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EDITORIAL COMMITTEE

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THE BRANCHIOBDELLIDAE (OLIGOCHAETA) OF NORTH AMERICAN CRAYFISHES

WITH THREE PLATES

BY

CLARENCE JAMES GOODNIGHT

CONTRIBUTION FROM THE ZOOLOGICAL LABORATORY OF THE UNIVERSITY OF ILLINOIS
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1940
VIII. Classification (continued)—

Subgenus Coronata new subgenus

*Cambarincola (Coronata) chirocephala* Ellis, 1919

*Cambarincola (Coronata) philadelphica* (Leidy, 1851)

*Cambarincola okadai* Yamaguchi, 1933, sp. dub.

Genus Xironogiton Ellis, 1919

*Xironogiton occidentalis* Ellis, 1919

*Xironogiton instabilius instabilius* (Moore, 1894)

*Xironogiton instabilius oregonensis* Ellis, 1919

Genus Xironodrilus Ellis, 1919

*Xironodrilus formosus* Ellis, 1919

*Xironodrilus pulcherrinus* (Moore, 1894)

*Xironodrilus pulcherrinus pulcherrinus* (Moore, 1894)

*Xironodrilus pulcherrinus dentatus* new subspecies

Genus Bdellodrilus Moore, 1895

*Bdellodrilus illuminatus* (Moore, 1894)

Genus Stephanodrilus Pierantoni, 1906

*Stephanodrilus obscurus* new species

Genus Triannulata new genus

*Triannulata magna* new species

*Triannulata montana* new species

Genus Pterodrilus Moore, 1895

*Pterodrilus alcicornus* Moore, 1895

*Pterodrilus distichus* Moore, 1895

*Pterodrilus durbini* Ellis, 1919

*Pterodrilus mexicanus* Ellis, 1919

Genus Cirrodrilus Pierantoni, 1905

*Cirrodrilus thysanosomus* (Hall, 1914)

Nomina nuda

IX. Biology

Host Specificity

Food Habits

Longitudinal Distribution of Branchiobdellids in a Stream

X. Conclusions

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Plates
I. INTRODUCTION

The Branchiobdellidae comprise a family of annelid worms which live on the bodies of crayfish. In the older literature this family has been designated as the Discodrilidae, but Hall (1914) showed this name to be untenable as there is no genus Discodrilus. This family is known from Europe, eastern Asia and Japan, and North and South America. So far as is known, these worms are always found on crayfish, but the question whether or not they are parasitic in their food habits is far from settled. The writer believes and will attempt to show that their food consists largely of diatoms and that they are for the most part non-parasitic.

The descriptions of the American branchiobdellids are scattered throughout a number of papers published in various sources, some of which are not generally available. The last paper dealing with the taxonomy of the American forms (Ellis, 1919) appeared twenty years ago. In no recent paper has there been any attempt at synthesis of all the described species by means of diagnostic keys. The last attempt at such synthesis was by Hall in 1914, but his material was so meager that his keys are inadequate, and over half the species now known were described after his paper was published. Except for a new species, inadequately described from poorly preserved material, he included no specific descriptions or comparisons.

Of the known species the locality records are from only a few well-known areas, and many are known from the type locality only. Thus the geographical limits of the species are poorly defined. The last important paper was by Ellis in 1919. He described in fine detail a number of new species and gave new locality records for a few old ones, but he presented few diagnostic keys and attempted very little synthesis.

The present study summarizes the existing information on American forms, presents diagnostic keys, further defines the range of the species, and adds four new forms which were encountered. In an attempt to evaluate the taxonomic importance of morphological characters, the family is divided into two natural groups, the forms with two pairs of testes being recognized as the basis for a new subfamily (Cambarincolinae). The present study also adds to the existing knowledge of the biology of the family.

II. ACKNOWLEDGMENTS

The writer wishes to express his sincere appreciation for the help given him by Professor H. J. Van Cleave, of the University of Illinois, under whose direction this investigation has been conducted. Throughout the
entire period of study Professor Van Cleave has given helpful advice and encouragement, thus contributing largely to whatever success this investigation has attained.

The writer is indebted to Dr. Carl L. Hubbs for permission to examine the material in the Museum of Zoology, University of Michigan, and for a place to work while at the museum. He also wishes to express his thanks to Dr. David H. Thompson for permission to examine the material in the collections of the Illinois State Natural History Survey, to Dr. Percy Moore for advice and criticism, to Dr. A. S. Pearse for material from North Carolina, to Dr. John D. Mizelle for specimens from Oklahoma, to Dr. James Sanders for specimens from South Dakota, to Dr. J. Henry Walker for material from Alabama and Florida, and to Dr. Edwin P. Creaser for information concerning the location of collections.

The writer is likewise indebted to his fellow graduate students, especially Dr. Harry G. Kimpel, for assistance in making field collections.

III. MATERIALS AND METHODS OF STUDY

Large amounts of material were available for this study. In general, two methods were employed to obtain this material: (1) actual collecting of crayfish and removing of worms, and (2) examining museum jars of preserved crayfish and obtaining the worms that had fallen to the bottom or still remained on the dead crayfish.

For fixing the worms, the best results were obtained with warm A.F.A. (85 parts 85% alcohol, 10 parts formalin, 5 parts glacial acetic acid). The crayfish were dropped into this solution and the fixed worms were gathered from the bottom after decanting. However, the worms fixed in formalin and higher grades of alcohol were found to be adequate for taxonomic studies, though slightly contracted. Worms were studied both from total mounts and from sectioned material. The best results with total mounts were obtained by running the worms up through the grades of alcohol and clearing in xylol, then mounting in balsam without staining. In some cases excellent results were also obtained by staining with a solution of four drops of Delafield's hematoxylin and four drops of Ehrlich's acid hematoxylin in 20 cc. of a saturated water solution of potassium alum, then destaining, neutralizing in running tap water, clearing, and mounting in balsam. Borax carmine was also used with some success.

While in most cases the significant taxonomic details could be demonstrated in total mounts by means of dorsal, ventral, and lateral views, these findings were checked by means of sections cut at 10 or 20 microns. Transverse, frontal, and longitudinal series were prepared.
Excellent results were obtained by staining the sections with Delafield’s hematoxylin, going up through alcohols to 70%, destaining in acid 70%, running down to water, and washing in tap water 30 minutes or longer, going up to 95% alcohol, counterstaining with eosin, clearing, and mounting in balsam. Heidenhain’s iron hematoxylin, with eosin as a counterstain, was used to some extent.

The paraffin ribbon was affixed to the slide with bakelite. A mixture of 2.0 grams gelatin, 1.0 grams phenol, 15 cc. glycerin, and 100 cc. distilled water was smeared on the slide, and the sections were floated on with 4% formaldehyde solution.

Of the twenty-two species included in this study, all but three have been studied from large amounts of material, many species being represented by hundreds of specimens.

Field observations were also carried on during this study to determine the abundance and distribution of the branchiobdellids.

IV. HISTORY OF INVESTIGATIONS ON THE BRANCHIOBDELLIDAE

Apparently the first published note of this group was by Rosell (1755). Braun in 1805 mentioned them in a description of some leeches. A few other papers, Müller (1806) and Savigny (1809), mention them also, but it was not until 1823 that the first taxonomic description was given. In that year Odier published in the Mémoires de la Société d’Histoire Naturelle de Paris a very fine description of the common branchiobdellid of western Europe which he called Branchiobdella Astaci. He believed it was a leech and closely related to the genus Hirudo. He gives (p. 75) the following characterization of the genus: “un corp contractile un peu aplati, composé de dix-sept anneaux, terminé par un disque préhensile; une tête oblongue, garnie de deux lèvres; une bouche armée de deux mâchoires cornées, triangulaires, dont la superficie plus grande, et point d’yeux.” He spends some time (p. 76) pointing out that this form was a leech and not a tipulid larva as one M. de Blainville had previously reported to the society.

Apparently no important work was published on the group for the next twenty years. Then in 1835 G. Henle reported a careful anatomical study in an article entitled “Ueber die Gattung Branchiobdella.” Vallot in two papers (1839 and 1845) also reported briefly on this group. Moquin-Tandon in his leech monograph of 1846 included a description of Branchiobdella.

Previous to 1851 all work on this family was by Europeans and on European species, but in that year Joseph Leidy published in the Proceedings of the Academy of Natural Sciences of Philadelphia (p. 209) a
description of an American species which he called *Astacobdella philadelphica*. There followed a series of brief papers by Europeans on branchiobdellid anatomy, but thirty-one years elapsed before the next significant taxonomic paper was published.

The next American paper was by Verrill (1873). In his synopsis of American leeches he republished Leidy’s description of 1851.

A series of papers published in Europe on European species next appeared. Whitman (1882) published a description of *Branchiobdella pentadonta*, a new species. Next appeared a number of papers on the anatomy and development of Branchiobdella. These were by various Europeans who were only incidentally interested in the group. These included Gruber, Lemoine, Voigt, Ostroumoff, Vejdowski, Rohde, Salensky, and others.

In 1894, forty-three years after Leidy’s paper, Moore published descriptions of “Some Leech-like Parasites of American Crayfish.” He included *Branchiobdella illuminata*, *B. pulcherrima*, *B. instabilis* new species, and *B. philadelphica* (Leidy) in his discussion. The following year, in another paper, he described a new genus, *Pterodrilus*, which included two new species, *P. alcicornis* and *P. distichus*. In 1895 Moore published a very fine account of the anatomy of *Bdellodrilus illuminatus* (Moore). This is the best general anatomical account yet published and the only one on an American species. He pointed out in this paper the need for more work on the nephridial system. This complicated system was worked out and the results were published the following year by Voinow on *Branchiobdella varians*. Moore in 1897 gave an excellent account of the nephridial system of *Bdellodrilus illuminatus*. Four years later, 1901, his monograph on the leeches of Illinois was published in which he mentioned the fact that in the collection *Bdellodrilus philadelphica* was found on *Cambarus diogenes* and *C. blandiingi*. This paper marks the end of Moore’s work on Branchiobdellidae. Afterwards he turned his attention largely to leeches.

F. Schmidt pointed out in his papers (1902 and 1903) that the musculature was more definitely similar to the Oligochaeta than to the Hirudinea. Some time later (1905) Pierantoni, an Italian, began to publish on the group, giving a description of *Cirrodrilus cirratus*, a new species from Japan. He followed this in 1906 by a brief general account of the genus Branchiobdella. In another paper (1906b) he described two new forms, *Branchiobdella tetradonta* from California and *B. digitata* from Japan. In the same year Smallwood, an American, gave an account of some observations on the life habits of some branchiobdellids in the neighborhood of Clear Lake, New York.

The year 1912 is a memorable one in the study of this group, for
in that year Pierantoni published the first monograph. In this he summarized the anatomy of branchiobdellids and showed that they are definitely Oligochaeta. He included several new species and all previous ones. He listed: *Cirrodrilus cirratus* Pier. from Japan, *Branchiobdella parasita* Henle, *B. pentadonta* Whitman, *B. hexadonta* Gruber, and *B. astaci* Odier from Europe; *B. minuta* n. sp. from Amur-Riff; *B. anatis* n. sp. and *B. dubia* n. sp. of unknown habitat; *Stephenodrilus sapporensis* Pier., *S. japonicus* n. sp. from Japan; *S. koreanus* n. sp. from Korea. From America he listed *Branchiobdella tetradonta* Pier., *B. americana* n. sp., *Edelodrilus pulcherrimus* (Moore), *B. instabilis* (Moore), *B. illuminatus* (Moore), *B. philadelphicus* (Leidy), *Pterodrilus alcicornus* Moore, and *P. distichus* Moore.

In the same year (1912) Ellis described a new American worm, *Cambarincola macrodonta* from Colorado. He included a brief key to some of the described forms. Two years later (1914) Hall briefly and inadequately described a new species from Utah which he called *Ceratodrilus thyssanosomus*. He also included a summary of locality records for American species and erected the superfamily Branchiobdelloidea. In 1915 Tannreuther published a cell lineage study using *Cambarincola philadelphica* as a subject. In 1918 Frank Smith included a few species in his chapter in Ward and Whipple’s “Fresh Water Biology.” In the same year Ellis listed species he collected around Douglas Lake, Michigan. In 1919 he published an account of “The Branchiobdellid Worms in the Collection of the United States National Museum.” He described as new *Xironodrilus formosus*, *Xironogiton occidentalis*, *Xironogiton oregonensis*, *Pterodrilus mexicanus*, *Pterodrilus durbini*, *Cambarincola vitrea*, *Cambarincola chirocephala*, and *Cambarincola inversa*. This is the best single article on the taxonomy of the American species, but no generic keys and few specific keys are included. This was Ellis’ last paper on the branchiobdellids. In 1928 Alessandra gave an account of a new European species, *Branchiobdella italica*.

