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EPIGEAN BRANCHIOBDELLIDS (ANNELIDA:
CLITELLATA) FROM FLORIDA

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In the early Pleistocene, most of Florida was covered by marine waters (Cooke, 1945:275) which reduced the peninsula to a few small islands. The distribution of the salt intolerant branchiobdellids of the state should present interesting zoogeographical problems. But, though confined to their crustacean hosts and, hence, able to go only where their hosts take them, they have evolved at a slower rate than the crayfishes (their principal hosts) (Holt, in press), they are not host specific and the paucity of species in the state as opposed to the richness of the crayfish fauna, make the solution of such problems difficult. Nonetheless, some tentative conclusions can be reached. In any case, little is known of the branchiobdellids of Florida, and as a part of efforts the objectives of which are to describe, classify and speculate on the evolution of the North American members of the order, the following is offered as a contribution towards these goals. The troglobitic branchiobdellids of Florida will be treated in another paper which is in preparation.

Much is known of the crayfishes of the state through the work of Hobbs, but I know of only three references to any branchiobdellids of the state. Goodnight (1940:34) recorded the presence of *Cambarincola philadelphicus*¹ in Punta Gorda,

¹ By direction of the International Code of Zoological Nomenclature, London, 1961, Article 30 (a) (i) (2), the gender of the generic name *Cambarincola* is masculine and it is so treated herein. A list of the required changes in species names is included in another paper (Holt, in press).

Florida: there is no reason to accept this record. Later, utilizing some 75 collections taken by Hobbs, Goodnight (1941) reported the occurrence of four species in the state. Most of his Florida records of *Cambarincola vitreus* Ellis (= *C. osceolai* Hoffman) and his species, *C. floridanus*, are accepted; but his report of *C. philadelphicus* (Leidy) and *C. chirocephalus* Ellis has not been confirmed and their occurrence in this area is not consonant with the known distribution of the two (Hoffman, 1963:349) and I have found specimens of only one Floridian species that even resembles these two closely related ones.

Hoffman (1963) extracted from *C. vitreus* a group of populations of the southern Coastal Plain, extending from the "panhandle" of Florida to "tidewater" Virginia, to which he gave the name *osceola*. This designation is accepted herein, though there are reasons for doubting its validity (see below under *C. osceolai*).

The taxonomic characteristics of the branchiobdellids and methods of handling the material have been discussed several times (cf. Hoffman, 1963, for those of the genus *Cambarincola*; Hobbs et al., 1967; other works of Holt). There is, therefore, little need for further comments herein on these topics except to note that I shall accept Hoffman's (1963:287) view that an undifferentiated prostate is a primitive feature, that in all figures the animals, or separately illustrated parts of them, are so oriented that the anterior portions are to the reader's right and that all measurements, made with an ocular micrometer, are to be regarded as approximations. For the measurements presented, the numbers within parentheses represent the ranges of the measurements on which the preceding average is based and the greatest diameter is always, unless otherwise indicated, that of segment VII.

Much of the material on which this paper is based is deposited in the National Museum of Natural History, Smithsonian Institution, including all holotypes, and such material is identified by the initials "USNM" preceding the catalogue numbers. In all cases, my catalogue numbers are given, identified by the initials "PCH," and material not in the collections

of the Smithsonian Institution are housed, under my care, at Virginia Polytechnic Institute and State University.

I am grateful to Mr. and Mrs. Chester A. Mann for the hospitality they extended to me and my wife during our collecting trips in Florida and to Mr. Mann for additional collections; to Mr. and Mrs. John E. Cooper for furnishing me with some valuable collections; to my wife whose aid makes my own collecting possible; and to the other collectors whose names appear in the "Material examined" sections below. To Dr. Horton H. Hobbs, Jr., I owe a triple debt for supplying specimens and furnishing or confirming host identifications and reading the manuscript. My travel for the purpose of collecting branchiobdellids was supported by NSF grants G-4439, G-9828 and GB-372.

ORIGINS OF THE BRANCHIOBDELLIDS OF FLORIDA

In general, the greatest diversity of Amercian branchiobdellids occurs in upland regions: the southern Appalachians, the Ozarks and the mountainous streams of the Pacific drainage. The plains of North America are inhabited, in contrast to their crustacean hosts, by relatively few species of the worms. Florida has over 30 species of crayfishes (Hobbs, 1942; 1958; and other papers), close to a third of which are troglobites; many of which are endemics. On the other hand, seven species of branchiobdellids from Florida are treated herein and a few others, cave dwelling ones, are known (their treatment is reserved for a paper in preparation on branchiobdellids that have been found in caves). Of these, none is known with certainty to be endemic, though it is highly likely that the cavernicolous species and *Cambarincola floridanus*, *C. manni* and *C. goodnighti*, the latter two newly described below, are endemics. The two new species of *Sathodrilus* described herein may be endemics, but since they are from the northern portion of the western panhandle of the state, it is doubtful if they are.

Hobbs (1942; 1958; and elsewhere) has cogently, and in convincing detail, discussed the evolution and history of the crayfishes of Florida. The few known species and the fact that the worms can move readily from one crayfish host to

another, precludes any such discussion of the origins of the branchiobdellids of the state. Yet a few tentative conclusions can be proposed.

The ranges and affinities of the species discussed herein are presented below with the treatment of each species. Briefly, these data may be summarized as follows.

Cambarincola manni, although it is related to the wide ranging *C. mesochoreus* Hoffman, has as its closest relative a primitive Mesoamerican species (Holt, in press). Yet it is the most common and wide ranging of Floridian branchiobdellids. One can only assume that its progenitors reached Florida in pre-Pleistocene times, perhaps as early as the Miocene, and survived subsequent inundations of the peninsula (Cooke, 1945:197, 275, 283, 288, 298) on islands or a greatly reduced peninsular area near the present central part of the state (utilizing the ancestral *Procambarus alleni*, a crayfish that according to Hobbs (1967) also has Mesoamerican affinities). After the post-Pleistocene lowering of sea level, it has migrated outward to occupy almost all of peninsular Florida, a territory that is only slightly breached by other species (Fig. 1).

C. goodnighti is another primitive species known only from a region that may have been on or near a body of land that persisted as such throughout the Pleistocene (Cooke, 1945: 275, 283, 288, 293, 298). Possibly, its progenitors survived farther to the northwest, or on one of the possible islands along "Trail Ridge." One cannot know.

The type-locality of *C. floridanus* in Taylor County probably was covered one or more times by interglacial Pleistocene seas, but the other known record of the species from Liberty County is on or near land that probably escaped the fluctuations of the late Cenozoic waters. It is a close relative of *C. philadelphicus* and most likely represents a somewhat modified invader of the *philadelphicus* stock into the Coastal Plain during a Pleistocene glacial advance.

Two species of *Cambarincola* are clearly not endemics. *C. osceolai* ranges widely over the southern Coastal Plain and its presence along the northern border of the "panhandle" of Florida may antedate the Pleistocene and go back to the

Pliocene (Cooke, 1945:112). Its presence in Levy County, however, is indubitably a post-Pleistocene extension of range.

The surprising find of *C. heterognathus* Hoffman in Leon and Calhoun Counties can only confirm the speculations as to the origins of *C. floridanus* and represents relics of a Pleistocene invasion of the Coastal Plain by a species now confined to the uplands of the southern Appalachians.

The two newly discovered species of the genus *Sathodrilus* are closely related and possibly sympatric. Their closest relative is *S. veracruzicus* from northern Veracruz, Mexico, which may have been carried there by the ancestors of the Mexicanus group of the genus *Procambarus*, i.e., by relatives of the postulated hosts of the ancestors of *C. manni* (Hobbs, 1967; Holt, in press). The members of the genus range from South Carolina to southern Mexico and all appear to be primitive. The presence of *S. hortonii* and *S. okaloosae* in the western "panhandle" can tell us little about the history of the genus, but suggests the survival there, and perhaps in southern Mississippi, of members of a genus that originated somewhere in the southern Appalachians or associated uplands and reached southern Mexico before mid-Miocene times (Holt, in press).

