla, Puebla, Mexico, May 1944 (erroneously recorded as May 1941 in Holt, 1968b:299).

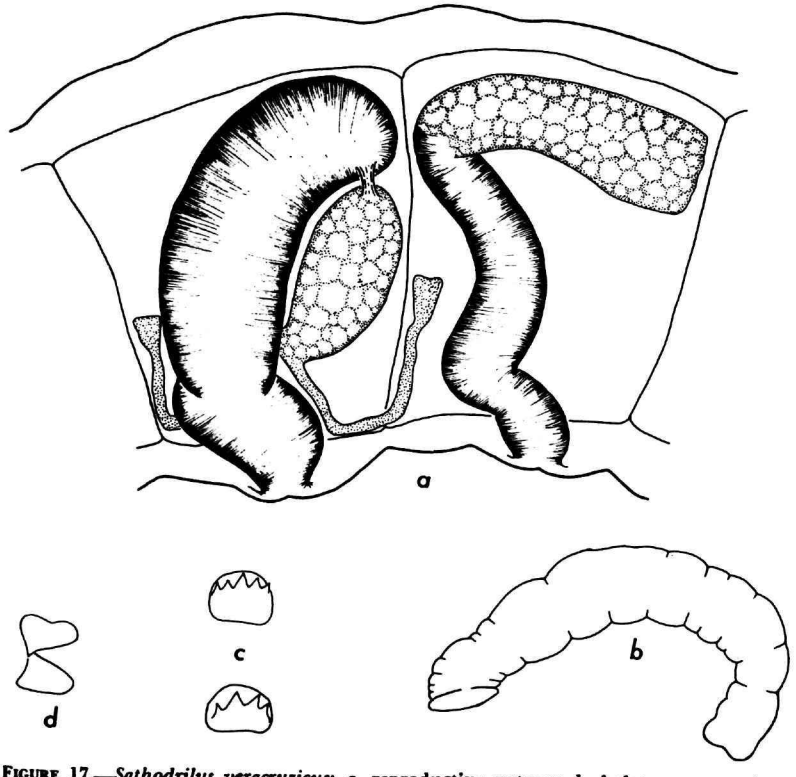

FIGURE 17.—*Sathodrilus veracruzicus*: *a*, reproductive systems; *b*, holotype; *c*, *en face* view of jaws; *d*, lateral view of jaws. (From Holt, 1968b.)

DIAGNOSIS (emended from Holt, 1968b:299).—Medium-sized, terete branchiobdellids; upper lip entire, lower with shallow median indentation; jaws heavy, dark, dental formula 1/4 or 5/4; bursa large, subequal to body diameter in length, bursal atrium less than 1/3 total bursal length; eversible penis composed of tube attached by few strands to inner wall of penial sheath; ejaculatory duct short, about 1/2 length of spermiducal gland; length of spermiducal gland about twice its diameter, about 1/3 that of bursa, tapering toward each end from prostatic protuberance, without deferent lobes; spermatheca with long narrow ectal duct, bulb globose.

AFFINITIES.—See *Sathodrilus prostates.*

HOSTS.—*Paracambarus paradoxus, Procambarus contrerasi, P. erichsoni, P. riojai.*

DISTRIBUTION.—*Sathodrilus villalobosi* is known from the states of Hidalgo and Puebla in the Interjacent Gulf Slope region of Mexico.

REMARKS.—A contradiction appears in my original treatment of this species. In the diagnosis (Holt, 1968b:299) it is said that *S. villalobosi* lacks oral papillae; in the discussion of the affinities of the