Stephenson published a monograph on the Oligochaeta in 1930, in which he gave a lengthy discussion of the Branchiobdellidae, including as valid genera: Branchiobdella, Cirirodrilus, Stephanodrilus, Edelodrilus, Pterodrilus, Ceratodrilus, Cambarincola, Xironodrilus, and Xironogiton. In 1932 H. Yamaguchi began writing on this group. He published several preliminary papers and finally in 1934 a monograph of the Japanese forms including nineteen species in three genera. In 1935 Evans collected worms in Champaign County, Illinois. He reported (1939) four species: *Cambarincola macrodonta*, *C. vitrea*, *C. chirocephala*, and *Edelodrilus illuminatus*. 
V. MORPHOLOGY OF THE BRANCHIOBDELLIDAE

Pierantoni (1912) in the first general monograph of the group characterizes the Branchiobdellidae as follows:

Corpo diviso in due regioni, una cefalica di tre segmenti con lobo preorale ventosiforme, bilobo o plurilobato, con o senza appendici digitiformi ed un’altra regione, del tronco, di II segmenti, terminata da ventosa e priva di setole.

Bocca provvista di due forti mascelle più o meno dentate.

 Sistema circolatorio fatto da un vaso dorsale con seno perienterico e da un vaso ventral riunito a quello da quattro paia di tronchi trasversali anteriori e da uno posteriore.

 Sistema escretore fatto da due paia di nefridii posti nei segmenti del tronco aprentisi per pori dorsali posti nel 4° e nel 9° segmento del tronco.

 Testicoli 1 o 2 paia, nel 5° e nel 6° e nel 7° segmento del tronco.

 Spermateca nel 5° segmento, impari; atrio ugualmente impari provvisto di pene e di condotti seminali pari in numero di due o di quattro, con corrispondenti paia di imbuti ciliata nel seg. 5° e nel 6°, trattenuti dai sepimenti posteriori corrispondenti; ovarii e pori femminili nel 7° segmento.

A. EXTERNAL CHARACTERS

The branchiobdellids are a homogeneous group of worms ranging from 1 to 12 mm. in length. The body consists of two parts, the head and the trunk. A caudal sucker is present at the posterior end of the body.

The head is somewhat cylinder-shaped. The mouth is surrounded by fleshy lips, which may or may not be lobed. In some forms the lobes may be extended into tentacles. Inside the mouth, at the base of the muscular ring or sucker, is a circllet of numerous minute papillae. The head shows a groove at the base of the lips and a median dorsal depression. The lack of definite segmentation has led to various interpretations of the number of annuli included. Pierantoni (1912) considered that the head consists of a prostomium and three segments; the prostomium represented by the peribuccal region, the first cephalic segment between the peribuccal ring and the dorsal pit, the second segment posterior to the pit, and the third, indistinct in most species, bordering the trunk region. According to Pierantoni there are three bilobed ganglia and three vascular commissures connecting dorsal and ventral vessels; so he concluded that the internal anatomy agreed with his three-segment theory. Moore (1895b:499) considered the peribuccal ring as a segment and so believed there are four head segments. Schmidt (1905) agreed with Pierantoni that there are only three, while Vejdowski (1884:39) thought that there are six or seven segments, since the ganglia are bilobed. Ellis (1912:482) and Stephenson (1930:796) agree with Moore. Stephenson (1930:796-797) summarizes the evidence for the four-segment head theory as follows:

It would, however, seem to be erroneous to describe the circumbuccal ring as a prostomium; it is obviously a peristomium, and the peristomium is universally the first true segment in the Oligochaeta. If so reckoned here, there would be
four segments in the head, the prostomium having disappeared (as, e.g., in Chaetogaster) as a distinct division. Moreover, in the Limicolae the first segment has no vascular commissures (apart from the arch uniting the anterior ends of the dorsal and ventral vessels); the first of the commissural vessels is in segment II. The vascular arrangement of the Branchiobdellidae, therefore, also indicates four segments to the head. Again F. Schmidt (1905) describes a thickening situated at the middle of the length of the pharyngeal connective on each side, which is due to an aggregation of nerve cells; a nerve is given off from the connective just above, and another from just below, this thickening, and these nerves pass forward to the buccal segment. The thickening is in addition to the buccal ganglion (with a visceral distribution), and seems to represent the proper ganglion of the buccal segment, so that again four cephalic segments seem to be indicated. Lastly, by counting four head segments the position of the genital apertures and organs is brought into line with that in the majority of genera of Lumbriculidae, with which the Branchiobdellidae are closely allied.

My own observations tend to support the four-segment theory.

The trunk region is variously shaped in different species. In some forms, as Cambarincola, it is cylindrical and relatively uniform in diameter throughout its entire length. In others as Xironodrilus, it is flattened and wider in segments VI and VII than in the others. Xironogiton is flattened and widest in the posterior segments.

Dorsal appendages are present in some forms. In Pterodrilus these consist of cylindrical fleshy protruberances along the median dorsal line of the body. In Cirrodrilus they extend transversely across the dorsal surface as a pointed band with usually six, sometimes seven or eight, points on the free margin. These dorsal appendages usually have ridges of transverse muscle fibers associated with them. Little is known of their function. Moore (1895a:450) first pointed them out on American species. He says:

Regarding the function of the dorsal organs there is little to say. A priori one would expect them to be respiratory, but the apparent entire absence of blood vessels, which are unrevealed after a careful study of sections would tend to throw strong doubt upon such an interpretation. Irregular spaces are evident here and there between the muscle fibres but these appear to be continuous with the intermuscular spaces which are developed between the circular and longitudinal muscle fibres of the body walls, and have not been traced into any communication with the body cavity. Until an opportunity is afforded of studying living examples in their proper habitat, and observing the uses to which these organs are put, no opinion can be vouchsafed.

Externally the trunk consists of eleven segments. The first eight are quite distinct and prominent. They are divided into two unequal parts by a sulcus towards the posterior fourth of the segment. The last three segments are smaller and less distinct. The last segments form the caudal sucker, the principal attachment organ of the worm. On a few species additional small, somewhat concave, glandular adhesive disks are present near the lateral margin of segments VIII and IX. This is true in Xironodrilus pulcherrimus (Moore) and Xironogiton occidentalis Ellis.

Pierantoni (1912) says the internal segmentation would correspond
to the external as there are nine ganglia on the trunk portion of the nerve cord and the most posterior of these corresponds to three. He shows this last by tracing the nerves that have their origin in the posterior ganglion.

Schmidt (1905) thinks otherwise, believing the last ganglion corresponds to five. This then would make the total number of trunk segments thirteen. My own observations on this point have been in no way conclusive but they tend to support Pierantoni's view.

**B. Body Wall**

The epidermis contains a great number of glands. Moore (1895b: 502) gives the best account of the epidermis and its glands in connection with his study of *Bdellodrilus illuminatus*:

The epidermis consists of ordinary epithelial cells, of non-nucleated protoplasm, and of gland cells, which are present in great number and variety. The epidermis proper presents little modification. The cellular elements are arranged with relation to the circular muscle fibers, which encircle the body walls at regular intervals and are so deeply imbedded in the epidermis that they are frequently almost in contact with the cuticle, only a thin layer of protoplasm separating them.

Concerning the epidermal glands, Moore (1895b:503) continues:

Glands are very richly developed in connection with the epidermis of *B. illuminatus*; and while all are constructed of similar elements, they differ much in size and arrangements of these elements. The elements are unicellular glands somewhat of the goblet cell type. In most cases they consist of an enlarged irregularly polyhedral body containing the nucleus, and tapering at one end into a slender, more or less elongated ductule. The only exceptions are those glands which are referred to as salivary and bursal glands.

Certain small mucous glands are very generally distributed over the skin; especially on the head, where they are regularly arranged in several transverse rows. They may be unicellular, or consist of three or four unicellular glands, the ductules of which are twisted or spiral.

On the sixth and seventh somites such glands become greatly increased in number and size; the body walls, particularly on the dorsal side, being little more than a thick glandular layer, which constitutes the clitellum. The unicellular glands are here aggregated in sub-globular or pyriform groups of from three to twenty or more, which extend inward to a length of from .03 mm. to .065 mm. Being arranged in a single stratum each cell forms part of the surface of the gland, close to which lies the deeply staining nucleus, in a mass of almost as deeply staining glandular protoplasm. The inner ends are glandular but clear and often unstained, and pass into ductules, which may be bound together into a fascicle, and either open in close proximity on the surface, or separate and open singly. In either case they wind a slightly spiral course, which is best seen in living animals, particularly when stained with methylene blue. The cell bodies have an average diameter of .011 mm., the ductules of .0018 mm., and a total length of about .05 mm.

The several cells in each group appear not to function simultaneously. Some have completely broken down into secretion while others are entirely protoplasmic.

Other masses of gland cells are developed in different parts of the epidermis. This is true in connections with the head, lips, and especially the posterior sucker. Concerning this last Moore (1895b:504) adds:

Glands similar to those described by Dorner, and more fully by Voigt, in Branchiobdella, are well developed in this species in relation to the posterior
sucker. The glandular masses, which largely fill the tenth and eleventh and part of the ninth somites, are pyriform, or aggregations of several pyriform groups. Large, granular, lightly staining cell bodies give rise to long slender ductules which, first united into fascicles, break up into smaller and smaller groups, and are finally distributed singly on all parts of the surface of the acetabulum. This arrangement is beautifully shown in living specimens. The ductules are filled with rounded granules, which may be forced from their mouths in living worms by pressure. The granules will emerge in strings, absorb water, swell, and run together in a very short time, forming a homogeneous mucus.

The body wall is then made up of epidermis, with its cuticular covering, and the muscle layers of circular and longitudinal muscle fibers. These muscle layers are arranged like those of most Oligochaeta with an outer circular and an inner longitudinal layer. According to Schmidt (1903), in Branchiobdella the cells of the circular layer regularly number twenty-five on each side of an ordinary segment; and each segment has its own system of longitudinal cells, forty-four in each half of the segment.

The cuticle is thin, transparent, colorless, nearly homogeneous and follows the epidermis, which secretes it, closely. It follows invaginations into the oral and sexual cavities. Cuticular markings are evident and appear to be different in different species. It is possible that these markings may furnish diagnostic characters. The writer hopes later to investigate this possibility.

The intersegmental septa, according to Moore, are formed of thin sheets of parallel dorso-ventral muscles arising from the ends of the longitudinal fibers. Septa practically disappear between the first four segments and are represented by thin slips that support the alimentary tract from the body walls. Septa are extremely well developed between the sexual somites.

The musculature of the posterior sucker is very well developed. Moore (1895b:509) says about Bdellodrilus illuminatus:

The musculature of the posterior sucker is complex, and well adapted to secure strength and mobility. The circular muscles undergo little change; but the longitudinal split up, by the branching of individual fibers, into a set which are the direct continuation of the body longitudinal fibers, a second set which pass dorso-ventrally across the body cavity, a third which radiate to the margins of the disc, and lastly a highly branched set which have become slightly displaced at their posterior ends, right or left from their original longitudinal direction, and consequently pass with a slight spiral turn from the body walls to the periphery of the sucker, where they cross and interface with their fellows having an opposite displacement.

C. Digestive System

The alimentary canal may be divided into several regions, the oral, pharyngeal, esophageal, intestinal, and anal. The mouth is situated between the lips into which the peristomium is divided. Aggregations of unicellular glands are developed from the margins and inner surfaces of the lips.
Posterior to these are slit-like dorsal and ventral infoldings of the epidermis and cuticle, bounded by a thickened epidermal pad. On the posterior walls of these invaginated pockets, the jaws are molded.

These jaws, one ventral and one dorsal, are solid chitinous plates. According to Ellis (1919:242) the primitive type is one with several sub-equal teeth. Modifications have progressed along one or both of two lines, namely, (a) reduction in number and (b) increase in size of some teeth correlated with reduction in size of others.