The branchiobdellid fauna of Florida is composed of descendants of several waves of invasion. It is dominated by members of the largest genus, and one of the most advanced, of the order. The primitiveness of the most widespread of these species in the state, and the presence of members of the primitive genus *Sathodrilus*, attest to an early invasion of Florida by branchiobdellids and confirm the earlier proposed hypothesis of the antiquity of the genera of the order (Holt, in press). The primitive species of *Cambarincola* survived on islands during the Pleistocene; the more advanced *C. heterognathus* and perhaps *C. floridanus* arrived in the northern parts of the state that were not covered by the interglacial seas during the Pleistocene as refugees from the north; *C. osceolai* may be a post-Pleistocene invader; and *S. hortonii* and *S. okaloosae* are relics persisting near or in their present range since much earlier, perhaps pre-Miocene, times. More one cannot say; there is little need at this time to attempt to correlate these speculations with Hobbs' hypotheses explain-

ing the origins of the crayfish fauna of Florida: the notorious absence of host specificity among these epizoötic worms makes such an effort entirely too complicated for anything beyond the meager speculations that there are parallel relationships between Floridian branchiobdellids and their hosts and those of Mesoamerica discussed above.

Genus *Cambarincola* Ellis, 1912

Astcobdella Leidy, 1851:206.

Branchiobdella.—Moore, 1894:427 (in part).

Bdellodrilus.—Pierantoni, 1912:24 (in part).

Cambarincola Ellis, 1912:481; 1918:51; 1919:25.—Hall, 1914:190.—Stephenson, 1930:801.—Yamaguchi, 1932:454; 1933:191; 1934:189.—Goodnight, 1940:30.—Holt and Hoffman, 1959:97.—Hoffman, 1963:271.—Hobbs et al., 1967:52.—Holt, 1969:197; in press.

Diagnosis: "Body terete without specialized projections [other than peristomial tentacles in some species]; 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." (Hobbs et al., 1967:52).

Remarks: Members of the genus *Cambarincola* constitute the dominant portion of the North American branchiobdellid fauna: they are found wherever other branchiobdellids occur on the continent (with the exception of the Great Salt Lake drainage and a few streams of the Coastal and Cascade Ranges of the Pacific drainage). In much of the Central and Coastal Plains they appear to be the only representatives of the order.

KEY TO THE FLORIDIAN SPECIES OF THE GENUS *CAMBARINCOLA*

- | | | |
|-------|--|---|
| 1 | Prostate undifferentiated | 4 |
| 1' | Prostate differentiated | 2 |
| 2(1') | Spermiducal gland reflexed; jaws subequal in size | |
| | <i>Cambarincola osceolai</i> | |
| 2' | Spermiducal gland not reflexed, jaws variable in size | 3 |
| 3(2') | Prostate subequal in length to spermiducal gland; jaws subequal in size | |
| | <i>Cambarincola floridanus</i> | |
| 3' | Prostate very short, about one-fourth length of spermiducal gland; upper jaw much larger than lower | |
| | <i>Cambarincola heterognathus</i> | |
| 4(1) | Spermiducal gland reflexed; prostate about one-half length of latter; ental end of prostate composed of nonglandular cells | |
| | <i>Cambarincola goodnighti</i> | |
| 4' | Spermiducal gland not reflexed; prostate subequal in length to latter; ental end of prostate with prostatic bulb | |
| | <i>Cambarincola manni</i> | |

Cambarincola manni, new species

Figures 1, 2

Type-specimens: Holotype, nine paratypes, USNM 48700 on *Procambarus fallax* (Hagen) taken from Lake Martha, at 612 E. Lake Martha Drive, Winter Haven, Polk County, by Chester A. Mann, 12 January 1964 (PCH 1793); one paratype, USNM 48701 on *Procambarus fallax* (Hagen) taken from canal between Lake Buckeye and Lake Fanny, Winter Haven, Polk County, by Chester A. Mann and Perry C. Holt, 20 April 1963 (PCH 1663); one paratype, PCH 1670, on *Procambarus fallax* (Hagen) taken from Lake Martha, Winter Haven, Polk County, by Chester A. Mann and Perry C. Holt, 20 April 1963; ten paratypes, PCH 1793, from the type-locality; five paratypes, PCH 1673, on *Procambarus paeninsulanus* (Faxon) taken from slough, 13 miles northwest of Inglis, Levy County, by Perry C. and Virgie F. Holt, 25 April 1963.

Diagnosis: Small branchiobdellids (average length approximately 2.0 mm); anterior segmental annuli of trunk segments not noticeably greater in diameter than posterior ones, though weak supernumerary muscles occur in anterior segments; jaws small, length about $\frac{1}{15}$ that of head, dental formula 5/4; bursa pyriform, about $\frac{1}{3}$ body diameter in length, penial sheath and bursal atrium subequal in length; ejaculatory duct short; spermiducal gland slender, length approximately $\frac{6}{7}$ that of bursa, its diameter about $\frac{1}{6}$ its total length, without obvious deferent lobes; prostate undifferentiated, subequal to spermiducal gland in length and diameter, with small clear ental bulb; length of ectal duct of spermatheca slightly greater than $\frac{1}{2}$ body diameter, spermathecal bulb globose without ental process.

Etymology: It is a pleasure to dedicate this species to its codiscoverer and my friend, Chester A. Mann, whose enthusiasm for natural history remains undiminished after a life time of its study.

Description: Specimens of *Cambarincola manni* are smaller than those of most of its congeners. The holotype has the following dimensions: total length, 2.1 mm; greatest diameter, 0.3 mm; head length, 0.3 mm; head diameter, 0.2 mm; diameter, segment I, 0.2 mm; diameter, sucker, 0.2 mm. The average dimensions of the holotype and four specimens selected from the type-series at random are as follows: total length, 2.1 mm (1.8–2.3 mm); greatest diameter, 0.3 mm (0.3–0.3 mm); head length, 0.3 mm (0.3–0.4 mm); head diameter, 0.3 mm (0.2–0.3 mm); diameter, segment I, 0.2 mm (0.2–0.3 mm); diameter, sucker, 0.2 mm (0.2–0.2 mm). The animals are, therefore, rather uniform in size and relatively slender.

The lips are entire, without indentations other than the usual lateral ones and there are no detectable oral papillae. My material is well preserved and if these structures were present, they should be readily seen. The peristomial sulcus is not unusually prominent. The head is marked by one other very shallow annular indentation or sulcus and there is only one pharyngeal sulcus.

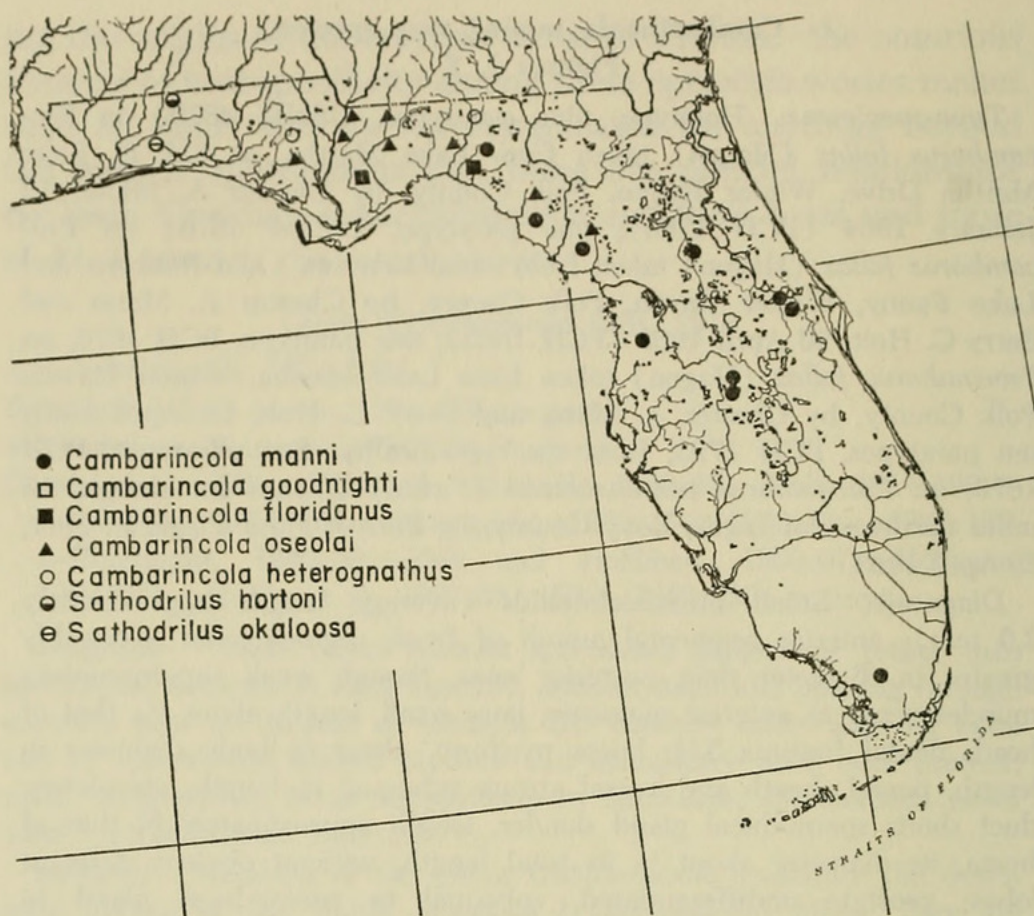


FIG. 1. Known distribution, excepting the doubtful records from Goodnight (1941) (see text, page 80), of the branchiobdellids of Florida.