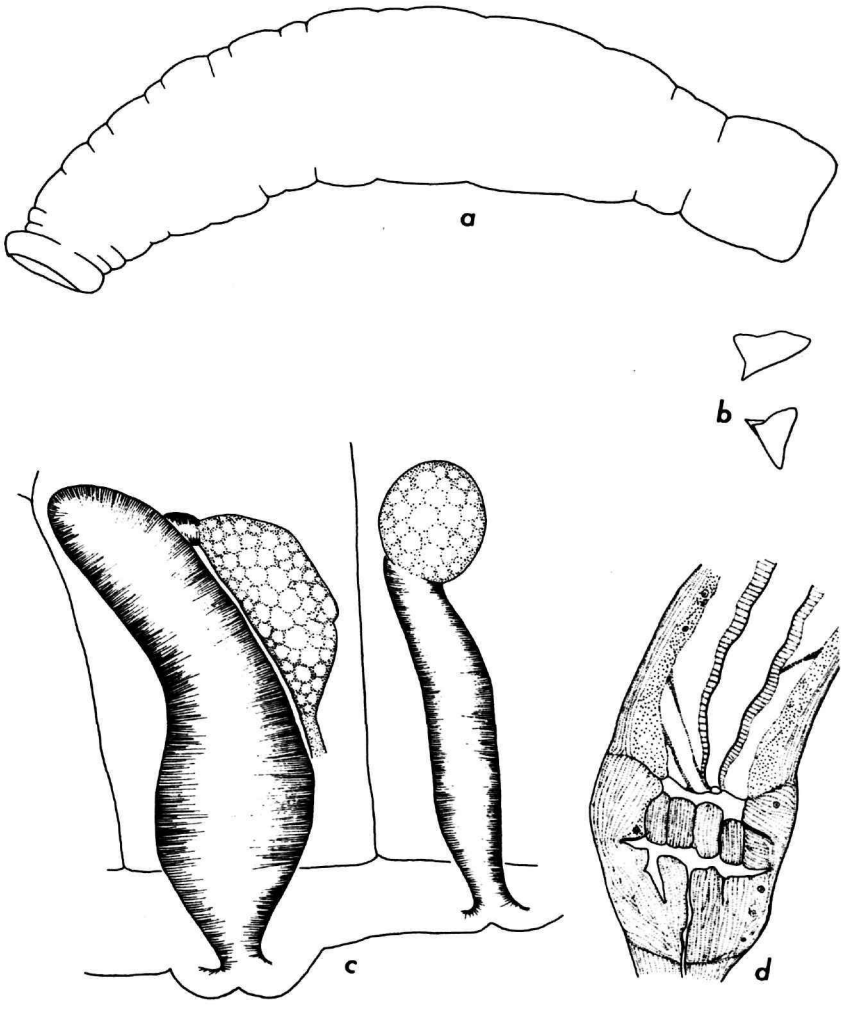

FIGURE 18.—*Sathodrilus villalobosi*: *a*, holotype; *b*, jaws; *c*, reproductive systems; *d*, longitudinal section of ectal part of penis and bursa. (From Holt, 1968b.)

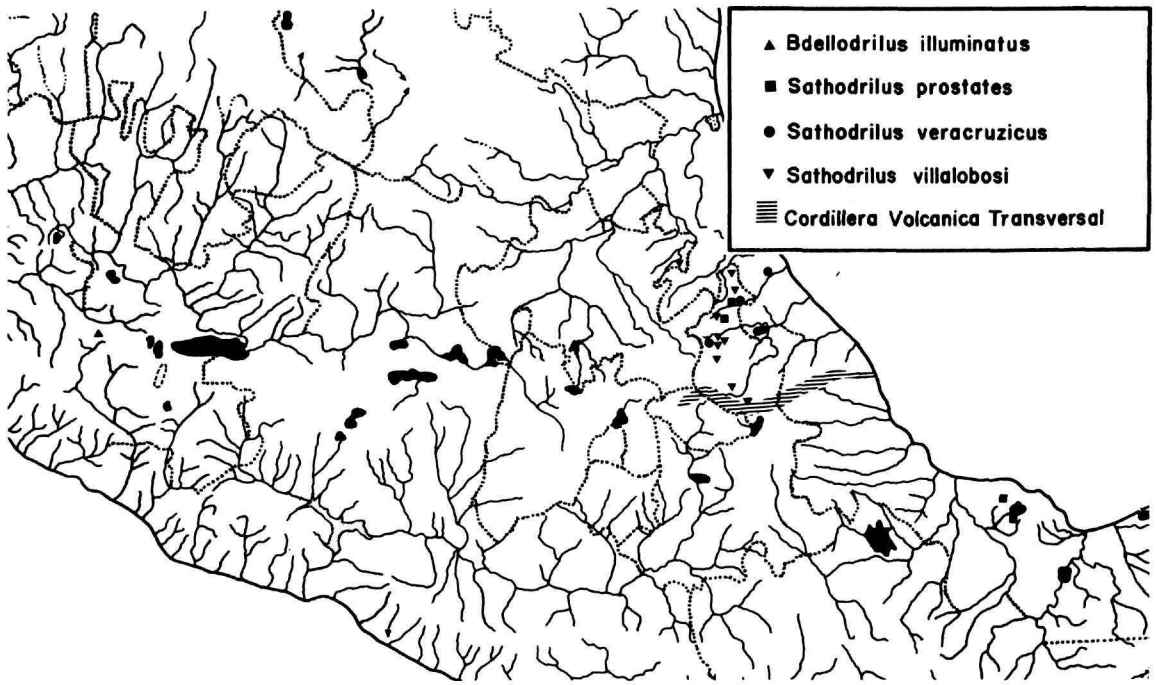

FIGURE 19.—Distribution of four species of Mexican branchiobdellids.