The jaws are provided with a powerful musculature. This is well described by Moore (1895b:511) for *Bdellodrilus illuminatus*:

The mechanism of the jaws is seen to be powerful and efficient. The muscular plates, with their radiating fibers, regulate the distance between the two jaws, approximating or separating them as the circular or radial fibers contract in turn. The circular muscles seem sufficiently powerful to bring the jaws together with crushing force. The protractor muscles carry the jaws forward (with a rotary or rocking movement on the muscular pads) against an object of attack, the lower jaw acting with its teeth as a hook, while the powerful retractor muscles of the upper jaw bring its toothed blade with a shearing motion between the ventral teeth. Thus is constituted an efficient pruning apparatus, the chief purpose of which is, I believe, the clipping off of branchial filaments of the crayfish host, from which the blood is then drawn. They are probably also used for mowing down the colonial infusorians which cluster along the borders of the branchial chamber, and remains of which are frequently seen with diatoms, etc. mixed with crayfish blood in the stomach of the worms examined.

The jaws mark the beginning of the pharyngeal region, which is characterized by great development of the musculature and which may function as a suction bulb. This region extends to the esophagus, which usually begins in the first body segment.

The esophagus is short and ill-defined. Its muscular coat is made of a sheet of circular and longitudinal muscles. This coat continues throughout the intestine, into which the esophagus rapidly merges. The intestine continues with various sacculations to the anus, situated in the dorsal half of segment X. In the second or third somite the peritoneum is modified to form chlorogogue cells which envelop the intestine except in the seventh somite. In the region of the dorsal blood vessel they arch over its walls. According to Moore (1895:513) they appear in surface view as "a mosaic of large polygonal cells, with straight closely fitted edges, possessing a large clear nucleus, and cytoplasm of a greenish brown color, due to the presence of numerous large granules and minute globules. In sections they appear more or less flattened, or prominently bulging, according to their position and the degree of contraction of the intestine." Being absent in the seventh segment they permit the maturing ova to come into close contact with the walls of the blood sinus, an important nutritive consideration.

The intestine in segments VIII and IX is a very narrow tube, the rectum. In the region of the anus the circular muscles increase to form a sphincter.
D. The Vascular System

According to Stephenson (1930:798) the vascular system of the Branchiobdellidae consists of a peri-enteric sinus, a dorsal and a ventral blood vessel, four pairs (three cephalic and one in front of the trunk) of vascular commissures in the anterior part of the body and one near the posterior end. Moore (1895b:514) found seven vascular arches present in *Bdellodrilus illuminatus*; four in the head and one each in segments I, VII, and IX. These connect the dorsal and ventral blood vessels.

In front of the third segment the dorsal vessel is large and pulsatile (the so-called heart) but posterior to this it loses its distinct identity and merges into the peri-enteric sinus. Moore (1895b:514) describes this sinus as follows:

The peri-enteric blood sinus, to which Voigt first especially called attention in Branchiobdella, is highly developed in the present species, in which it exists as a continuous space between the muscular and epithelial coats of the intestine, extending from the third to the eighth somites inclusive, and breaking up at each end into a system of passages and lacunae having a retiform arrangement. The sinus has an average depth of .05 mm., and is without true walls other than the intestinal coats between which it lies. It is crossed by numerous protoplasmic strands and columns which bind its walls together, and remind one of the stalactites and columns of a limestone cave. These become larger and more frequent towards the ends of the sinus, which they finally interrupt so much as to convert it into the terminal plexuses mentioned.

Throughout its entire length the ventral blood vessel lies in contact with the dorsal side of the nerve cord and passes through the ganglia of each segment in a deep groove. The ventral vessel terminates in the tenth segment in a pair of large trunks which arch around the intestine, and pass forward to empty into the dorsal region of the peri-enteric sinus, thus forming the beginning of the dorsal enlargement, which here receives the dorsal ends of the plexus of the blood passages.

Concerning the connecting lateral arches in *Bdellodrilus*, Moore (1895b:516) continues:

In the seventh somite it [the ventral blood vessel] gives off a pair of large ovarian vascular arches, which empty into the dorsal enlargement of the peri-enteric sinus. The supra-neural vessel terminates in the tenth somite in a pair of large trunks, which arch around the intestine, and pass forward to empty into the dorsal region of the peri-enteric sinus, thus forming the beginning of the dorsal enlargement, which here receives the dorsal ends of the plexus of blood passages. Of the seven pairs of lateral arches mentioned, a labial and three cephalic pairs, in the pharyngeal region, arise from the anterior prolongation of the heart; an oesophageal pair which owing to their great length are often looped into the succeeding somite, arise from the anterior end of the heart itself; a large pair of ovarian arches, which are more or less imbedded in the maturing ova, lie in the posterior part of the seventh somite; and the seventh pair, the largest of all, posteriorly connect the supra-neural vessel with the peri-enteric sinus. The walls of the supra-neural and lateral vessels are very delicate and non-contracile. At wide intervals, nuclei, which resemble those of the peritoneal cells, may be detected, but I have found no traces of cell boundaries.
E. Respiratory System

In the Branchiobdellidae, as in many aquatic Oligochaeta, there are no specialized organs of respiration. Respiratory exchange simply takes place in general through the body wall.

F. Excretory System

The excretory system of the group consists of two pairs of nephridia. Those of the anterior pair are placed asymmetrically and open in the dorsal part of segment III just behind septum II/III. They may open either through a single pore or through paired pores. As mentioned, they are not symmetrical, so the one may extend from segment III to I, and the other posteriorly from III to IV. The nephridia of the posterior pair are symmetrical and situated in segment VIII, opening to the outside just behind furrow VIII/IX.

The best accounts of the finer anatomy of the branchiobdellid nephridium are furnished by Moore (1897) and by Voinow (1896). These studies are well summarized by Stephenson (1930:224-226), who says:

Each nephridium begins in an open ciliated funnel, of which the lips are formed of two marginal cells; the single central cell bears a long ciliary flame, and unlike that of Lumbricus is tubular and surrounds the whole funnel below the marginal cells; this is followed by the stalk of the funnel, also composed of a single cell.

The next region constitutes the special peculiarity of the Branchiobdellid nephridium; it is called by Moore the plexus region. In the undisturbed condition of the organ it forms a compact lobulated mass; but when this is slightly teased apart it is seen to consist of a single tube, alternately swollen out and contracted; in each swelling there is a labyrinth of branching and anastomosing canals, while in each contracted part the lumen is single. At each contracted part is a nucleus, and here also on the inner surface of the wall is a ciliary flame; both nuclei and flames are absent from the parts occupied by the plexuses. The tube is to be considered as intracellular, the territory of each cell consisting of one of the narrowed sections of the tube and the adjacent parts of the swellings on each side. The plexus region is granular and yellowish and appears to be a seat of considerable excretory activity.

The looped portion of the organ succeeds the plexus region. It consists of two loops, a longer and a shorter, the longer with an irregular and twisted course, the shorter less tortuous. Each limb consists of a series of drainpipe cells, and the two limbs of a loop are apposed and mostly fused together. In the long loop are seen at intervals nuclei and accompanying ciliary flames—twelve of each; in the connecting tube between the two loops is a single nucleus and flame, and in the short loop ten nuclei but only one flame. On the inner surface of the tube in this region are seen peculiar minute rod-like markings, most numerous at the turning-point of the long tube; these are occasioned by a lining coat of bacteria.

The wall of the long loop is only slightly granular, that of the short stains deeply and is very densely granular, the granules being disposed in radial lines. In the walls of the short tube, in the living organ, are seen granules exactly similar to others contained within the enlarged peritoneal cells which invest the loops, and similar granules occur also in its lumen. The cells, therefore, deposit solid particles in the lumen of the tube, in addition to passing in fluids containing matters in solution. Accumulations of disintegrated coelomic corpuscles are stated by Moore to be found in all parts of the nephridial lumen.
The duct passes along the plexus region, the zigzags of which are arranged on it as on a supporting axis, then surrounds the neck of the funnel in a small loop, undergoes a thickening of the wall in which are several small diverticula of the lumen, and enters the body wall. It consists of about ten cells, but no cilia.

The peritoneal covering is constituted by large cells with elongated processes extending outwards into the coelomic cavity. These cells apparently also take part in the excretory process.

G. THE NERVOUS SYSTEM

The branchiobdellids have a pair of supra-esophageal ganglia lying just posterior to the dorsal jaw pad. According to Moore the two ganglia are united across the median line by a cord of nerve cells and a fibrous commissure. Each bears posterior lobes which are in turn divided into large external and small internal parts and connected to the main ganglion by three strands of nervous tissue. The circum-esophageal connectives extend as thick strands of nerve fibers with a partial covering of nerve cells from the ganglia. They pass around the pharynx and each bears a bilobed stalked ganglion just before they join. They unite to form the ventral nerve cord, and just posterior to this anastomosis form two pairs of larger ganglia. This makes four pairs of double ganglia within the limits of the head (see four-segment head theory above).

Numerous nerve fibers arise from the circum-esophageal connectives and the supra-esophageal ganglion and pass forward to the peristomial region. These end in the circum-oral hairs and oral papillae.

The ventral nerve cord consists of two distinct halves throughout its length. It enlarges at the ganglia and narrows in the inter-gangliar intervals.

In the body segments there are eight pairs of bilobed ganglia and a posterior ganglionic mass called the anal ganglion. This ganglion is composed of several pairs of ganglia, three according to Moore and five according to Schmidt. The fifth and sixth ganglia are displaced to the right of the median line by the spermatheca and male atrium. Three pairs of nerves arise from the region of each pair of ganglia, one from each end and one from the transverse constriction. They supply the body walls, going between the two layers of muscles and splitting up as they proceed. The first and second nerves supply the major annulus; the third splits, one branch going also to the major annulus, the other branch supplying the minor annulus.

A thin muscular sheath encloses the nerve cord for its entire length and includes the ventral blood vessel.

H. THE REPRODUCTIVE SYSTEM

The male organs are situated in segments V and VI. In the genus Branchiobdella a pair of testes is present in segment V. In all other known genera an additional pair is present in segment VI. The sperms
are liberated directly into the body cavity, and in mature worms the testes cannot be detected. One or two pairs of vasa deferentia and funnels (depending on the number of testes) are present. The two vasa deferentia of each pair unite and all open within a single atrium. The atrium consists of a dilated ental portion and an ectal portion that is a narrow short bursa. The penis, which may or may not be eversible, is situated within the bursa. According to Michaelson, the atrium may be provided with glands near the place of entry of the vasa deferentia, but these are never compacted into a single prostate. In some genera an accessory sperm tube is present. This consists of a blind tube extending dorsally and anteriorly from the bursa.

The female reproductive system is situated in segment VII. A pair of ovaries is situated on the posterior face of septum VI/VII. In sexually mature worms large eggs are often present in segment VII. The oviducts are represented by two funnel-like pores in the ventro-lateral walls in the posterior part of segment VII. These pores are ciliated. A glandular clitellum forms about these genital segments. A spermatheca is present in segment V. It is unpaired and opens in the mid-ventral line about the middle of the segment. It is quite variable in form in different species. The blind end is usually free but may be attached by means of a peritoneal investment.

VI. RELATIONSHIPS OF THE BRANCHIOBDELLIDAE

From their general appearance, the presence of jaws, the absence of setae, and the posterior sucker, the Branchiobdellidae were originally considered leeches. Odier (1823) in the first taxonomic description of the group has a sub-title of "Nouveau Genere d'Annelides de la Famille des Hirudinées." Leidy (1851) and Verrill (1873) considered the American branchiobdellids to be leeches. They were omitted by Beddard (1895) in his monograph on the Oligochaeta, and Michaelson (1900) failed to include them in his monograph in the Tierreich series. Later Michaelson (1919b) insisted that they were Oligochaeta and closely related to the Lumbriculidae.

In 1903 F. Schmidt showed that the musculature in the Branchiobdellidae is definitely like that of the Oligochaeta and unlike that in most Hirudinea. Pierantoni (1912) in his monograph discussing their anatomy as Oligochaeta notes how closely they resemble Mesoporodrilus. Michaelson (1919b) shows how the peculiar characters of the branchiobdellids are merely adaptations to parasitic life and could be derived from other Oligochaeta. The short body and posterior sucker are apparently adaptations to the habitat. The pharynx, he says, is a sucking apparatus, and the pro stomum is absent. Both these characters are present in Chaetogaster, a
BRANCHIOBDELLIDAE OF CRAYFISHES—GOODNIGHT

genus of Naididae the members of which are carnivorous and sometimes ectoparasitic. Michaelsen further compares the jaws to the pair of buccal stylets with chitinous tips in the buccal cavity of certain Enchytraeidae.

Since their genital organs are so much like those of the Lumbriculidae, it is generally agreed that they have a common origin with that family. Both these families have the combined male ducts opening to the outside on the segment that contains the hinder pair of testes. In many respects the Branchiobdellidae are only modified Lumbriculidae. Their relationships are shown in the accompanying diagram from Stephenson (1930:705).