The body outline is generally smooth, though rather weak or rudimentary supernumerary muscles of the anterior segmental annuli are present in at least the anterior segments and the intersegmental furrows are prominent in some specimens.

The jaws, although somewhat small, are similar to those of other members of the genus that are of overall small body size and possess a $5/4$ dental formula. The basal portions are light brown; the sharp pointed and widely spaced teeth are almost colorless.

The size and proportions of the spermiducal gland and prostate are distinctive. The spermiducal gland is unusually slender, though of usual histological appearance. The prostate is subequal in length and diameter to the spermiducal gland, and similar (undifferentiated) to it histologically. A small, clear ental bulb of the prostate is present.

The bursa is proportionately larger than other structures of the male efferent apparatus, is pyriform in shape, with the bursal atrium composing about $1/2$ of its total length, and there is a suggestion in the appearance of the retracted penis (no specimens with the penis protruded have been seen) that it may be of disproportionate length when

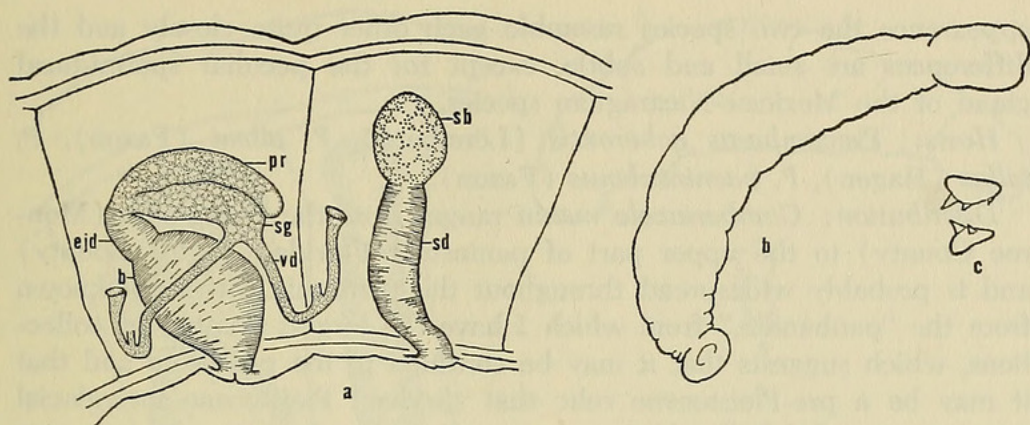


FIG. 2. *Cambarincola manni*, n. sp. *a*, reproductive organs of holotype; *b*, same, lateral view; *c*, same, lateral view of jaws. Abbreviations: *b*, bursa; *ejd*, ejaculatory duct; *pr*, prostate; *sb*, spermathecal bulb; *sd*, spermathecal ectal duct; *sg*, spermiducal gland; *vd*, vas deferens.

protruded, but none that it is eversible. The ejaculatory duct is short, subequal in its length and diameter.

The spermatheca possesses a long ectal duct, its length approximately $\frac{2}{3}$ the diameter of segment V. It terminates entally in a relatively small, thin-walled bulb without any evidence of an ental process.

Variation: None, other than in size and the aforementioned prominence of the intersegmental furrows (probably a result of the effect of different fluids used in the collection and preservation of specimens).

Affinities: The relationships of *C. manni* lie with a group of species that have been designated the *Mesochoreus* section which are characterized by an undifferentiated prostate (which was originally thought to be without an ental bulb [Hoffman, 1963:320]). Among these species only two need to be mentioned. *Cambarincola mesochoreus*, with a rather wide range in the United States (from the Canadian border to southern Louisiana), is a larger worm (2.8–4.2 mm in length) with a much more prominent spermiducal gland and prostate than *C. manni*. It also possesses a "slender, elongate, subfusiform [spermatheca, which] curving dorsolateral around the gut, [expands] laterally, and [is] attenuated to a blunt ental process near the middorsal portion of the segment" (Hoffman, 1963:307–308), as opposed to the globose spermathecal bulb without an ental process in *C. manni*.

A second species which resembles *C. manni* and, indeed, may be its closest relative, is known from Rio Tapalapa and Lake Catemaco in southern Veracruz, Mexico, and Lake Nicaragua in Nicaragua (Holt, in press). This species differs from *C. manni* in the total absence of dorsal ridges, the occurrence of a smaller bursa, a spermiducal gland with a peculiar heavily granulated ental portion, in possessing a prostate which arises farther entad to its junction with the spermiducal gland and in a spermatheca with a shorter ectal duct and an ental process. This would seem to be a formidable list of differences, but in size and overall

appearance the two species resemble each other quite closely and the differences are small and subtle, except for the peculiar spermiducal gland of the Mexican-Nicaraguan species.

Hosts: *Procambarus acherontis* (Lönnberg), *P. alleni* (Faxon), *P. fallax* (Hagen), *P. paeninsulanus* (Faxon).

Distribution: *Cambarincola manni* ranges from the Everglades (Monroe County) to the upper part of peninsular Florida (Taylor County) and is probably widespread throughout the peninsula. It is not known from the "panhandle," from which I have the largest number of collections, which suggests that it may be confined to the peninsula and that it may be a pre-Pleistocene relic that survived Pleistocene interglacial times on one of the islands that remained above salt water.

Material examined: Other than the types listed above, six specimens, USNM 48702 on *Procambarus fallax* (Hagen) and *P. paeninsulanus* (Faxon) taken from a roadside stream on U.S. Highway 98, 11.6 miles east of Enconfina River, Taylor County, by Perry C. and Virgie F. Holt, 18 April 1958, (PCH 746); one specimen, USNM 48703, on *Procambarus alleni* (Faxon) taken from Everglades drainage ditch, 2.0 miles east of intersection of State Road 94 on U.S. Highway 41, Monroe County, by Perry C. and Virgie F. Holt, 24 April 1963, (PCH 1671); six specimens, USNM 48704, host unknown, taken from slough 5.0 miles northwest of Brooksville on U.S. Highway 98, Hernando County, by Perry C. and Virgie F. Holt, 25 April 1963, (PCH 1672); four specimens, USNM 48705, host unknown, taken from a slough on U.S. Highway 98, 9.0 miles southeast of Taylor-Dixie County line, Dixie County, by Perry C. and Virgie F. Holt, 25 April 1963, (PCH 1674); twenty specimens, on *P. acherontis* (Lönnberg) taken at Palm Springs, Seminole County, by John E. and Martha R. Cooper, January 1965, (PCH 2373).

***Cambarincola goodnighti*, new species**

Figures 1, 3

Type-specimens: Holotype, USNM 48706, one paratype, USNM 48707, and one paratype, PCH 2607, on *Procambarus fallax* (Hagen), and *P. paeninsulanus* (Faxon) taken 5.6 miles north of St. Augustine, St. John County. (Collector and date unknown.)

Diagnosis: Small branchiobdellids (about 1.7 mm in length), anterior segmental annuli slightly greater in diameter than minor ones (weak supernumerary muscles present, dorsal ridges obscure); jaws small, length less than $\frac{1}{10}$ that of head, light brown, dental formula $5/4$, lateral teeth of lower jaw small, obscure; bursa about $\frac{1}{3}$ body diameter in length, with prominent atrial fold, penial sheath short; ejaculatory duct short, its length subequal to its diameter; spermiducal gland long, slender, bent upon itself, without deferent lobes; prostate undifferentiated, subequal in diameter to that of spermiducal gland, ending entally in thick-walled bulb at level of flexure of latter; spermatheca with very long ectal duct curving dorsally over gut, spermathecal bulb globose, lying on opposite side of gut from ectal duct.