species then known (Holt, 1968b:307) it is said that *S. villalobosi* and *S. veracruzicus* possess such papillae. The paratypes, somewhat overcontracted, do not appear to have oral papillae. The much better preserved material from Aqua Fria (PCH 1593), collected by me and my field companions, have oral papillae. It is likely that these structures are often impossible to see in specimens that are overly contracted or poorly preserved and it is not known whether there is intraspecific variability in the presence or absence of them or whether or not they are of any real taxonomic value.

The dental formula is also apparently more variable than the original description would indicate (Holt, 1968b:301). In some, presumably younger specimens, the dental formula is 5/4, but the lateral teeth are small and perhaps wear away with age.

Literature Cited

Berry, James W., and Perry C. Holt
1959. Reactions of Two Species of Branchiobdellidae (Oligochaeta) to High Temperatures and Low Oxygen Tensions. *Virginia Agricultural Experiment Station, Virginia Polytechnic Institute, Technical Bulletin,* 141:1–11, figures 1–3.

Bishop, John E.
1968. An Ecological Study of the Branchiobdellid Commensals (Annelida—Branchiobdellidae) of Some Mid-western Ontario Crayfish. *Canadian Journal of Zoology,* 46:835–843, figure 1, tables 1–3.

Blackford, Susan
1966. A Study of Certain Aspects of the Ecology and Morphology of Branchiobdellid Annelids Epizoic on *Callinectes sapidus.* Unpublished honors thesis, Newcomb College, Tulane University, 34 pages, figures 1–3.

Brown, George G.
1961. Some Ecological Studies of the Branchiobdellidae Found in Sinking Creek, Giles County, Virginia. Unpublished masters thesis, Virginia Polytechnic Institute, 67 pages, figures 1–5.

Causey, David
1955. Branchiobdellidae in Arkansas. *Proceedings, Arkansas Academy of Science,* 7:43–46, figures 1–4.

Ellis, Max M.
1912. A New Discodrilid Worm from Colorado. *Proceedings of the United States National Museum,* 42 (1912):481–486, figures 1–5.
1918. Branchiobdellid Worms (Annelida) from Michigan Crawfishes. *Transactions of the American Microscopical Society,* 37 (1) :49–51.

1919. The Branchiobdellid Worms in the Collections of the United States National Museum, with Descriptions of New Genera and New Species. *Proceedings of the United States National Museum,* 55 (2267): 241–265, figures 1–18, plates 10–13.

Goodnight, Clarence J.

1940. The Branchiobdellidae (Oligochaeta) of North American Crayfishes. *Illinois Biological Monographs,* 17 (3) :1–75, plates 1–3.

1941. The Branchiobdellidae (Oligochaeta) of Florida. *Transactions of the American Microscopical Society,* 60 (1) 69–74, figures 1–4.

1943. Report on a Collection of Branchiobdellids. *The Journal of Parasitology,* 29 (2) :100–102, figures 1–5.

Hall, Maurice C.

1914. Description of a New Genus and Species of the Discodrilid Worms. *Proceedings of the United States National Museum,* 48 (2071) :187–193, figures 1–3.

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

1969. Evolutionary Trends in the Ostracod Family Entocytheridae, with Notes on the Distributional Patterns in the Southern Appalachians. In Perry C. Holt, editor, The Distributional History of the Biota of the Southern Appalachians, Part I: Invertebrates. *Virginia Polytechnic Institute, Research Division Monograph,* 1:179–190, figures 1–21.

Hobbs, Horton H., Jr.

1971. The Entochytherid Ostracods of Mexico and Cuba. *Smithsonian Contributions to Zoology,* 81:1–55, figures 1–31.

Hobbs, Horton H., Jr., Perry C. Holt, and Margaret Walton

1967. The Crayfishes and their Epizoötic Ostracod and Branchiobdellid Associates of the Mountain Lake, Virginia, Region. *Proceedings of the United States National Museum,* 123 (3602) :1–84, figures 1–22.

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

1958. The Exoskeleton of a Freshwater Crab as a Microhabitat of Several Invertebrates. *Virginia Journal of Science,* new series, 9 (4) :395–396.

Hoffman, Richard L.