Diagram of Relationships (After Stephenson, 1930)

Michaelsen (1919b: 152) points out the similarity between leeches and oligochaetes and that the most significant difference is the position of the testes, posterior to the ovaries in Hirudinea and anterior in the Oligochaeta. So he proposes the following natural classification of annelids:

KREIS ANNELIDES
I. Klasse Archiannelides
II. Klasse Chaetopoda
   1. Ordnung Protochaeta
   2. Ordnung Polychaeta
III. Klasse Clitellata
   1. Ordnung Oligochaeta
   2. Ordnung Hirudinea
IV. Klasse Echiuroidea
V. Klasse Sipunculoidea

The two families, Branchiobdellidae and Acanthobdellidae, link the Oligochaeta and Hirudinea inseparably. Frank Smith (1920) reported this work in English, and at the time seemed to agree with the proposed classification.
VII. CHARACTERS OF TAXONOMIC SIGNIFICANCE

Stephenson (1930:796) calls the Branchiobdellidae a homogeneous group. However, even though they are very similar in structure, there are distinct generic and specific differences. Below are discussed the various morphological characters which the writer believes to be of diagnostic significance.

A. Body Shape

While the shape of the body is somewhat variable it seems to correlate fairly well with other characters as a basis for generic description. For example, the flattened shapes of Xironodrilus and Xironogiton, as described above (page 13), are quite distinctive.

B. Dorsal Appendages

The presence of distinct dorsal appendages, described above, has been used by Moore (1895a) as a generic character in establishing the genus Pterodrilus and followed by Ellis (1919) in describing additional species of this genus. Yamaguchi (1934:180) doubts the generic value and perhaps even the specific value of these dorsal appendages:

The dorsal appendages are known to be present in several species belonging to Pterodrilus and Ceratodrilus. According to Moore (1894) [1895a], Pt. alciornus and Pt. disticus are provided with dorsal transverse ridges and wing-like or cylindrical appendages located in the free margin of the ridges. Ceratodrilus thyssanosomus also bears dorsal appendages extending from the dorsal transverse ridges (Hall, 1914). Digitiform dorsal appendages have been described in two Japanese species, Stephanodrilus cirratus and St. uchidai, which was at that time referred to Ceratodrilus (Yamaguchi, 1932a). The digitiform appendages of these species are mounted on dorsal transverse ridges which become lamelliform in cirratus, while in uchidai the ridges are rather inconspicuous so that the present writer overlooked them in his previous work (1932a). According to Moore (1894), the dorsal transverse ridges of Pt. alciornus are supported by dorsal segmental muscle fibers connecting the anterior with the posterior covering of hypodermis. Similar dorsal muscle fibers are also found in the dorsal transverse ridges of cirratus and uchidai. In the former species these fibers are quite conspicuous in highly developed ridges. The dorsal segmental fibers seen in these three species are found only on the dorsal side and are distinguishable from longitudinal muscles running the whole body length by their position and short length. The muscle fibers are probably identical to the "Langsmuskulzelle des Nebensystems" described by Schmidt (1903) in his study on the musculature of Branchiobdella parasita. Stephanodrilus sapporensis is destitute of dorsal appendages but is marked by a low conspicuous ridge supported by a few dorsal segmental muscles. In other species of Stephanodrilus, i.e., in St. inukuii n. sp., St. megalodontatus n. sp., etc., neither dorsal transverse ridges or dorsal appendages are present. The dorsal segmental muscles could not be detected in these species. From these facts it seems to the present writer that the dorsal ridges appear along with the development of the dorsal segmental muscles. In a previous paper (1932a) it is stated that in Ceratodrilus uchidai = Stephanodrilus uchidai the dorsal digitiform appendages are present in the six trunk somites III-VIII, each somite bearing twelve of them. As the result of examination on abundant specimens of the species collected from various localities it has been clear that there are several intergrades in regard both to number of somites bearing appendages and to the appendages on each somite. Some forms are also provided with appendages in the
six trunk somites III-VIII but they are variable in number according to the
somites (maximum 12 and fewer in the more anterior ones). In others the appen-
dages are more reduced in number and disappear in several anterior somites,
finally disappearing altogether in all trunk somites. In these several forms the
dorsal transverse ridges are always present accompanying the dorsal segmental
muscle fibers. According to Ellis (1920) [1919] description and figures, Pterodrilus
durharni seems to be also provided with dorsal transverse ridges, but to be destitute
of distinct appendages except two "horns" found in the eighth trunk somite.
Moreover, Branchiobdella kobayashii n. sp. has dorsal transverse ridges supported
by dorsal segmental muscle fibers while Br. orientalis n. sp., and Br. pentadonta
and others are destitute of the ridges. Judging from these facts, those provided
with the dorsal transverse ridge, or dorsal segmental muscles, are not distinctly
separated from those lacking them.

However, it seems to the writer that Yamaguchi's position is some-
what unjustified and that at least with the American forms the dorsal
appendages are of generic significance. For example, in Pterodrilus,
while there are specific differences, the appendages are similar enough to
allow grouping into one genus. It seems that Yamaguchi has grouped
forms diverse enough to be in several genera in the genus Stephanodrilus.
In regard to Stephanodrilus uchidai, he is not even sure he is dealing with
only one species. He merely says: "As the variation occurs in series all
seem to belong to a single species."

C. Peristomium

The character of the peristomium appears to be of specific taxonomic
value but not generic. Pierantoni (1912) believed the presence of a
plurilobate peristomium to be of generic significance. Ellis (1919:256),
when reviewing the genus Cambarincola, first expressed doubt of this
view. He questioned it as follows:

One of these characters, "the pluri lobate prostomium" is particularly note-
worthy in this connection as it is used by Pierantoni to differentiate Stephanodrilus
in his generic key. The two species C. philadelphica and C. chirocephala have
lobate lips similar to the lips of Stephanodrilus japonicus Pierantoni as figured
by Pierantoni. Neither Stephanodrilus koreanus Pierantoni nor Stephanodrilus
japonicus Pierantoni, however, are figured with accessory sperm tubes, and the
accessory sperm tube is present in species of Cambarincola. Pierantoni also
figures Branchiobdella digitata Pierantoni, a species having but a single pair of
testes (Pierantoni), with a pluri lobate prostomium, showing that the lobate lip
character occurs in that group of species.

Yamaguchi (1934:182) expresses the writer's view when he says:

The bilobate or pluri lobed peristomium which was regarded as one of the
generic characters by Pierantoni (1912) seems to be of no significance for generic
value, because the two kinds of peristomia are found in one genus as will be
stated below. In the genus Branchiobdella a pluri lobed peristomium is found in
Br. digitata, Br. niinata (Pierantoni 1912) and Br. parasita (Whitman 1882),
while other species have a bilobed peristomium. On the other hand, Cambarin-
cola chirocephala, C. philadelphica (Ellis 1920) [1919] and C. okadai (Yamaguchi
1933) are provided with a pluri lobed peristomium, but other species belonging to
the genus are provided with a bilobed peristomium. Though the present writer
(1932a) distinguished the funnel shaped peristomium from that not funnel shaped,
the distinction is not clear in several species.
D. JAWS

The number and arrangement of teeth on the jaws seem to be of specific importance, although there is considerable individual variation in some species. Variations in the dental formulae of several different species are given by Ellis (1919), from which the accompanying tables have been adapted.

Table I.—Variations in the Dental Formula of Xironodrilus formosus Ellis

<table>
<thead>
<tr>
<th>Locality</th>
<th>Dental formulae</th>
</tr>
</thead>
<tbody>
<tr>
<td>Irondale, Anderson, Ind.</td>
<td>3 4 17 13 4 1</td>
</tr>
<tr>
<td>Noblesville, Ind.</td>
<td>1 1 4 .. 2 ..</td>
</tr>
<tr>
<td>Charlevoix, Mich.</td>
<td>.. .. 2 1 ..</td>
</tr>
<tr>
<td>Vincennes, Ind.</td>
<td>.. .. .. ..</td>
</tr>
<tr>
<td>Number of specimens</td>
<td>4 5 24 14 6 1</td>
</tr>
</tbody>
</table>

Table II.—Variations in the Dental Formula of Xironodrilus pulcherrimus (Moore)

<table>
<thead>
<tr>
<th>Locality</th>
<th>Dental formulae</th>
</tr>
</thead>
<tbody>
<tr>
<td>Blowing Rock, N. C.</td>
<td>2 .. 6 ..</td>
</tr>
<tr>
<td>Cheat River, W. Va.</td>
<td>.. .. ..</td>
</tr>
<tr>
<td>Cheat Bridge, W. Va.</td>
<td>.. .. 3 ..</td>
</tr>
<tr>
<td>Shavers Fork, W. Va.</td>
<td>.. .. 1 1</td>
</tr>
<tr>
<td>Cheat River, W. Va.</td>
<td>.. 1 8 ..</td>
</tr>
<tr>
<td>Indian Creek, W. Va.</td>
<td>.. 1 .. ..</td>
</tr>
<tr>
<td>Queens, W. Va.</td>
<td>.. .. 7 1</td>
</tr>
<tr>
<td>Trubies Run, W. Va.</td>
<td>.. 1 4 ..</td>
</tr>
<tr>
<td>Baileyville, W. Va.</td>
<td>.. .. .. ..</td>
</tr>
<tr>
<td>Number of specimens</td>
<td>2 5 30 2</td>
</tr>
</tbody>
</table>

Table III.—Variations in the Dental Formula of Xironogilon oregonensis Ellis

<table>
<thead>
<tr>
<th>Locality</th>
<th>Dental formulae</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eugene, Ore.</td>
<td>1 8 3 2 ..</td>
</tr>
<tr>
<td>Sequallichew Lake, Wash.</td>
<td>.. .. 4 1 3</td>
</tr>
<tr>
<td>Number of specimens</td>
<td>1 8 3 6 1 3</td>
</tr>
</tbody>
</table>
From a total of 37 specimens of Xironogiton instabilis (Moore) examined from various localities in New York, Virginia, West Virginia, and North Carolina, Ellis found 16 with a 4-4 formula, 11 with a 5-4 formula, and 10 with a 5-5 formula.

We could go on citing other species, the great variation in formulae of Cambarincola philadelphica (Leidy), etc., but this is sufficient to show that in nearly all species sufficiently studied there is a great diversity of dental formulae.

However, in spite of this variation, individual formulae are sufficiently similar to be of specific importance. In fact Yamaguchi (1934:184) suggests that in some cases the dentition may be of generic importance when he uses it as a character to separate Stephanodrilus and Cambarincola as follows:

<table>
<thead>
<tr>
<th>Stephanodrilus</th>
<th>Cambarincola</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dorsal dental plate…. Provided with seven or more teeth, median one larger than lateral ones.</td>
<td>Provided with five teeth, a large median and four small lateral ones.</td>
</tr>
<tr>
<td>Ventral dental plate…. Similar in dentition to the dorsal plate.</td>
<td>Provided with four teeth, having no median unpaired teeth (except in C. okadai bearing same dentition as dorsal plate).</td>
</tr>
</tbody>
</table>

The writer considers the dentition and general shape of the jaws to be of specific but not generic importance.

E. Position of Caudal Sucker

Whether the sucker is ventral, as in Xironodrilus, Xironogiton, etc., or terminal, as in Cambarincola and others, seems to be of some generic significance when correlated with the general shape of the body.

F. Shape of Gut

While the gut varies considerably in shape, depending on the amount of food present and the amount of contraction of the specimen, its general shape may in some cases be used as an additional specific diagnostic character. However, it is not an important taxonomic character.

G. Pharyngeal Diverticula

Ellis (1919:243) says:

From the sections studied the number and position of the major pharyngeal diverticula and the presence or absence of buttress-like supports of connective tissue attached to the intersegmental partitions were considered of taxonomic value. The major pharyngeal diverticula may be seen to best advantage in sagittal sections but may be located in good whole mounts of compressed worms. These pharyngeal diverticula are not to be confused with the slight invaginations of the pharyngeal wall nor with the fold in the pharyngeal wall near the posterior end of the pharynx (found in many preserved specimens), due to the pushing forward of the esophageal portion of the alimentary canal so that the anterior end of the esophagus partly telescopes the posterior end of the pharynx.
But Yamaguchi (1934:183) throws doubt on the importance of pharyngeal diverticula:

But it was difficult for the present writer to distinguish the “major pharyngeal diverticula” from the “slight invaginations.” It seems to be quite doubtful, therefore, whether one should consider the number and position of the “major pharyngeal diverticula” as an important taxonomic character.