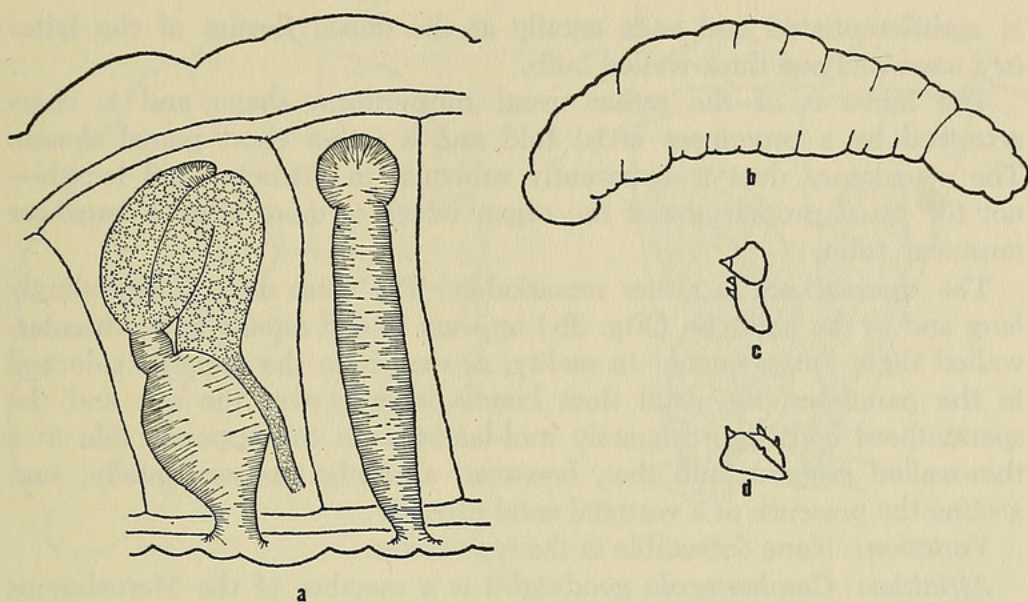


FIG. 3. *Cambarincola goodnighti*, n. sp. *a*, lateral view of reproductive organs of holotype; *b*, same, lateral view; *c*, oblique view of upper jaw; *d*, oblique view of lower jaw.

Etymology: I take pleasure in naming this worm for my friend Clarence J. Goodnight, whose studies of North American branchiobdellids furnished the stimulus for my studies of them.

Description: Specimens of *Cambarincola goodnighti* are rather small worms. The holotype has the following dimensions: total length, 1.7 mm; greatest diameter, 0.4 mm; head length, 0.3 mm; head diameter, 0.2 mm; diameter, segment I, 0.25 mm; diameter, sucker, 0.25 mm. The paratypes are of comparable size and dimensions.

The lips each have median indentations. There are no oral papillae. Two internal pharyngeal sulci are present, the posterior one the smaller. Externally, the head is marked by a prominent sulcus which corresponds in position to the anterior internal one; the peristomial sulcus is likewise prominent and the diameter of the peristomium is noticeably less than the greatest diameter of the head.

The anterior annuli of the body segments are greater in diameter than the posterior ones, but only slightly so: the animals do not present the sawtoothed appearance, in lateral view, of species with prominent dorsal ridges. The anterior nephridiopore is obscure. The clitellum is well developed on segment VII, but less so on VI.

The jaws are not large, subequal in size, distinctly brown, and the dental formula is 5/4. The teeth are not prominent and the lateral teeth of the lower jaw are small and difficult to see.

The spermiducal gland is long, extending beyond the dorsal border of the gut where it is sharply bent upon itself. Its ental end is not marked by deferent lobes and begins at the dorsal apex of the bursa. The prostate, of approximately the same diameter as the spermiducal gland,

is undifferentiated and ends entally at the dorsal flexure of the latter in a narrowed and thick-walled bulb.

The bursa is of the rather usual subpyriform shape and is characterized by a prominent atrial fold and a rather short penial sheath. The ejaculatory duct is apparently subequal in diameter and length—not the usual proportions of the organ which is more often a narrower muscular tube.

The spermatheca is rather remarkable. The ectal duct is exceedingly long and in the holotype (Fig. 3b) appears to end entally in a muscular-walled slight enlargement. In reality, as seen from the opposite side and in the paratypes, the ectal duct bends dorsally over the gut and the spermatheca ends approximately mid-laterally on the opposite side in a thin-walled globose bulb that, however, abruptly narrows entally, suggesting the presence of a vestigial ental process.

Variation: None detectable in the type-series.

Affinities: *Cambarincola goodnighti* is a member of the Mesochoreus section of the genus, but differs from other members of the section in that the undifferentiated prostate possesses an ental bulb with a thick wall and an obscure lumen. The spermiducal gland is almost identical to that of *C. vitreus*, *C. osceolai* and a new species (Holt, in press) from the Rio San Juan of the Rio Grande drainage in Nuevo León, Mexico. The Mexican animal lacks an ental bulb of the prostate; *C. vitreus* and its closely allied relative, *C. osceolai*, have differentiated prostates. *C. goodnighti* differs from these species in the structure of the spermatheca: they have a shorter ectal duct and an ovoid or clavate bulb without an ental process. In addition, the prominent external sulcus of the head is absent in the closest relatives of *C. goodnighti*. *Cambarincola goodnighti* is a relatively primitive member of the Mesochoreus section.

Hosts: *Procambarus fallax* (Hagen), *P. paeninsulanus* (Faxon).

Distribution: Known only from the type-locality.

Material examined: The type-series.

Cambarincola floridanus Goodnight, 1941

Figures 1, 4

Cambarincola floridana Goodnight, 1941:73.—Hoffman, 1963:368.

Cambarincola floridanus.—Holt, in press.

Type-specimens: "From Taylor County, Florida, 6.8 miles south of Lamont; collected March 18, 1939, on *Cambarus fallax* Hagen, by H. H. Hobbs [Jr.]" (Goodnight, 1941:73). Holotype, USNM 20570.

Diagnosis: (Based on material from Liberty County, Florida.) Medium large branchiobdellids (approximate total length 3.0 mm); anterior annuli of body segments greater in diameter than posterior ones; jaws subequal in size, dark brown, dental formula 5/4; bursa moderately large, $\frac{1}{3}$ or more body diameter in length, subpyriform, with prominent atrial fold; spermiducal gland with prominent posterior

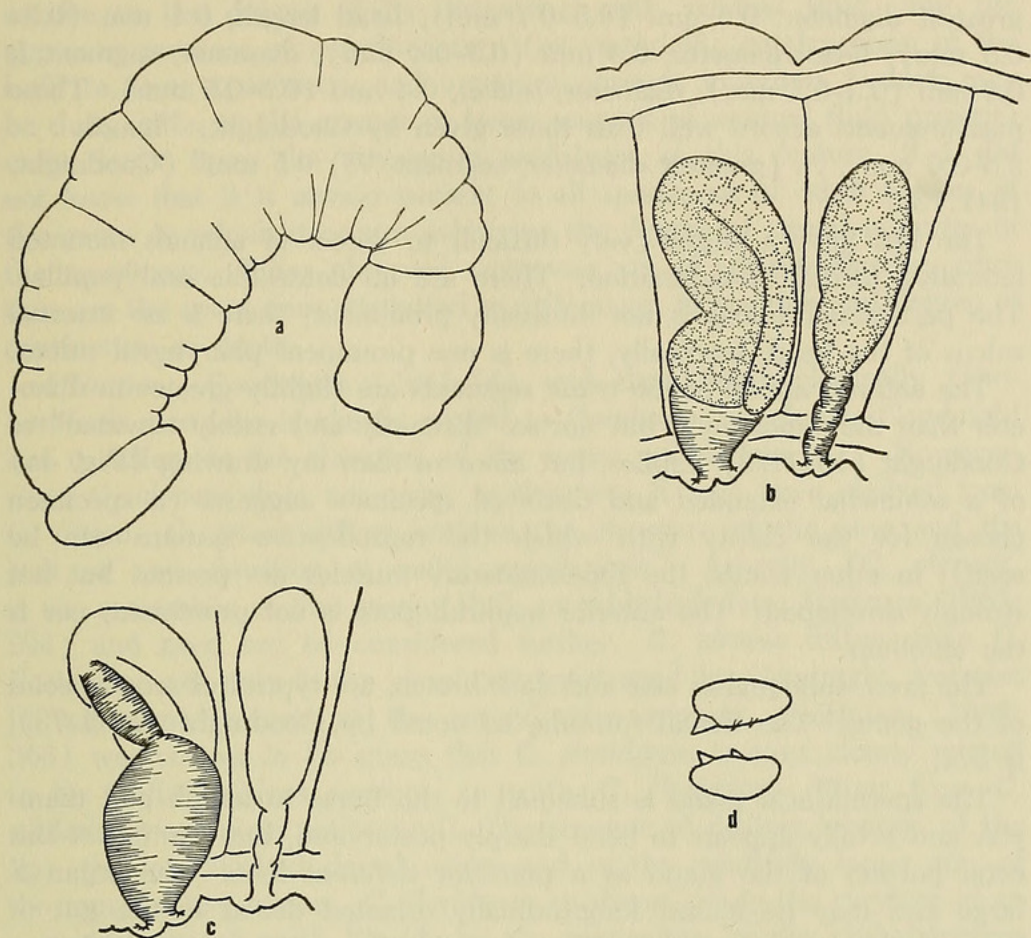


FIG. 4. *Cambarincola floridanus* Goodnight, *a*, lateral view of specimen from Liberty County, Florida; *b*, same, reproductive organs; *c*, same, mesial view of reproductive organs; *d*, same, lateral view of jaws.

deferent lobe, relatively thick, subequal to bursa in length; prostate differentiated, subequal to spermiducal gland in length, with small, obscure ental bulb; spermatheca with clavate to subovate bulb.