1963. A Revision of the North American Annelid Worms of the Genus *Cambarincola* (Oligochaeta: Branchiobdellidae). *Proceedings of the United States National Museum,* 114 (3470) :271–371, figures 1–79.

Holt, Perry C.

1949. A Comparative Study of the Reproductive Systems of *Xironogiton instabilius instabilius* (Moore) and *Cambarincola philadelphica* (Leidy) (Annelida, Oligochaeta, Branchiobdellidae). *Journal of Morphology,* 84 (3) :535–572, plates 1–4.

1953. Characters of Systematic Importance in the Family Branchiobdellidae (Oligochaeta). *Virginia Journal of Science,* new series, 4 (2) :57–61.

1960a. The Genus *Catatodrilus* Hall (Branchiobdellidae Oligochaeta) with the Description of a New Species. *The Virginia Journal of Science,* new series, 11 (2): 53–77, plates 1–4.

1960b. On a New Genus of the Family Branchiobdellidae (Oligochaeta). *The American Midland Naturalist,* 64 (1) :169–176, figures 1–7.

1963. A New Branchiobdellid (Branchiobdellidae: *Cambarincola*). *Journal of the Tennessee Academy of Science,* 38 (3) :97–100, figures 1–2.

1964. A New Branchiobdellid (Annelida) from Costa Rica. *Tulane Studies in Zoology,* 12 (1) :1–4, figures 1–4.

1965. The Systematic Position of the Branchiobdellidae (Annelida: Clitellata). *Systematic Zoology,* 14 (1): 25–32, figures 1–3.

1967. The Status of the Genera *Branchiobdella* and *Stephanodrilus* in North America with Description of a New Genus (Clitellata: Branchiobdellida). *Proceedings of the United States National Museum,* 124 (3631) :1–10, figures 1–4.

1968a. The Branchiobdellida: Epizoötic Annelids. *The Biologist,* 50 (3–4) :79–94, figures 1–2.

1968b. New Genera and Species of Branchiobdellid Worms (Annelida: Clitellata). *Proceedings of the Biological Society of Washington,* 81:291–318, figures 1–9.

1968c. The Genus *Pterodrilus* (Annelida: Branchiobdellida). *Proceedings of the United States National Museum,* 125 (3668) :1–44, figures 1–12.

1969. The Relationships of the Branchiobdellid Fauna of the Southern Appalachians. *In* Perry C. Holt, editor, The Distributional History of the Biota of the Southern Appalachians, Part 1: Invertebrates. *Virginia Polytechnic Institute, Research Division Monograph,* 1:191–219, figures 1–10.

Holt, Perry C., and Richard L. Hoffman

1959. An Emended Description of *Cambarincola macrodonta* Ellis, with Remarks on the Diagnostic Characters of the Genus (Oligochaeta: Branchiobdellidae). *Journal of the Tennessee Academy of Science,* 34 (2) :97–104, figures 1–6.

Leidy, Joseph

1851. Contributions to Helminthology. *Proceedings of the Academy of Natural Science of Philadelphia,* 5:205–209.

Ludwig, Hubert

1886. Pages 782–783, in Johannes Lennis, *Synopsis der drei Naturreiche.* Hanover.

McManus, Lawrence R.

1960. Some Ecological Studies of the Branchiobdellidae (Oligochaeta). *Transactions of the American Microscopical Society,* 79 (4) :420–428.

Martin, Paul S., and Byron E. Harrell

1957. The Pleistocene History of Temperate Biotas in Mexico and Eastern United States. *Ecology,* 38 (3) : 468–480, figures 1–15.

Moore, J. Percy

1894. On Some Leech-like Parasites of American Crayfishes. *Proceedings of the Academy of Natural Sciences of Philadelphia,* 1893:419–428, plate 12.

1895a. *Pterodrilus,* A Remarkable Discodrilid. *Academy of Natural Sciences of Philadelphia,* 1895, (part 3): 449–454.

1895b. The Anatomy of *Bdellodrilus illuminatus,* an American Discodrilid. *Journal of Morphology,* 10 (2): 497–540, plates 28–32.

1897. On the Structure of the Discodrilid Nephridium. *Journal of Morphology,* 22 (1) :327–380, figures 1–49.

Odier, Auguste

1823. Memoire sur le Branchiobdelle, Nouveau Genre d'Annelides de la Famille de Hirudinees. *Mémoires de la Société d'Histoire Naturelle de Paris,* 1:71–78, plate 4.