The writer agrees with Yamaguchi that their taxonomic value is doubtful.

H. Opening of the Anterior Nephridia

The paired or unpaired condition of the pores by which the anterior nephridia open to the outside seems to be of generic importance. For example, Cambarincola has a single pore while Xironodrilus, Xironogiton, and Branchiobdella have paired pores.

In the genus Stephanodrilus, Yamaguchi (1934) has described *S. korecanus* Pierantoni as having a single pore while all the remaining species of the genus have paired pores. But here again, in this diverse genus, several genera may well be included.

I. Number of Testes

The genus Branchiobdella is separated from all other genera by the presence of a single pair of testes located in segment V. All other known genera have two pairs located in segments V and VI. This has been the basis of separating the two subfamilies, Branchiobdellinae and Cambarincolinae.

J. Accessory Sperm Tube

The accessory sperm tube, described by Ellis (1912) as a generic character of Cambarincola, consists of a blind tube arising from the spermatic vesicle and extending anteriorly. This is, according to Yamaguchi, homologous to the blind tube present in other species of other genera. It is very distinct and can clearly be seen in cleared whole mounts. It seems to be of generic importance, occurring in the genera Cambarincola and Xironogiton.

K. Penis

Certain genera, as Cambarincola, appear to have non-eversible penes, while others, as Cirrodrilus, are eversible. The character of the penis provides characters which are constant within certain groups, and therefore seems to be of generic significance.

L. Shape of the Spermatheca

The various shapes of the spermatheca seem to be of specific significance but have no generic importance with possibly one exception, namely, the bifid spermatheca of *Bdellodrilus*. However, only one species of this genus is known, and further study may reveal that this character is of specific value only.
VIII. CLASSIFICATION OF THE AMERICAN BRANCHIOBDELLIDAE

In the following classification, the characterizations of the Class and Order are translations from Michæelsen (1919:153).

PHYLUM ANNELIDA.—Triploblastic coelomate worms characteristically having a metanephridial excretory system, a ventral nervous system, and a dorsal blood vessel. Segmentation is typical but not universal.

CLASS CLITELLATA.—Annelids with well-developed outer and inner metamerism, without parapodia, and without feelers, tactile cirri and ordinary cirri, mostly without gills; hermaphroditic. Gonads in a few definite segments. Clitellum present. Development is direct; in the main, fresh-water and land animals.

ORDER OLIGOCHAETA.—Clitellum present, mostly with setae in the skin. Segments mostly single or slightly and unequally divided. Coelom well developed, large. Testes anterior to the ovaries, generally one or two pairs.

SUPERFAMILY BRANCHIOBDELLOIDEA Hall, 1914

Body divided into two regions, a head and a trunk, the latter terminated by a sucker; without setae; mouth provided with two chitinous jaws; two pairs of nephridia; testes in pairs in fifth or in fifth and sixth segment; ovaries in the seventh segment; unpaired spermatheca in the fifth.

FAMILY BRANCHIOBDELLIDAE

With the characteristics of the superfamily.

In the present study the writer has become impressed with the fact that the family Branchiobdellidae contains two distinct groups of genera. The sharpness of this distinction warrants the recognition of two separate subfamilies. In proposing Branchiobdellinae and Cambarincolinae as new subfamilies, the following diagnosis is presented:

BRANCHIOBDELLINAE.—Branchiobdellidae with only one pair of testes, located in the fifth segment.

CAMBARINCOLINAE.—Branchiobdellidae with two pairs of testes, located in the fifth and sixth segments.

SUBFAMILY BRANCHIOBDELLINAE new subfamily

Branchiobdellid worms having one pair of testes and male funnels located in the fifth segment.

Type and only genus: Branchiobdella Odier, 1823.
GENUS BRANCHIOBDELLA Odier, 1823

Branchiobdella, Stephenson 1930:800.

With the characteristics of the subfamily; spermatheca simple, not bifid; penis eversible; no accessory sperm tube; anterior nephridia opening to the outside by separate pores in segment III; body cylindrical, not flattened; without body appendages.

Type species: Branchiobdella astaci Odier, 1823, from western Europe.

KEY TO AMERICAN SPECIES OF THE GENUS BRANCHIOBDELLA

1. Dorsal and ventral jaws dissimilar with a 5-4 dental formula; peristomium entire.............Branchiobdella americana Pierantoni, 1912
2. Dorsal and ventral jaws similar with a 4-4 dental formula; peristomium bilobed..................Branchiobdella tetradora Pierantoni, 1906

Branchiobdella tetradora Pierantoni, 1906


Description (based on Pierantoni 1912):
Peristomium divided into two lips, a dorsal and a ventral; head distinctly separated from body. Body rather uniform throughout, not enlarged in median portion. Posterior sucker cup-like, not very prominent. Length about 2.0 mm.
Jaws similar, bearing four equal teeth placed in a row, the two median ones sometimes a little shorter than the outer ones.
Spermatheca shaped like an hour glass, with a short passage tube "condotto di uscita." Atrium enlarged and sack-shaped.
Type: From Klamath River, Calif., on Astacus klamathensis.
Previous locality record: Pierantoni, 1906b, N.S. 2 (No. 11)—Klamath River, Calif., on Astacus klamathensis.
Remarks: The present writer has not examined this form.

Branchiobdella americana Pierantoni, 1912


Description (based on Pierantoni 1912):
Peristomium entire, a little enlarged to form a sucker; head very distinct from body, circumbuccal ring of papillae present; body not
"swollen" towards the middle; body semi-cylindrical; posterior sucker slightly prominent; clitellum slightly visible.

Length about 5.0 mm.

Jaws unequal, the dorsal provided with a large median tooth and with two pairs of smaller median teeth; the ventral with two large teeth and two smaller ones.

The spermatheca in this species is in the form of an hour glass with short neck; without terminal process. The male atrium is slightly enlarged.

Type: Material from Texas on _Cambarus viridis_ (according to Pierantoni), _C. latimanus_, and _C. hayi_, and from Raleigh, N. C., on _C. rusticus, C. immuns_, and _C. sp._

Previous locality records:
1. Texas, on _Cambarus viridis, C. latimanus_, and _C. hayi_.
2. Raleigh, N. C., on _C. rusticus, C. immuns_, and _C. sp._

Allen 1933:119
1. Durham, N. C.

New locality records:
1. Cleveland, N. Y., on _Cambarus bartoni robustus_.

Remarks: The material examined by the writer from Cleveland, N. Y., agreed very well with the above description. However Pierantoni failed to mention the large everted penis, which was quite evident in the writer's specimens.

SUBFAMILY CAMBARINCOLINAE new subfamily

Branchiobdellid worms having two pairs of testes and male funnels located in the fifth and sixth segment.

Type genus: Cambarincola Ellis, 1912.

KEY TO THE GENERA OF SUBFAMILY CAMBARINCOLINAE

1. (a) Body with appendages.................................................. 2
   (b) Body without appendages........................................... 3
2. (a) Appendages in the form of blunt cylindrical projections along the median dorsal line of body................................................... _Pterodrilus_ Moore, 1895
   (b) Appendages in the form of pointed bands encircling the dorsal surface of the body............................................ _Cirrodrilus_ Pierantoni, 1905
3. (a) Accessory sperm tube present...................................... 4
   (b) Accessory sperm tube absent..................................... 5
4. (a) Body cylindrical, not flattened, posterior end not conspicuously enlarged, anterior nephridia opening to the outside through a single pore........... _Cambarincola_ Ellis, 1912
   (b) Body flattened, posterior end enlarged, so that body is racket- or spatula-shaped, anterior nephridia opening to the outside through separate pores........................................... _Xironogiton_ Ellis, 1919
5. (a) Pair of large clear glands in each of the nine postcephalic segments; spermatheca bifid...................................................... 6
   (b) Without a pair of large clear glands in each of the nine post-cephalic segments; spermatheca not bifid........................................... 6
6. (a) Major annulations of body segments secondarily divided especially noticeable in the median segments .................. Triannulata new genus  
(b) Major annulations of body segments not secondarily divided .............. 7  
7. (a) Body flattened; sucker ventral .................. Xironodrilus Ellis, 1919  
(b) Body not flattened; sucker terminal .......... Stephanodrilus Pierantoni, 1906

GENUS CAMBARINCOLA Ellis, 1912  
Cambarincola, Stephenson 1930:801-802.  

With the characteristics of the subfamily; spermatheca simple, not bifid; accessory sperm tube present; bursa but not penis eversible; anterior nephridia opening to the outside through a common pore situated on a median dorsal papilla; body cylindrical not flattened; without body appendages.  
Type species: Cambarincola macrodonta Ellis, 1912.  

KEY TO THE SUBGENERA OF CAMBARINCOLA  
1. Upper lip composed of four subequal lobes ................. Coronata new subgenus  
2. Upper lip entire excepting a small median emargination .............. Cambarincola new subgenus

SUBGENUS CAMBARINCOLA new subgenus  

With the characteristics of the genus Cambarincola; upper and lower lip entire excepting a small median emargination in all but C. inversa which has two small lobes in the base of the emargination.  
Type species: Cambarincola macrodonta Ellis, 1912.  

KEY TO THE AMERICAN SPECIES OF THE SUBGENUS CAMBARINCOLA  
1. (a) Major annulation of segment VIII visibly and distinctly elevated over minor annulations .................. Cambarincola elevata new species  
(b) Major annulations of segment VIII not distinctly elevated over minor annulation ......................................................... 2  
2. (a) Upper jaw with three prominent teeth; if, as in a few specimens, five teeth are present the two lateral ones are very small .................. Cambarincola inversa Ellis, 1919  
(b) Upper jaw not as above but with five noticeable teeth .............. 3  
3. (a) Middle tooth of upper jaw long and prominent when compared with the small lateral teeth .................. Cambarincola macrodonta Ellis, 1912  
(b) Middle tooth of upper jaw longer than the other four teeth but small enough that all five teeth may be considered subequal .................. Cambarincola vitrea Ellis, 1919
Cambarincola (Cambarincola) macrodonta Ellis, 1912


Description from Ellis 1912:481-486:

"Body rather slender when extended, slightly arched ventrally, circular in cross section in all regions, greatest diameter in the fifth or sixth segment, shortest diameter in the first segment, sloping gradually from the fifth segment to the first and rather abruptly from the sixth segment to the acetabulum; greatest diameter of the head always less than the greatest diameter of the body; greatest diameter of the body 5 to 8 in the body length; head distinct, elongate in extended specimens; length of the head greater than the greatest diameter of the body in extended specimens (greatest diameter of the body 1.1 to 1.3 in the length of the head), equal to or less than the greatest diameter of the body in contracted individuals (length of the head 1 to 1.3 in the greatest diameter of the body); greatest diameter of the head 1.2 to 1.4 in the greatest diameter of the body.

"Head composed of four annulations; the first or anterior cephalic annulation very prominent, of less diameter than the second annulation, tapering forward, from 2.3 to 3.3 in the total length of the head, depending upon the degree of contraction, composed largely of two fleshy lips—a dorsal and a ventral—of which the dorsal is very slightly the longer; the other three annulations very indistinctly marked, so that the remainder of the head appears to be but a single piece; first seven or eight body segments showing a rather distinct biannulation, the anterior portion of each segment being of the greater diameter; acetabulum terminal, of moderate size, from 1 to 1.25 in the greatest diameter of the head; genital papillae on segments 5 and 6, quite conspicuous in large specimens.

"Mouth terminal, or very slightly ventral, its opening rather diamond shaped, with the greatest dimension at right angles to the dorso-ventral line, guarded by two large lips, each of which bears several tiny papillae on its inner surface and a few minute hairs on its outer edge near the median line; each lip entire with the exception of a single slight emargination in the median line, which may be entirely wanting; dental plates very dark-brown to black, situated at or just in front of the junction of the first and second cephalic annulations; dorsal plate roughly triangular in outline when seen from the front, middle portion of the base excavated so that the two corners extend beyond the rest of the plate as two horns, anterior face with two rather prominent teeth on each side near the edge of the plate, the tooth nearer the apex on each side being pointed and larger than the basal tooth, apex produced into a single large cylindrical tooth with a conical point; ventral plate with an excavated base like that of the dorsal plate, the anterior face bearing a single small
knob-shaped tooth on each side near the base, apex produced into two large cylindrical teeth, each with a conical point.