Description: Goodnight (1941:73) presented a rather short diagnostic description which includes nothing of value in reference to the reproductive systems, a practice current among students of the branchiobdellids at the time he wrote. Hoffman and I have examined the holotype and both of us have made free-hand sketches of it. "This specimen is mounted laterally, but the reproductive system[s] cannot be made out with certainty" (Hoffman, 1963:368). Since, because of correspondences in the structures that can be seen in it, I am convinced that my specimens are conspecific with Goodnight's holotype, it seems appropriate that I present a description based on these animals.

Specimens of *Cambarincola floridanus* are medium sized members of the genus. Averages of measurements of five mature animals from Liberty County are as follows: total length, 2.8 mm (2.4–3.2 mm)

greatest diameter, 0.6 mm (0.5–0.7 mm); head length, 0.4 mm (0.3–0.5 mm); head diameter, 0.3 mm (0.3–0.4 mm); diameter, segment I, 0.3 mm (0.3–0.4 mm); diameter, sucker, 0.4 mm (0.2–0.5 mm). These measurements accord well with those given by Goodnight: "length . . . 2.5–3.0 mm . . . (greatest diameter, segment VI) 0.5 mm" (Goodnight, 1941:73).

The lips have a slight (very difficult to detect in animals mounted laterally) median emargination. There are no detectable oral papillae. The peristomial sulcus is not unusually prominent; there is no external sulcus of the head; internally, there is one prominent pharyngeal sulcus.

The anterior annuli of the trunk segments are slightly greater in diameter than the minor ones, but not so "distinctly and visibly elevated" as Goodnight (1941:73) implies, but more so than my drawing (Fig. 4a) of a somewhat extended and distorted specimen suggests (a specimen chosen for the clarity with which the reproductive systems can be seen); in other words, the supernumerary muscles are present but not strongly developed. The anterior nephridiopore is not prominent, nor is the clitellum.

The jaws, subequal in size and dark brown, are typical of most species of the genus. The dental formula, as noted by Goodnight (1941:73), is 5/4.

The spermiducal gland is subequal to the bursa in length and diameter and ectally appears to bend sharply posteriorad, but I interpret this ectal portion of the gland as a posterior deferent lobe. The organ is large and may lie almost longitudinally oriented dorsal to the gut or variously bent in a lateral position alongside the gut mesal to the bursa. The prostate is about $\frac{1}{2}$ the diameter of the spermiducal gland and subequal to the latter in length. The ental bulb of the prostate is obscure and easily overlooked in most specimens.

The ejaculatory duct is relatively short. The bursa is characterized by its relatively large size, as noted by Hoffman (1963:368), and the disproportionately thick muscular wall of the penial sheath.

The spermatheca has a long, but not unusually so, ectal duct. The bulb is oblong ovate to clavate in mature animals and in some specimens there is a thickening of its ental end that is suggestive of an ental process.

Variation: The variation in size of specimens of *C. floridanus* is no more than usual among most species of the genus. The reproductive organs do show a greater amount of variation. The bursa is rather constant in proportional size and position, but the spermiducal gland appears to differ considerably in shape and position between individuals: a variation I am inclined to ascribe to the large size of the organ and the various positions in the coelom that it may assume. More disturbing is my observation that it possesses a posterior deferent lobe: the vasa deferentia are impossible to trace in my material, or essentially so, thus this lobe could, with a better series of specimens, be shown to be only an ental flexure of the gland as a whole. The spermathecal bulb, as noted above, differs in shape among my specimens; a difference I

ascribe to the degree of its distension with seminal fluid. But the apparent presence of a rudimentary (or vestigial?) ental process of the bulb in some specimens, and apparent absence in others (which may be due, again, to the greater or lesser amount of seminal fluid present) casts doubt upon the taxonomic usefulness of this feature, if I did not know that it is always present in all specimens of other species of the genus in which it occurs, whatever the degree of sexual maturity of the specimens. Other observed variations are of no significance, since they are the usual ones attributed to differences in position and degree of contraction at death.

Affinities: Goodnight (1941:74) said that "morphologically *Cambarincola floridana* is closely related to *Cambarincola elevata* Goodnight but it differs in the elevation of the major annulations . . . However, since *C. elevata* does not occur in this area it may have evolved from *C. vitrea*. *C. vitrea* differs both in the structure of the jaws and the lack of any elevation of major annulations." Actually, "*C. elevata*" is not a member of the genus (Holt, unpublished data; Hoffman, 1963: 294) and need not be considered further. *C. vitreus* differs from *C. floridanus*, not only in the characters mentioned by Goodnight, but also in important features of the reproductive systems. Hoffman (1963: 368) was correct in his guess that *C. floridanus* is most closely related to his Philadelphicus section: in truth, *C. floridanus* differs from *C. philadelphicus* most noticeably in the absence of distinct lobation of the lips, the less marked dorsal ridges and in the relatively larger size of the reproductive organs. *C. floridanus* is almost surely the survivor of an early invasion of north Florida by the progenitors of the Philadelphicus section.

Hosts: *Procambarus fallax* (Hagen) [= *Cambarus fallax* (from Goodnight, 1941:73)], *Procambarus spiculifer* (LeConte).

Distribution: Known only from the type-locality and one locality in Liberty County.

Material examined: The holotype, USNM 20570; in addition, 11 specimens, USNM 48708 (PCH 665), on *Procambarus spiculifer* (LeConte) taken 1.6 miles north of Hosford, Liberty County, by H. H. Hobbs, Jr., and C. W. Hart, Jr., 5 September 1955.

Cambarincola osceolai Hoffman, 1963

Figures 1, 5

Cambarincola osceola Hoffman, 1963:330

Cambarincola osceolai.—Holt, in press.

Type-specimens: "Holotype and seven paratypes, USNM 29943, from *Procambarus paeninsulanus* and *Cambarus uhleri* collected along Dry Creek, 3.1 miles north of Iron City, Seminole County, Georgia, by Horton H. Hobbs [Jr.,] and C. W. Hart, September 9, 1955" (Hoffman, 1963: 330).

Diagnosis: "A small species of the Vitrea group, very similar to the

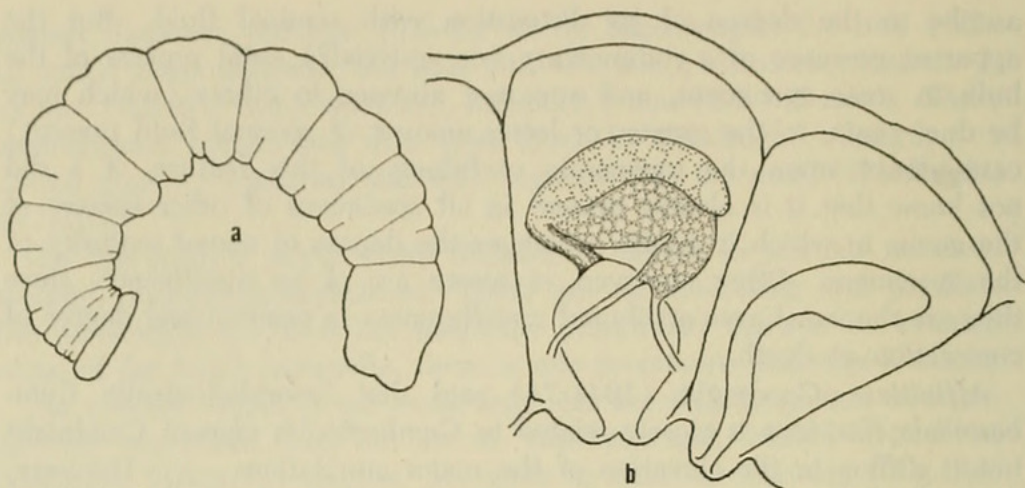


FIG. 5. *Cambarincola osceolai* Hoffman (after Hoffman, 1963).
a, lateral view of specimen from Calhoun County, South Carolina;
b, same, reproductive systems.

typical species and possibly a geographic race of it, but differing in the much smaller diameter of the prostate in comparison with that of the spermiducal gland, as well as by differences in the jaw sizes at least in the populations of the two that are geographically most approximate" (Hoffman, 1963:330).