Pierantoni, Umberto

1912. Monografia dei Discodrilidae. *Annuario del Museo Zoologico (R. Universita) Napoli,* new series, 3 (24) :1–28, figures 1–20, plate 5.

Rioja, Enrique

1940. Datos sobre los Branchiobdellidae de Xochimilco, Zempoala y Texcoco. *Sobretiro de los Anales del Instituto de Biología,* 11 (1) :249–253, figures 1–4.

1943. Anotaciones sobre Branquiobdeliodos Mexicanos. *Sobretiro de los Anales del Instituto de Biología,* 14 (2) :541–546.

Stephenson, J.

1930. *The Oligochaeta.* 978 pages, 242 figures. Oxford: Oxford University Press.

Vejdovsky, Franz

1884. *System und Morphologie der Oligochaeten.* 166 pages, 14 plates. Prague: F. Řivnáč.

Yamaguchi, Hideji

1933. Description of a New Branchiobdellid *Cambarincola okadai,* n. sp., Parasitic on American Crayfish Transferred into a Japanese Lake. *Proceedings of the Imperial Academy [of Japan],* 9 (4) :191–193, figures 1–2.

1934. Studies on Some Japanese Branchiobdellidae with some Revisions on the Classification. *Journal of the Faculty of Science, Hokkaido Imperial University,* series 6, 3 (3) :177–219, figures 1–17, plates 12, 13.

Young, Willard

1966. Ecological Studies of the Branchiobdellidae (Oligochaeta). *Ecology,* 47 (4) :571–578, figures 1–3.

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Copy must be typewritten, double-spaced, on one side of standard white bond paper, with 1½″ top and left margins, submitted in ribbon copy with a carbon or duplicate, and accompanied by the original artwork. Duplicate copies of all material, including illustrations, should be retained by the author. There may be several paragraphs to a page, but each page should begin with a new paragraph. Number consecutively all pages, including title page, abstract, text, literature cited, legends, and tables. The minimum length is 30 pages, including typescript and illustrations.

The *title* should be complete and clear for easy indexing by abstracting services. Taxonomic titles will carry a final line indicating the higher categories to which the taxon is referable: "(Hymenoptera: Sphecidae)." Include an *abstract* as an introductory part of the text. Identify the *author* on the first page of text with an unnumbered footnote that includes his professional mailing address. A *table of contents* is optional. An *index,* if required, may be supplied by the author when he returns page proof.

Two *headings* are used: (1) text heads (boldface in print) for major sections and chapters and (2) paragraph sideheads (caps and small caps in print) for subdivisions. Further headings may be worked out with the editor.

In *taxonomic keys,* number only the first item of each couplet; if there is only one couplet, omit the number. For easy reference, number also the taxa and their corresponding headings throughout the text; do not incorporate page references in the key.

In *synonymy,* use the short form (taxon, author, date:page) with a full reference at the end of the paper under "Literature Cited." Begin each taxon at the left margin with subsequent lines indented about three spaces. Within an entry, use a period-dash (.—) to separate each reference. Enclose with square brackets any annotation in, or at the end of, the entry. For *references within the text,* use the author-date system: "(Jones, 1910)" and "Jones (1910)." If the reference is expanded, abbreviate the data: "Jones (1910:122, pl. 20: fig. 1)."

Simple *tabulations* in the text (e.g., columns of data) may carry headings or not, but they should not contain rules. Formal *tables* must be submitted as pages separate from the text, and each table, no matter how large, should be pasted up as a single sheet of copy.

Use the *metric system* instead of, or in addition to, the English system.

Illustrations (line drawings, maps, photographs, shaded drawings) can be intermixed throughout the printed text. They will be termed *Figures* and should be numbered consecutively; however, if a group of figures is treated as a single figure, the components should be indicated by lowercase italic letters on the illustration, in the legend, and in text references: "Figure 9*b*." If illustrations (usually tone photographs) are printed separately from the text as full pages on a different stock of paper, they will be termed *Plates,* and individual components should be lettered (Plate 9*b*) but may be numbered (Plate 9: figure 2). Never combine the numbering system of text illustrations with that of plate illustrations. Submit all legends on pages separate from the text and not attached to the artwork. An instruction booklet for the preparation of illustrations is available from the Press on request.

In the *bibliography* (usually called "Literature Cited"), spell out book, journal, and article titles, using initial caps with all words except minor terms such as "and, of, the." For capitalization of titles in foreign languages, follow the national practice of each language. Underscore (for italics) book and journal titles. Use the colon-parentheses system for volume, number, and page citations: "10(2):5-9." Spell out such words as "figures," "plates," "pages."

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