"Pharynx narrowing just behind the dental plates, with a distinct dorsal diverticulum near the junction of the second and third cephalic annulations and a ventral diverticulum slightly caudad, the mouths of the two diverticula producing an irregular enlargement of the pharynx in the third annulation; esophagus narrow, occupying the first body segment, near the middle of which it drops to the floor of the body cavity; crop or post-esophageal portion of the alimentary canal extending through segments 2 and 3, rising gradually to the center of the body, increasing steadily in diameter, caudad, and showing little or no constriction at the junction of segments 2 and 3 unless distended with food; stomach large, almost filling segment 4, marked off by definite constrictions; intestine proceeding as a straight tube of slightly less diameter than that of the stomach through the center of segments 5 and 6; in segment 7 becoming somewhat narrowed, swinging dorsally and to the left side of the body in the anterior portion of the segment, and returning much narrower to the right of the median line in the posterior portion of the segment, leaving segment 7 near the dorsal wall of the body cavity; continuing in the anterior portion of segment 8 much narrower, crossing again to the left side and descending to the center of the segment, enlarging in the posterior portion of the segment, but leaving segment 8 near the center as a small tube; the rectum beginning in segment 9, passing diagonally through this segment to its dorsal wall, opening dorsally in the median line in the anterior portion of segment 10.

"Living animals colorless and quite transparent excepting the alimentary canal (which was a pale green in the specimens observed), and the gonads; body quite contractile."

Type: U.S.N.M. No. 53794 from Boulder, Colo., on Cambarus diogenes Girard. Length 4.65 mm.

Previous locality records:
Ellis 1912:481—
Ellis 1919:251—
1. Fort Clark, Tex., on C. clarkii.
2. New Orleans, La., on C. diogenes ludovicianus.
4. Lake Lapondre, Morgan City, La., on C. clarkii.
5. Frierson, La., on C. blandingii acutus.
6. Las Vegas, N. M., on C. galliatus.
7. Muldon, Miss., on C. hagenianus.

New locality records:
1. Leaf River, Ill., on C. virilis.
3. Champaign Co., Ill., on *C. virilis*, *C. immunis*, and *C. propinquus.*
4. Oakwood, Ill., on *C. propinquus.*
5. Botetourt Co., Va., on *C. bartonii.*
6. Meni, Ark., on *C. menae.*
8. Omaha, Neb., on *C. immunis.*

Remarks: The above quotation describes very accurately this species which has little variation despite its large geographical range.

*Cambarincola (Cambarincola) vitrea* Ellis, 1919


Description from Ellis 1919:257-258:

"Body and head subterate, little if at all depressed; diameter of the head approximately equal to that of segment II, usually slightly greater than that of segment I; body segments II to VIII subequal, segments V, VI, and VII when distended with sex cells slightly wider than segments III and IV; segments posterior to VIII narrowing rather rapidly to the caudal sucker, the diameter of which is less than that of the head; all body segments easily visible in side view: major annulations distinct, but very slightly elevated above the minor annulations; head divided into three subequal parts, the anterior being the most distinct of the three; lips two, subequal, each with a small, median emargination; major pharyngeal diverticula two, the dorsal slightly anterior to the ventral; a few short bristles present on each lip; dental formula 5-4: . . . . alimentary canal straight, following the mesial line of the body, maximum enlargement in segment IV; anterior nephridia opening to the outside through a common pulsatile pore on the dorsal surface of the major annulation of segment III; spermatheca simple and tubular; testes present in segment V and VI, vasa deferentia from segments V and VI meeting the atrium in segment VI; accessory sperm tube present: largest specimen examined, 4.7 mm.

"This species superficially resembles *Xironodrilus formosus* Ellis, both in body form and type of jaws. In addition to the several generic characters by which these two species may be separated, it may be noted that the jaws, although having the same number of teeth and the same general form, are quite different."

Type: U.S.N.M. 17668 from Douglas Lake, Mich., on *Cambarus virilis* Hagen. Length: 310 mm.

Previous locality records:

Ellis 1918:49-51—

1. Douglas Lake, Mich., on *Cambarus virilis.*
2. James Island, Potagannissing Bay, Mich., on *C. virilis.*
3. Three miles up Potagannissing River, Drummond Island, Mich., on *C. virilis.*
5. Echo Lake, Grand Island, Lake Superior, Mich., on *C. propinquus.*
Ellis 1919:257-258—

1. Rhinelander, Wis., on C. virilis.
2. St. Vrain, Colo., on C. immunis.
3. Rolla, Mo., on C. virilis.
5. Lake Huron, Cheboygan, Mich., on C. propinquus and C. virilis.
7. Wellington, Ill., on C. virilis.
8. Urbana, Ill., on C. virilis.
10. St. Marys River, Fort Wayne, Ind. (host not given).
11. Mouth of Carp River, St. Martin’s Bay, near Straits of Mackinac, on C. virilis.

New locality records:

1. Leaf River, Ill., on C. virilis.
2. Lake Geneva, Wis., on C. virilis.
4. Oakwood, Ill., on C. propinquus.
5. Punta Gorda, Fla., on C. sp.
6. Stillwater, Okla., on C. sp.
7. Tuscaloosa, Ala., on C. sp.
8. Cleveland, N. Y., on C. bartonii.
11. Indianapolis, Ind., on C. rusticus.
12. Lisbon, N. D., on C. virilis.
13. Dallas, Tex., on C. simulans.
14. Hayward, Wis., on C. virilis.
15. Marathon, Wis., on C. virilis.
16. Pittsville, Wis., on C. virilis.
17. Glen Flora, Wis., on C. virilis.
18. Swastika, Ontario, on C. virilis.
19. Holcombe, Wis., on C. virilis.
20. Noxubee County, Miss., on C. mississippiensis.

Remarks: This form could be confused with Cambarincola macrodonta, but it is easily distinguished by the difference in tooth structure as outlined above.

Cambarincola (Cambarincola) elevata new species
(Pl. I, Fig. 3; Pl. II, Fig. 5)

Description:

Length of mature worms varying between 2.0 and 3.0 mm. The head diameter approximately equal to segment II, slightly greater than segment I. Segments increasing in diameter to segment VI or VII which is about 0.4 mm, in a worm 2.5 mm. long, then decreasing rapidly to the caudal sucker, whose diameter is slightly less than the head; sucker terminal; body little if at all depressed. Major annulations distinct; all
except segment VIII but very slightly elevated over minor annulations; major annulation of segment VIII distinctly and visibly elevated over the minor annulation so as to almost obscure it.

Head divided into three subequal parts: peristomium divided into two lips each with a slight median emargination. Jaws small, about 15-20 microns in a 2.5 mm. worm with a tooth formula of 5-4. The alimentary canal is straight following the mesial line of the body with the maximum enlargement in segment IV; anus present in the dorsal half of segment X.

Two pairs of testes present, one pair in segment V and one pair in VI; vasa deferentia joining the atrium in VI; distinct accessory spermatheca tube present in VI. Bursa but not penis eversible. Ovaries in segment VII; spermatheca in V consists of three parts, a short muscular portion near the spermathecal pore, a short middle tubular portion, and large dorsal globose part, resembling the spermatheca of *Xironodrilus formosus*; anterior nephridia opening to the outside through a common pore in the dorsal half of segment III.

Holotype: From Leaf River, Ill. on *Cambarus virilis*.

Paratypes: From Macoupin Creek near Carlinville, Ill., on *Cambarus virilis*; Buck Creek near Penfield, Ill., on *C. virilis*; Leaf River near Byron, Ill., on *C. virilis*; Seven Mile Creek, Rock River Drainage, Ill., on *C. virilis* and *C. propinquus*; and Lake Geneva, Wis., on *C. virilis*.

Additional material: Farmington, Mo., on *C. punctimanus*; Iowa River, Iowa, above Junction of Upper Iowa River; Oxford, Ontario.

Remarks: This species is closely related to *C. vitreus*, but differs in the elevation of the major annulation of segment VIII and in the shape of the spermatheca which is simple and tubular in *C. vitreus*. The holotype will be deposited in the United States National Museum, and paratypes in the collection of Dr. H. J. Van Cleave, of the University of Illinois, and in the collection of the writer.

*Cambarincola (Cambarincola) inversa* Ellis, 1919


Description from Ellis 1919:259-260:

"Body rather elongate and more or less terete; width of the head approximately equal to that of segment I; body segments increasing in width regularly and gradually from segment I to segment VI, which is the widest segment of the body; segments VII and VIII slightly narrower than segment VI; body posterior to segment VIII narrowing rapidly to the caudal sucker: all eleven body segments visible in side view and nine or more visible in dorsal view; caudal sucker termino-ventral, its diameter less than that of the head; each segment slightly constricted anteriorly and posteriorly, so that the segmental junctions are distinct; head subcylindrical, its anterior third defined by a groove or constrict-
tion; length of the head in a moderately expanded specimen slightly less than the length of the first two body segments; lips, two, the upper slightly longer than the lower; the lower lip with a distinct median emargination; upper lip like the lower, but with two small lobes in the base of the emargination; oral bristles present; dental formula 3-4, varying 3-3 to 5-4; upper jaw with three large teeth, of which the middle one is the longest, all three directed forward—that is, away from the base of the jaw; dental ridge of the upper jaw usually with a small tubercle in the position of the teeth of the "e" order—that is, if the jaw were five-toothed (teeth were found on these tubercles in two specimens, the tooth point in each case being very small); lower jaw with two large teeth and two small lateral teeth; upper jaw 20 micra wide, lower jaw 17 micra wide in an expanded worm measuring 3.6 mm.; major pharyngeal diverticula two, one dorsal and one ventral; anterior nephridia alternating in segments II and III, opening to the outside in segment III through a common pore in the dorsal surface of the major annulation of segment III: spermatheca simple, long, and tubular, not bifid; testes present in segments V and VI, vasa deferentia from segments V and VI meeting in the strium in segment VI; alimentary canal straight, increasing in diameter in segment I, much expanded in segments II, III, and IV, in which segments it forms an almost continuous pouch; intestine narrowing in the posterior half of segment IV; alimentary canal following the mesial line of the body through segments V to IX, swinging dorsad through segment IX to anal opening on the dorsal surface of segment X."

Type: U.S.N.M. No. 17680 from Eugene, Ore., on Astacus klamathensis.

Previous locality records:
Ellis 1919:259—
1. Eugene, Ore., on Astacus klamathensis.

New locality records:
1. Twenty-two miles from Vintago, Wash., on A. sp.
2. Klamath, Ore., from A. troxbridgii.
3. Deer Creek, Ore., on A. klamathensis.
7. Odessa, Wash., on A. klamathensis.
8. St. Helens, Ore., on A. troxbridgii.
10. Cestasso Creek, Ore., on A. troxbridgii.
12. Vernonia, Ore., on A. troxbridgii.
13. Silver Creek, Harney County, Ore., on A. gambelii.
14. Young River, Ore., on A. klamathensis.

Remarks: Although a great many specimens were studied, little variation was encountered.
SUBGENUS CORONATA new subgenus

With the characteristics of the genus Cambarincola; upper lip composed of four subequal lobes, which may be extended as digitiform tentacles; lower lip composed of two subequal lobes which may be extended also; middle tooth of upper jaw long and prominent, almost obscuring lateral ones.

Type species: *Cambarincola philadelphica* (Leidy, 1851)

**KEY TO THE AMERICAN SPECIES OF THE SUBGENUS CORONATA**

1. Major annulations of body segments distinctly and visibly elevated over minor annulations.................... *Cambarincola chirocephala* Ellis, 1919
2. Major annulations of body segments not elevated over minor annulations ....................................... *Cambarincola philadelphica* (Leidy, 1851)

*Cambarincola (Coronata) chirocephala* Ellis, 1919


Description from Ellis 1919:263-264:

“General body form that of *Cambarincola philadelphica* (Leidy); body segments evident, major annulations of segments especially in contracted specimens, distinctly and visibly elevated above the minor annulations; body segments increasing regularly and gradually in diameter from segment I to segment VI or VII, and decreasing slightly from segment VIII to the caudal suckers; body terete; head large, equalling the first two body segments in length and exceeding the first segment in width; lips two, upper composed of four subequal lobes which may be extended into four distinct digitiform tentacles, or may be so flattened as to give the lip an almost entire outline; lower lips of two larger, subequal lobes which are usually somewhat extended; a very small intermediate lobe at the junction of the upper and lower lip on each side of the mouth; major pharyngeal diverticula two, a dorsal and a ventral, the dorsal diverticulum being slightly cephalad of the ventral; dental formula 5-4; upper jaw very large, its width two or three times that of the lower jaw, teeth of the “a” and “b” orders on each side very small, less than one-sixth of the height of tooth “a.” The jaw appearing to have but one tooth when examined under low power magnification; . . . . anterior nephridia opening to the outside through a common pore in segment III; spermatheca simple, bulbous; testes in segments V and VI, vasa deferentia from segments V and VI meeting in segment VI.”