Material examined: In addition to that cited by Hoffman (1963:333, Fig. 31), the following material has been examined: five specimens, USNM 48709, on *Procambarus paeninsulanus* (Faxon) taken from a cypress swamp, 6.0 miles south of Lamont on State Highway 257, Jefferson County, by Perry C. and Virgie F. Holt, 25 April 1963, (PCH 1675); five specimens, USNM 48710, on *Procambarus paeninsulanus* (Faxon) taken 2.0 miles west of Bloxham on State Highway 20, Liberty County, by Perry C. and Virgie F. Holt, 26 April 1963, (PCH 1676); five specimens, USNM 48711, on *Procambarus spiculifer* (LeConte) taken 9.0 miles west of Greensboro, Gadsden County, by Perry C. and Virgie F. Holt, 26 April 1963, (PCH 1677); five specimens, USNM 48711, on *Procambarus spiculifer* (LeConte) taken on U.S. Highway 80 at eastern edge of Quincy, Gadsden County, by Perry C. and Virgie F. Holt, 26 April 1963, (PCH 1678).

Remarks: The description of *Cambarincola osceolai* and its affinities with *C. vitreus* are thoroughly discussed by Hoffman (1963:330–332) and the only thing that needs to be added here is that I share his suspicion that *C. osceolai* is a geographical variant of *C. vitreus*. However, until such time that I can study with more thoroughness specimens from Mississippi and Alabama, I prefer to retain his name for the Florida worms. Both *C. vitreus* and *C. osceolai* are inhabitants of streams of the plains: *C. vitreus* is widespread in the Central Plains of the Mississippi Valley and the Great Lakes region; *C. osceolai* is known from Florida and Georgia to eastern Virginia (Hoffman, 1963:327, Fig. 31).

Both are members of the *Philadelphicus* section that differ from *C. floridanus* in the smaller and strongly reflexed spermiducal gland. Goodnight's (1941:72-73) records of *C. vitreus* in Florida may be provisionally accepted as records of *C. osceolai* for the northern part of the state, though I have not plotted them in Figure 1. I suspect strongly that many of his records of this species, particularly in the central and southern portions of the peninsula, apply to *C. manni* which is much more widespread and is superficially similar, but differs markedly in reproductive systems (see above, under *C. manni*).

Cambarincola heterognathus Hoffman, 1963

Figures 1, 6

Cambarincola heterognathus Hoffman, 1963:362

Cambarincola heterognathus.—Holt, in press.

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

Diagnosis: "Immediately recognizable by the remarkably dissimilar jaws alone. In addition, the male reproductive system is reduced in size and the prostate gland is less than half the length of the spermiducal gland" (Hoffman, 1963:362).

Material examined: In addition to that cited by Hoffman (1963:363-364), eight specimens, USNM 48712, on *Cambarus rogersi rogersi* (Hobbs), taken at Horse Shoe Bay, Leon County, by H. H. Hobbs, Jr., 27 November 1936 (PCH 1795); one specimen, PCH 2719, on *P. rogersi campestris* taken from roadside ditch, 10.3 miles south of Jackson County line on State Highway 71, Calhoun County, by Horton H. Hobbs III, 11 August 1968.

Remarks: The discovery in my collections of a slide labelled "*Cambarincola philadelphica*" in Dr. Hobbs' handwriting that bore a specimen of *C. heterognathus* was most surprising. At my request, Dr. Hobbs searched the original collection of *Cambarus r. rogersi* and found additional specimens that undoubtedly must be assigned to *C. heterognathus*, a species that I long ago recognized as distinct and that is adequately described by my student, Hoffman. The affinities of the species lie with the *Philadelphicus* section and though species from Mesoamerica (Holt, in press) and the western United States are now known (Holt, unpublished data) to have equally disparate jaws, they are different from those of *C. heterognathus*, and the reproductive systems of all of these species are markedly different and none is closely related to the others.

The previously known range of *C. heterognathus* is a coherent one that is confined to the southern Appalachians (Hoffman, 1963:363, Fig. 74; Holt, 1969:206-207). There can be little doubt that the populations of the species in northern Florida are disjunct and the only plausible

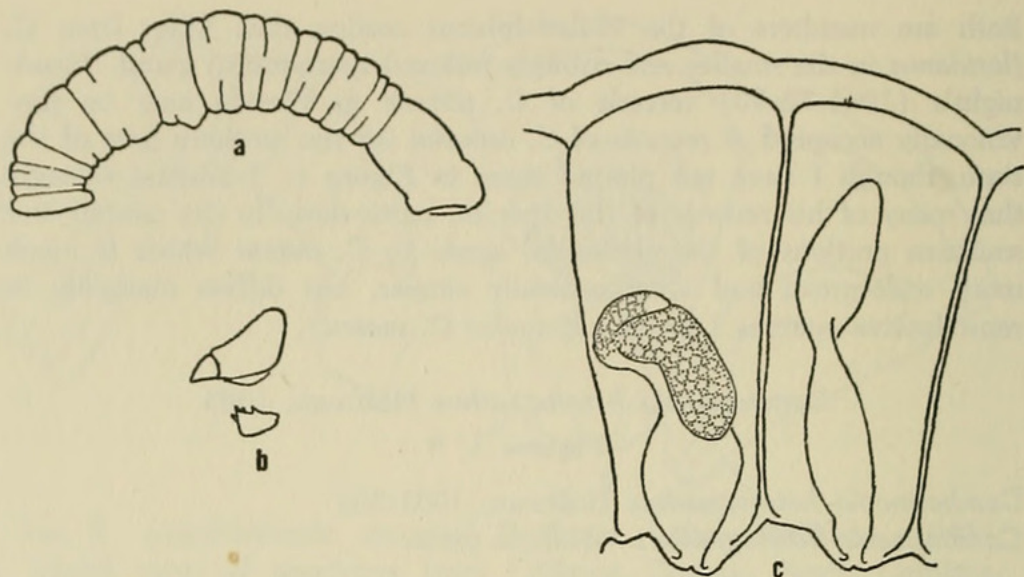


FIG. 6. *Cambarincola heterognathus* Hoffman (after Hoffman, 1963). *a*, lateral view of paratype; *b*, same, jaws in lateral view; *c*, same, reproductive organs.

explanation is that they are relics of an invasion during a Pleistocene glaciation. The two localities from which *C. heterognathus* is known lie on opposite sides of the Apalachicola bluff area. A number of other disjunct species of plants and animals of Appalachian origin are found in this region. It is possible that *C. heterognathus* is at least a facultative inhabitant of the gill chambers of its hosts and, if this is so, the fact that its Floridian host is a burrowing crayfish would aid its survival in an area now so unlike its ancestral home in the Appalachians.

Genus *Sathodrilus* Holt, 1968

Sathodrilus Holt, 1968:294.

Diagnosis: "Medium sized branchiobdellid worms (known species 1.5 to 4.6 mm in average length) with two pairs of testes; unpaired nephridiopore on dorsum of segment III; body terete, without peristomal tentacles or dorsal projections on trunk segments; spermiducal gland with vasa deferentia entering entally; prostate, if present, consisting of bulb-like prostatic protuberance on anterior or dorsal border of spermiducal gland; ejaculatory duct present; penis eversible, but attached by cytoplasmic strands to inner wall of penial sheath and without cuticular hooks; spermatheca with or without ental process" (Holt, 1968:294).

Remarks: The two new species of *Sathodrilus* described below are geographically intermediate between the previously recorded localities from which the genus is known in South Carolina, northern Georgia, and Mexico (the latter with species on both sides of the ancient, mid-Miocene, Cordillera Volcánico Transversal). They do not, however, invalidate the previous conclusion (Holt, 1968:295) that the genus is a relatively

primitive one. These species and those previously described, must be considered as phylogenetic relics of a stock once much more common and widespread.

A key to the species cannot be presented herein because of the danger of creating nomina nuda, but a comparison of the following diagnoses with those in Holt (1968; in press [Mexican species]) will readily separate all the known species of the genus.

***Sathodrilus hortonii*, new species**

Figures 1, 7

Type-specimens: Holotype, USNM 48713, two paratypes, USNM 48714, two paratypes, PCH 2716, on *Cambarus d. diogenes* Girard and *Cambarus* sp. Hobbs taken from Pond Creek 2.1 miles northeast of Laurel Hill, Okaloosa County, 10 August 1968, by H. H. Hobbs III.