Type: U.S.N.M. No. 17713, from Rolla, Mo., on *Cambarus virilis.*

Previous locality records:

Ellis 1919:263--

1. Rolla, Mo., on *Cambarus virilis.*
New locality records:
1. Leaf River, Ill., on C. virilis.
2. Champaign County, Ill., on C. virilis, C. blandingii acutus, and C. propinquus.
3. Oakwood, Ill., on C. propinquus.
4. Cleveland, N. Y., on C. bartonii.
6. Alpha, Ky., on C. placidus.
9. Highlands, Ala., on C. rusticus.
10. Indianapolies, Ind., on C. rusticus.
12. Mott, N. D., on C. virilis.
13. Iowa City, Iowa.

Remarks: These observations have been confirmed by the writer in numerous specimens examined. Especially notable are the elevated major annulations mentioned above, giving a saw-toothed appearance to the margins in total mounts.

*Cambarincola (Coronata) philadelphiica* (Leidy, 1851)


Description from Ellis 1919:261-263:

“In the original description of this species Leidy gives the following: ‘Head campanulate, terminated by a circular or elliptical crenated lip, fringed with very minute stiff hairs; dental plates brown, nearly equal, forming an isosceles triangle, with the base longest and attached, apex of superior plate ending in a sharp conical point with several minute denticulations on each side; apex of inferior plate bifurcated into two points, with two minute denticulations on each side.’ From this description the lower jaw may be regarded as a six-toothed jaw, having two large apical teeth and two small teeth on each side. The upper jaw is not so easily understood. The upper jaw bears “x” teeth, if x equals 1 plus Y, in which statement “y” is more than two (several minute denticulations, according to Leidy). This interpretation of the upper jaw would give a minimum of seven teeth: that is, one large tooth plus at least three teeth on each side.

“Moore [1894] figures a specimen which he assigns to Leidy’s species, having jaws of the dental formula 7-10. The upper jaw as figured has...
one large apical tooth, and three small denticles on each side, and the lower jaw has two large teeth, and four small denticles on each side. Moore’s figure of the head of this worm shows that the upper lip is composed of four distinct but small lobes, and the lower lip of two large subequal lobes. At the junction of these upper and lower lips on each side is a small intermediate lobe. These six lobes are small enough to fall in Leidy’s description of a “circular or elliptical, crenated lip.”

“From the examination of a large series of specimens and a study of many living individuals at Douglas Lake, Michigan, the usual dental formula of this species seems to be 5-4. The upper jaw has one large tooth with two small denticles on each side and the lower two large teeth with two small denticles. The variation in the number of teeth figured and described may be accounted for by the fact that the sides of both upper and lower jaws of this species often bear small tubercles below the small denticles—that is, toward the base of the jaw—and these small tubercles could easily be confused with teeth. As understood in this paper, a tooth or denticle is a tubercle on the dental face bearing a distinct tooth cap. These tooth caps are lighter in color than the dental ridge, have 5 definite points and definite form. Two specimens from Tillance Creek, W. Va., one from Indian Creek, W. Va., and one from Douglas Lake, Michigan, had jaws with more teeth—that is, definite teeth with tooth caps—that is, the regular 5-4 type, showing that some variation does occur.

“The plurilobate condition of the prostomium is regular and definite, the upper lip having four subequal lobes, the lower, two large, subequal lobes with a small, often inconspicuous lobe present at the junction of the upper and lower lip on each side of the mouth. In the living worms it was observed that the four lobes of the upper lip and to a less extent the two lobes of the lower lip could be extended to form distinct tentacles on the lips. Several specimens from various localities were found in the collections, killed with these tentacles fully extended. Most of the preserved specimens examined showed these tentacles, the lobes of the lips being extended beyond the level of the lips so that the tentacles, although small, were distinct. It was also found that worms of this species could flatten the entire lip, so that the lobes were scarcely visible. Preserved specimens which had been killed with the lips in this flattened condition were separated often with difficulty from individuals of the first group of species of this genus, but close examination in nearly every case showed the regular emarginations marking the location of the lobes of the lips. The lobes were easily seen in a young worm less than three hours old which was examined in water. This worm extended and con-
tacted the lobes in the same manner as an adult. Cambarincola philadelphia was the most variable species studied.”
Previous locality records:
Leidy 1851:209—
Moore 1894:428—
1. Philadelphia, Pa., and Watanga Co., N. C.
Moore 1901:542—
1. From Illinois on Cambarus diogenes and C. blandingii.
Ellis 1918:50—
Ellis 1919:260-261—
2. Chenowith Creek, between Beverly and Elkins, W. Va., on C. bartonii carinirostris.
4. Right Hand Fork at Queens, W. Va., on C. obscurus.
5. Rock House River, near Baileyville, W. Va., on C. dubius.
7. Crane Creek, W. Va., on C. bartonii veteranus.
9. Cheat River near the Pike, W. Va., on C. bartonii carinirostris.
10. Tilhance Creek, Black Creek Valley, W. Va.
11. Indian Creek, tributary of the Elk River in Kanawha County, W. Va.,
    on C. bartonii veteranus.
12. Stone Coal Creek between Buckhannon and Weston, W. Va., on C. obscurus.
13. War Creek, headwaters of the Big Sandy in McDowell Co., W. Va., on C. dubius.
14. Coney Creek, Bainbridge, Pa., on C. bartonii.
15. Stony Man Mountain, Va., on C. bartonii.
18. Wytheville, Va., on C. bartonii.
19. Scholarie Creek, Green Co., Catskills, N. Y., on C. bartonii.
20. Spring Branch, three miles east of Mammoth Cave, Ky., on C. bartonii tenebrosus.
22. East River, W. Va., on C. bartonii.
23. Trubies Sun, W. Va., on C. obscurus.
24. Between Paoli and Wyandotte, Ind., on C. rusticus.
27. Rhinelander, Wis., on C. diogenes.
30. Bloomington, Ind., on C. Propinquus.
32. North Judson, Ind.
New locality records:
1. Alama, Temporal, and Vera Cruz, Mexico, on C. blandingii acutus.
2. Oakwood, Ill., on C. propinquus.
3. Highland, N. C., on C. bartonii.
4. Fargo, N. D., on C. immunis.
5. Indianapolis, Ind., on C. rusticus.
6. Van Buren, Mo.
7. Green County, Mo., on C. neglectus.
8. Wilburton, Okla., on C. longimonus.
10. Mad River, Emory, Ohio.
11. Loup Creek, W. Va.

Remarks: The internal characters of this species omitted by Ellis are well summarized by Leidy in his original description (1851:209):

"Body whitish, translucent; sides nearly parallel, a little broader posteriorly, sixteen alternately broad and narrow segments exclusive of head and posterior end. Head campanulate, terminated by a circular or elliptical crenated lip, fringed with very minute stiff hairs, one two-thousandth of an inch long. Acetabulum circular, one-sixth or one-fourth of a line in diameter; mouth elliptical. Dental plates brown, nearly equal, forming an isosceles triangle, with the base longest and attached apex of superior plate ending in a sharp conical point; with several minute denticulations on each side. Stomach capacious, nearly filling the anterior eight alternately broad and narrow segments posterior to the head. Anus dorsal, one-fifth of a line from the acetabulum. Generative opening ventral, anterior to the anal aperture. Length, one to four lines; breadth, one-sixth to one-half of a line. Head, one-sixth to one-half of a line long."

This species has a wide, short, cylindrical spermatheca. It possesses the characteristics of the genus.

Cambarincola okadai Yamaguchi, 1933, sp. dub.

Description from Yamaguchi 1933:191-193:

"Recently through the kindness of Prof. Dr. Y. Okada the present writer had an opportunity to examine several specimens of a branchiobdellid worm attached to the sternal surface and appendages of crayfish formerly transferred from America into Lake Chuzenji, Nikko. The specimens were collected by him in 1928 and preserved in formalin. They are undoubtedly referable to the genus Cambarincola Ellis 1912, and seem to me to represent a new species, though closely related to the American species, C. philadelphia and C. chirocephala. . . .

"The preserved specimens are whitish in color and more or less transparent. The body is rather elongate and cylindrical, and in most speci-
mens it slightly curves dorso-ventrally with the ventral side concave. The head is broader than the first trunk segment and is distinctly demarcated from the latter by a constriction. The trunk segments gradually widen from I to VI and then become narrower towards the posterior portion. Among the specimens examined, the largest is 7 mm. long and 0.5 mm. wide at the widest trunk segment. The dorsal part of the peristomium is provided with four distinct sagitiform appendages, while the ventral part is thick and slightly bilobed. The mouth is surrounded by about sixteen circumoral papillae, which are also found in other genera, such as Ceratodrilus, Stephanodrilus. Both the dorsal and ventral dental plates are slightly brown in color and of similar shape, forming an isosceles triangle with the base longest. Each plate has a large conical tooth forming the apex of the plate, and two small denticles on each side. Unlike Ceratodrilus and Pterodrilus, the worm is destitute of trunk appendages. The spermathecal pore and the male sexual aperture each open on a slightly elevated papilla in the midventral line in trunk segments V and VI respectively. The oviduct pores are paired, situated on the ventro-lateral sides of trunk segment VII. The anterior nephridia open in a common median dorsal pore on trunk segment III. The digestive tract runs almost straight from the mouth to the anus. Two pharyngeal diverticula, one dorsal and the other ventral, are present. The testes and funnels are paired in trunk segments V and VI; the body cavity of these segments is filled with abundant male reproductive cells in different developmental stages. The spermatheca is tubular and not bifid. The spermathecal vesicle is bifid, having the accessory sperm tube, so named by Ellis (1912).

"Remarks:—The present species has plurilobate peristomium which is present among the genus only in C. philadelphia, C. chirocephala and C. homodonta. [Later placed in the genus Stephanodrilus (Yamaguchi 1934:200-201).] Though closely related to C. philadelphia and C. chirocephala in nearly all characters, is distinguishable from them in the dental plates especially in the ventral plate; according to Ellis (1920), there are two large teeth and two small denticles in C. philadelphia and four subequal denticles in C. chirocephala, while the new species has a ventral plate provided with a large apical tooth and two small denticles on each side.

"Ellis [1919] pointed out that the primitive type of dental plates in branchiobdellids is probably a subequal five-toothed form. According to him, the type is represented by the formula C-B-C-B-C. Therefore both the dorsal and ventral plates of the new species, provided with a large median tooth are denoted by the formula, c-b-A-b-c. As to the dentation C. philadelphia and C. chirocephala are similar to the new species in the dorsal plate, but the ventral plate of C. philadelphia is shown as c-b-
b-c lacking the large median tooth, and that of *C. chirocephala* is indicated by the formula c-B-B-c showing the disappearance of the median tooth and the increase in size of the inner pair. From the difference of the dentition in the ventral plate, it seems to the writer to be right to recognize the Japanese worm as distinct from *C. philadelphica* and *C. chirocephala*.

“So far as the writer knows, there has been no report on crayfishes from Lake Chuzenji and adjacent districts except these newly transferred from America. The present species was probably introduced from America together with the American crayfish. However it is very noticeable that the present species and *C. homodonta* [Later placed in genus Stephanodrilus (Yamaguchi, 1934:200-201)], both occurring in Japan, have the dentition of the *homodonta*-type, while in all species belonging to the genus *hitherto* found in America the dorsal and the ventral plates are different in dentition.”

Remarks: This species appears to the writer to be identical with *Cambarincola philadelphica*, as it differs from it only in the dentition of the lower jaw, and *C. philadelphica* is an extremely variable form, as outlined above.

**GENUS XIRONOGITON** Ellis, 1919

Xironogiton, Stephenson 1930:802.

With the characteristics of the subfamily; spermatheca simple, not bifid; each nephridium of the anterior pair opening to the outside through a separate pore in the dorsal half of segment III; a distinct accessory sperm tube present in segment VI; body distinctly depressed; posterior segments wider and flatter than the anterior segments; posterior sucker ventral; segment IX much reduced so body appears to be composed of eight or fewer segments; alimentary canal looped once or twice in segment VII.

Type species: *Xironogiton instabilissimus oregonesis* Ellis, 1919.