Diagnosis: Medium sized branchiobdellids (holotype 2.2 mm in length); only first two and last three body segments with detectable annuli; jaws small, approximately $\frac{1}{12}$ length of head, medium brown, dental formula $5/4$, lateral teeth very small; bursa elongate, about $\frac{1}{4}$ body diameter in length, bent posteriorad under gut; ejaculatory duct short; spermiducal gland slightly longer than bursa, its diameter about $\frac{1}{13}$ its length; histologically homogeneous; prostatic protuberance absent; spermatheca with distinct spermathecal bursa; spermathecal bulb narrowed, elongated, thick walled.

Etymology: It is with pleasure that I name this species for the son of my mentor, Horton H. Hobbs III, its discoverer.

Description: *Sathodrilus hortonii* is composed of medium sized worms. The holotype has the following dimensions: total length, 2.2 mm; greatest diameter (segment VI), 0.5 mm; head length, 0.3 mm; head diameter, 0.2 mm; diameter, segment I, 0.25 mm; diameter, sucker, 0.25 mm. The average dimensions of the type-series are as follows: total length, 2.7 mm (2.2–3.4 mm); greatest diameter (segment VI), 0.5 mm; head length, 0.3 mm (0.3–0.3 mm); head diameter, 0.2 mm (0.2–0.2 mm); diameter, segment I, 0.25 mm (0.2–0.3 mm); diameter, sucker, 0.2 mm (0.2–0.25 mm).

The upper lip is divided into four very indistinct lobes that are not apparent under the lower powers of the microscopes; the lower, separated by deep but broad indentations from the upper, is entire. No oral papillae are detectable. The peristomial sulcus is shallow and there are no other external furrows of the head. Internally, other than that in which the jaws lie, there is one prominent anterior sulcus and another smaller posterior one.

The first two body segments are longitudinally compressed and only with difficulty can they be seen to be composed of two annuli each and both are filled with muscles that are attached to the gut producing an "oesophagus." Segment VIII and succeeding ones to the sucker are normal in appearance. Segments III–VII show no external or internal signs of being divided into annuli. The body cavities of these

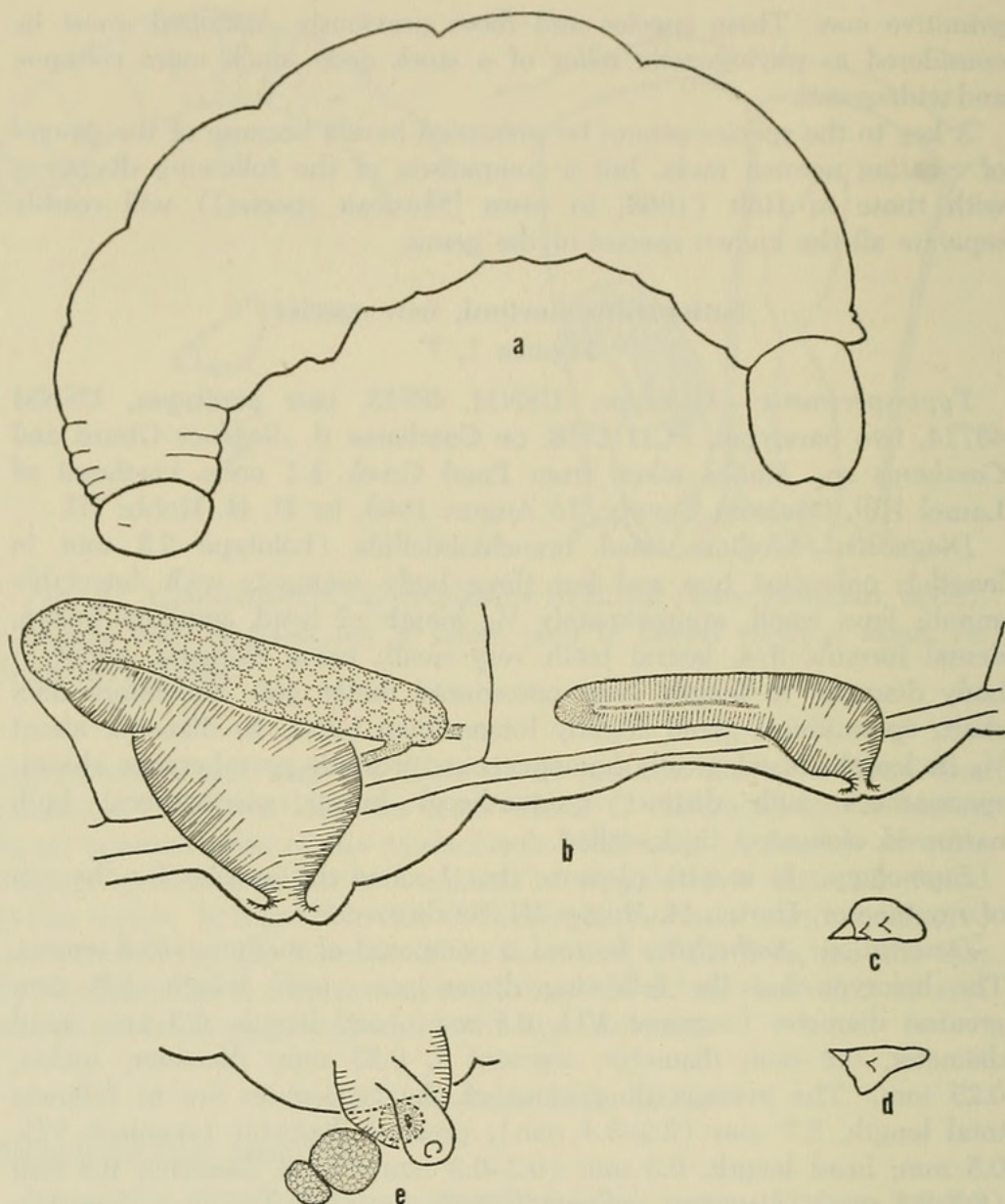


FIG. 7. *Sathodrillus hortonii*, n. sp. *a*, lateral view of holotype; *b*, same, reproductive organs; *c*, same, upper jaw; *d*, same, lower jaw; *e*, everted portions of male system (see text).

segments are distended by the gut which is filled with a yellowish material composed mostly of what appear to be globules of fat (I have never before seen material similar to this in any branchiobdellid and have no idea as to what it may be). The body wall is exceedingly thin, thinner than in any branchiobdellid known to me. The nephridiopore can be seen in its usual position, but is insignificant in size and the anterior nephridia are apparently reduced and pressed between the gut and body wall in such a way that they cannot be discerned in whole mounts of the worms.

The jaws are small, medium brown, with a dental formula of 5/4; the lateral teeth are small and indistinct.

The slender spermiducal gland lacks any detectable evidence of the presence of a prostatic protuberance or of any differentiated regions. The vasa deferentia and the male funnels cannot be seen in my material and only with difficulty can a very few clumps of spermatozoa be seen to lie in the all but obliterated space between the gut and body wall of segments V and VI.

The bursa is elongate ovoid in shape and there is little indication externally of its division into penial sheath and atrial portions. A series of zig-zag transverse folds in the penial sheath indicates that the penis is eversible. Its cuticular inner lining (when everted) appears to be attached by cytoplasmic strands to the inner wall of the penial sheath. The atrial portion of the bursa is also eversible. A specimen (Fig. 7e) from which the male reproductive system seems to have been mechanically squeezed confirms, somewhat uncertainly, these comments. The penis is an everted, cuticular tube, the bursa is also everted, but the spermiducal gland is lying, at least partially, outside the body and this cannot be the normal copulatory position of this organ. In animals with the penis retracted, both the spermiducal gland and bursa are compressed underneath the gut and hardly extend dorsad beyond the latter's ventral border.

The ejaculatory duct (Fig. 7b) is short and thick.

The spermatheca is, to my knowledge, unique among the branchiobdellids. The spermathecal pore opens immediately into a thick-walled, subglobose spermathecal bursa (Holt, 1960:64) which passes entally into a narrow, thick-walled, blindly ending tube. This tube resembles the ental process of the spermatheca of other species but it appears, however, to contain spermatozoa, which, if true, means that it is homologous to the spermathecal bulb of other branchiobdellids.

Variation: None of note.

Affinities: See below, p. 101.

Hosts: *Cambarus d. diogenes* (Girard), *C. sp.*

Distribution: Known only from the type-locality.

Material examined: The type-series.

***Sathodrilus okaloosae*, new species**

Figures 1-8

Type-specimens: Holotype, USNM 48715, five paratypes, USNM 48716, two paratypes, PCH 2720, on *Procambarus evermani* (Faxon) and *P. versutus* (Hagen), taken 1.0 mile east of Santa Rosa County line on U.S. Highway 90, Okaloosa County, 12 August 1968, by Horton H. Hobbs III.

Diagnosis: Small branchiobdellids (average length of type-series, 1.5 mm); with dorsal ridges on major annulations; jaws dark brown, teeth reflexed posteriorad, dental formula 1/4 (?3/4); bursa about $\frac{2}{3}$ body diameter in length, lessening in diameter towards apex, penial sheath

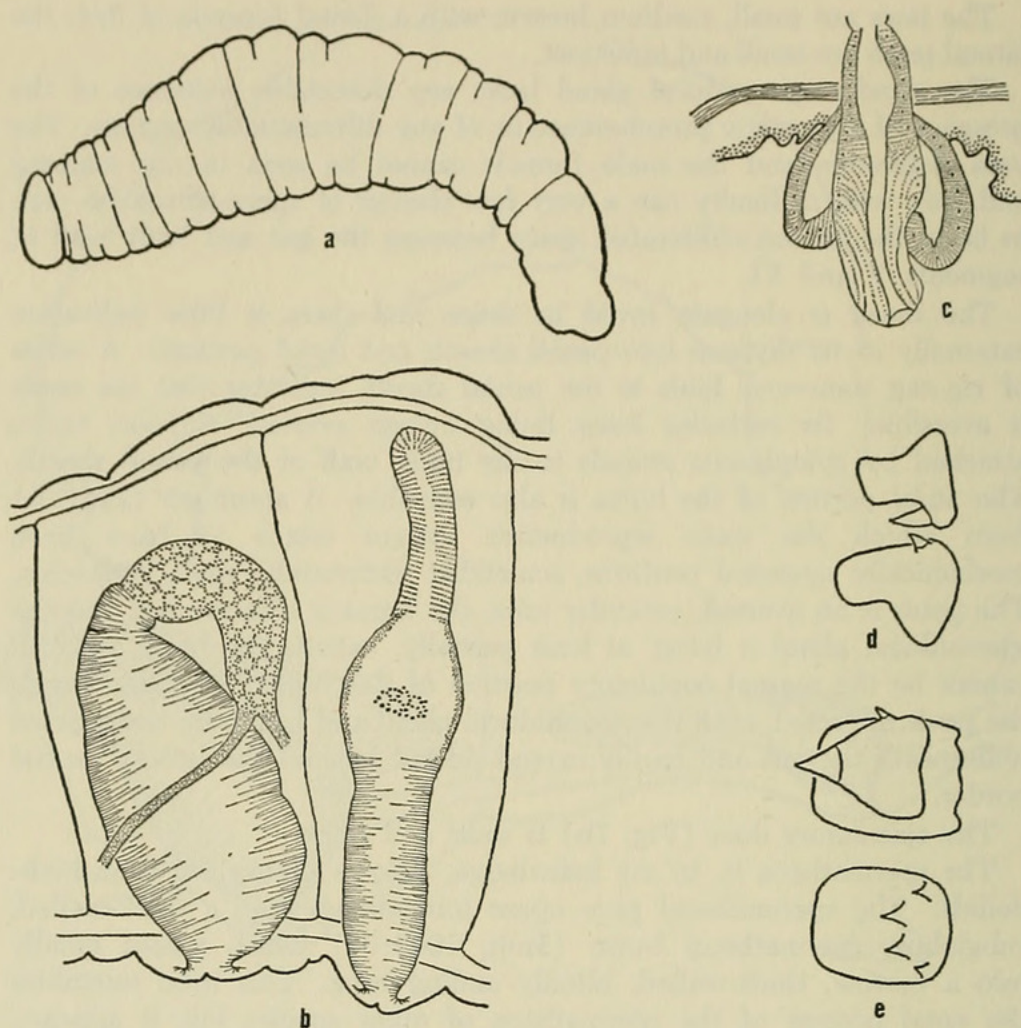


FIG. 8. *Sathodrilus okaloosae*, n. sp. *a*, lateral view of holotype; *b*, same, reproductive organs; *c*, everted penis of paratype; *d*, lateral view of jaws of holotype; *e*, en face view of jaws of paratype.

approximately $\frac{1}{2}$ total length, atrial fold prominent; ejaculatory duct short, thick; spermiducal gland short, about $\frac{2}{3}$ length of bursa, bent ventrad at midlength, no prostatic protuberance, no deferent lobes; spermatheca long, with ental end reaching dorsal border of segment, ectal duct long, ental process long, shorter median bulb only slightly greater in diameter than ectal duct.

Etymology: For Okaloosa County, Florida, within which is the type-locality.

Description: Specimens of *Sathodrilus okaloosae* are small worms. The holotype has the following dimensions: total length, 1.6 mm; greatest diameter (segment VI), 0.3 mm; head length, 0.3 mm; head diameter, 0.2 mm; diameter, segment I, 0.2 mm; diameter, sucker, 0.2 mm. The average dimensions of the holotype and four paratypes are as follows: total length, 1.5 mm (1.1–1.9); greatest diameter, 0.2 mm

(0.2–0.3 mm); head length, 0.3 mm (0.3–0.4 mm); head diameter, 0.2 mm (0.2–0.2 mm); diameter, segment I, 0.2 mm (0.15–0.2 mm); diameter sucker, 0.2 mm (0.15–0.2 mm).

The lips are entire, the upper distinctly longer than the lower. There are no oral papillae. Externally there is a faint, shallow sulcus which corresponds to one prominent internal one.

The trunk segments are distinct; the anterior (major) annuli bear relatively low dorsal ridges. The state of preservation is such that one can only guess at the position of the anterior nephridiopore; presumably it is in the usual middorsal position on segment III.

The jaws are peculiar and diagnostic. They consist of rather broad and thick rectangular plates that bear a raised ridge anteriorly on which the teeth are set. Most unusually, although the teeth point posteriorad in all branchiobdellids, the tooth bearing ridge and the teeth of *S. okaloosae* are bent backward in a very distinctive manner (Figs. 8d, e). The upper jaw bears one very large tooth, and in one paratype a small lateral one is present on one side; I cannot determine in my material whether the normal dental formula is $1/4$ (which it appears to be) or $3/4$ (which I think is more likely). The dental ridge of the lower jaw is not so highly elevated as that of the upper one, but the four teeth, subequal in size, that it bears are as sharply reflexed. Both jaws are dark brown and massive in appearance, though their anterioposterior dimension is only about $1/7$ that of the head.

The spermiducal gland is not well preserved in the holotype, the specimen in which it is best seen, but it appears to be of usual histology, lacks any sign of a prostate, lies high in its segment, runs a short distance anteriorad from its junction with the ejaculatory duct, bends ventrad, and is formed entally by the closely placed union of the vasa deferentia at approximately the midlength of the bursa.

The bursa is elongate ovoid, with a slight constriction demarcating the penial sheath and atrium. The penial sheath composes about $2/3$ of the organ and the eversibility of the penis is indicated internally by transverse folds. There is a heavily muscular atrial fold. In two of the paratypes the penis is everted (Fig. 8c) and its eversible nature is clear, with thin cytoplasmic strands connecting its inner cuticular lining to its outer wall and the ejaculatory duct. The latter is short, thick and heavily muscular.

The spermatheca is distinctive. It is composed of a long muscular ectal duct, a median thin-walled portion that contains a small quantity of spermatozoa and a long ental process that is subequal to the ectal duct in length and of indeterminate nature (muscular or glandular).

Variation: None that can be discerned in the type-series.

Affinities: The absence of a prostatic protuberance allies *Sathodrilus okaloosae* with *S. veracruzicus* and *S. hortonii* from both of which it is otherwise quite different. Only *S. megadenus* and *S. hortonii* have ental processes of the spermatheca. *S. hortonii* has a spermathecal bursa and is unique in this respect. Both *S. hortonii* and *S. okaloosae* have bursae

and penes that are similar to those of *S. carolinensis*. The jaws of *S. horton* are similar to those of other species of the genus; those of *S. okaloosae* are distinctly different from those of any branchiobdellid known to me. The presence of ental processes of the spermatheca and the absence of a prostatic protuberance relate the two species from Florida more closely to each other than either is related to other members of the genus. Their nearest relative seems to be *S. veracruzicus*.

Hosts: *Procambarus evermanni* (Faxon), *P. versutus* (Hagen).

Distribution: Known only from the type-locality.

Material examined: The type-series.

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