**KEY TO THE SPECIES OF THE GENUS XIRONOGITON**

1. (a) Glandular concave disks near the lateral margin of the ventral surface of segments VIII and IX; body usually spatula-shaped... ..........................Xironogiton occidentalis Ellis, 1919
   (b) No conspicuous glandular disks near the lateral margin of the ventral surface of segments VIII and IX; body usually lance-shaped... 2

2. (a) Two teeth of the longest pair in the upper jaw separated by but one tooth; if two long teeth are contiguous the inner one is the longer... Xironogiton instabilissimus instabilissimus (Moore, 1894)
   (b) Two teeth of the longest pair in the upper jaw separated by two teeth; if two long teeth are contiguous the outer one is usually the longer... Xironogiton instabilissimus oregonesis Ellis, 1919
Xironogiton occidentalis Ellis, 1919


Description from Ellis 1919:248-249:

"Body segments elongate and distinctly depressed; body segments I to VIII distinct, each slightly constricted at its anterior and posterior ends giving the segmental junctions sharp definition; segment IX greatly reduced so that the body appears to be composed of but eight segments; segments expanding gradually and regularly in width to segment VII, which is the widest body segment; segment XIII almost as wide as segment VII; segments IX and X so narrow and inconspicuous that the caudal sucker appears to be inserted under the posterior half of segment VIII; head large, its anterior third defined by a groove; lips two, each with a slight median emargination, otherwise entire; a few short transparent bristles on the margins of the lips; major pharyngeal diverticula three, two dorsal and one ventral; the ventral diverticulum about midway between the levels of the two dorsal diverticula; dental formula 6-6 . . . . but with the two teeth of the "a" order unequal in size; tooth plan of upper jaw C-B-a-a-B-C, teeth of the "C" order being slightly smaller than those of the "B" order but larger than those of the "a" order, the two "a" teeth unequal; difference in size of teeth slight so that the jaws approach the subequal-toothed jaw type; anterior nephridia alternating in segments II and III, opening to the outside through separate pores on the dorso-lateral surface of segment III; spermatheca simple; testes present in segments V and VI; vasa deferentia from segments V and VI joining the atrium in segment VI; a long accessory sperm tube present; alimentary canal not conspicuously expanded in the first three segments, wider in segment IV, increasing in diameter in segments V and VI, narrowing in segment VII, in which segment the intestine forms a more or less definite "s"-shaped curve; intestine narrowing rapidly in the anterior half of segment VIII and continuing as a somewhat crooked tube to the anal opening on the dorsal surface of the posterior half of segment IX: because of the reduced condition of the segment IX, the anal opening is subterminal; adhesive disks on segment XIII prominent, those on segment IX inconspicuous.

"The two specimens from which this species was described measured 4.5 and 5 mm., respectively. X. occidentalis resembles a large, much extended specimen of X. instabilis (X Moore). It is easily separated from that species by the glandular disks on the ventral surface of segments VIII and IX and by the distinct segmental junctions."

Type: U.S.N.M. No. 17639 from Crab Creek, Wash., on Astacus klamathensis. Length 4.5 mm.

Previous locality records:——
Ellis 1919:248——
1. Crab Creek, Wash., on Astacus klamathensis.
New locality records:
1. Vernonia, Ore., on *A. troxbridgii*.
2. Harney Co., Ore., on *A. gambelii*.
3. Young River, Ore., on *A. klamathensis*.

Remarks: The additional material studied agreed with the above description except in regard to size, as worms were found which were 6.0 mm. long, distinctly larger than any Ellis studied.

*Xironogiton instabilius instabilius* (Moore, 1894)


Description from Moore 1894:425-427:

"Body in a state of contraction very short and stout, the posterior four segments forming a flattened disk-shaped expansion which is scarcely longer than broad; the first four body segments are much more narrow, but increase somewhat in breadth to the fourth, posterior to which the increase is very rapid to the seventh; the eighth is slightly narrower and develops lateral wing-like flaps, which, sloping ventralward, bound a decided ventral concavity in this region; posteriorly they embrace the sucker-bearing segments. The head and anterior segments are terets. Under normal conditions the large head is considerably broader than the following segments, which form a neck-like constriction, to which the head is attached by a very mobile fold, forming a distinct annulus. The emarginated lips are slightly crenulated, and form an almost continuous muscular thickening around the mouth. The postoral constriction is well-marked, but not so deep as in *B. pulcherrima*. Numerous short stiff hairs fringe the lips and head, and in young individuals are present on the body segments also.

"The dark brown jaws are provided with four strong curved conical teeth, which diverge slightly; the outer pair are symmetrical, the left tooth of the middle pair is much larger than the right; this being the case in both jaws in nearly all of the many specimens examined.

"The acetabulum resembles that of *B. pulcherrima* in being directed ventralward. Its diameter is greater than that of the first or second body segments. Bi-amulation is conspicuous on the anterior four post-cephalic segments only.

"The alimentary canal is strongly sacculated in the fourth and fifth segments, in the sixth is pushed to the left side by the development of the atrium (this occurs in adults only), in the seventh is thrown into a complete double transverse loop which passes first to the right and then
to the left, and finally passes directly to the anus in the ninth body segment. The spermatheca is very small and inconspicuous, while the penis-sac is well developed, and possesses a long vermiliform appendage (atrium) which forms a loop dorsally over and around the intestine. Sexual and nephridial openings as in *B. pulcherrima*.

"In contraction the body of this species is shaped like a short-handled racket; in extension it has the outline of an Indian club from dorsal and ventral views.

Length of mature animal .................... 5.5 mm.
Maximum breadth ............................. 1.3 mm.
Diameter of acetabulum ...................... 3 mm.
Transverse diameter of jaw .................. 0.048 mm.
Length of cocoon without pedicle ............ 0.35 mm.

"The cocoons resemble those of the last described species, but are frequently provided with an apical fibrous tuft. They are invariably attached (to the extent of my experience) to the palmar surface of the propodite of the great chelae. The animals themselves are largely restricted in their distribution to the same segments of the limb, and are usually to be found in numbers clustered at the base of the pinchers to which position the form of the body peculiarly adapts them; for while the constricted anterior region, by reason of its tenuity, easily escapes crushing between the closing limbs of the chela, in which position it is frequently liable to be caught, the important organs of reproduction and digestion are massed together near the base of attachment, entirely out of reach of danger from this source. Frequently they wander to other parts of the same pair of limbs, or even to the two pairs of ambulatory limbs following."

Type: From Watauga Co., N. C., and Delaware Co., Pa.
Previous locality records:
Moore 1894:427—
Smallwood 1906:100—
1. Lake Clear, Franklin Co., N. Y.
Ellis 1919:252—
1. Stony Man Mountain, Va., on Cambarus bartonii.
2. West Branch of Clinmark Creek, North Rose, N. Y., on C. bartonii robustus.
3. Trubies Run, a tributary of the Buckhannon River, 7 miles above Buckhannon, W. Va., on C. obscurus.
5. Chenowith Creek between Beverly and Elkins, W. Va., on C. bartonii carinirostris.
7. Right Hand Fork of Chenowith Creek, a tributary of the Cheat River, Queens, W. Va., on C. obscurus.
New locality records:
1. Cleveland, N. Y.

Remarks: Moore adequately describes the material studied, which did not present much variation.

**Xironogiton instabilius oregonensis** Ellis, 1919


Description from Ellis 1919:249-251:

"Body distinctly depressed, general outline of contracted specimens racket- or flask-shaped, extended specimens conspicuously wider in the posterior half of the body than in the anterior; head and body segments I and II subequal and subterete; segment IV distinctly wider than segment III and somewhat depressed; segments V to VIII conspicuously wider than the anterior portion of the body, rather completely fused at the segmental junctions so that the segmental junctions are not clearly defined as they are in the anterior four segments; maximum width of the body in segment VII; segments V and VIII subequal; segmental margins of segments V to VIII broadly flattened forming a conspicuous shelf beyond the thicker portion of the body; segment IX greatly reduced, not prominent in dorsal view; caudal sucker large, ventral, its width in contracted specimens about equal to that of the head; head large, in contracted specimens exceeding the first two body segments in size; head divided into two rather distinct units, the anterior being slightly shorter than the posterior; lips two, each with a median emargination; dental formula 5-4 or 6-5, varying from 4-4 to 7-6 . . . . major pharyngeal diverticula three, two dorsal and one ventral; each anterior nephridium opening to the outside through a separate pore in segment III; spermatheca in segment V, small and simple, subglobose with a small dorsal tubular portion, not bifid; testes in segments V and VI; vasa deferentia from segments V and VI joining the large atrium in segment VI; accessory sperm tube present and well-developed; alimentary canal rather straight in segments I to V, maximum enlargement in segment V, intestine more or less displaced (usually to the right) in segment VI depending upon the state of the enlargement of the reproductive organs in that segment; intestine forming two rather distinct loops in segment VII, decreasing rapidly in diameter from segment VII to the anal opening on the dorsal surface of segment IX; largest specimens examined was strongly contracted and measured 2.0 mm. in length."

Type: U.S.N.M. No. 17639 from Eugene, Ore., on **Astacus klamathensis** Stimpson.
Previous locality records:
Ellis 1919:249-251—
1. Eugene, Ore., on Astacus klamathensis.
2. Sequalitchew Lake, Pierce Co., Wash.

New locality records:
1. 22 miles from Vintage, Wash., on A. sp.
2. Klamath, Ore., on A. troebridgii.
3. Deer Creek, Ore., on A. troebridgii.
5. St. Helens, Ore., on A. troebridgii.
11. Evanston (Bear River), Wyo., on A. gambelli.

Remarks: Ellis believed this form to be a distinct species on the basis of the tooth differences as outlined above. However, additional material has shown considerable overlap in tooth formula and so the present writer believing this worm to be a western subspecies of the eastern form described by Moore, here presents Xironogiton oregonensis as a subspecies under the name Xironogiton instabilius oregonensis.

GENUS XIRONODRILUS Ellis, 1919

Xironodrilus, Stephenson 1930:802.

With the characteristics of the subfamily; spermatheca simple, not bifid; no accessory sperm tube; each nephridium of the anterior pair opening to the outside through a separate pore in the dorsal half of segment III; body depressed; caudal sucker ventral; at least nine segments visible in dorsal view; a glandular concave disk near each lateral margin of the ventral surface of segments VIII and IX; segments I to IX distinct; alimentary canal straight.

Type species: Xironodrilus formosus Ellis, 1919.

KEY TO THE SPECIES OF THE GENUS XIRONODRILUS

1. (a) Middle tooth of the upper jaw the longest tooth if teeth are odd in number; if teeth are even in number, the middle pair is the longest

Xironodrilus formosus Ellis, 1919

(b) Middle tooth of the upper jaw shorter than either of the two teeth adjoining it

Xironodrilus pulcherrimus pulcherrimus (Moore, 1894)

2. (a) Dental formula 3-3

Xironodrilus pulcherrimus dentatus new subspecies

(b) Dental formula varying from 4-4 to 5-5
Xironodrilus formosus Ellis, 1919

Description from Ellis 1919:244-245:

"Body rather elongate and distinctly depressed; width of the head approximately equal to that of segment I and less than that of segment II; body segments increasing in width regularly from segment I to segment VII; segment VII usually the widest segment of the body (In strongly contracted specimens and in specimens in which segment VII is not distended with sex cells, segments VII and VIII are usually about the same width, or segment VIII may be slightly wider than segment VII); nine body segments distinct and easily seen in the dorsal view; each segment slightly constricted anteriorly and posteriorly so that the junctions of the segments are evident; segments narrowing regularly and rapidly from the middle of segment VIII to the caudal sucker; diameter of caudal sucker less than or barely equal to the width of the head; head subcylindrical, its anterior third defined by a groove or constriction; lips two, the upper slightly longer than the lower; both upper and lower lips with small but rather definite median emargination, otherwise entire; margins of the lips bearing a few short, transparent bristles; tooth formula usually 5-4 or 5-5, varying from 4-3 to 6-5; . . . . tooth plan of both jaws c-B-A-B-c, upper jaw sometimes c-B-A-B-c-d; width of lower jaw 24 micra (in worm 1.4 mm. body length) to 30 micra (in worm 2.8 mm. body length) major pharyngeal diverticula three, two dorsal and one ventral, the ventral diverticulum about midway between the levels of the two dorsal diverticula; anterior nephridia alternating in segments II and III (of 44 specimens examined on this point 25 had the nephridium in segment II on the right side and that in segment III on the left; 17 had the nephridium in segment II on the left side and that in segment III on the right; and two individuals had both nephridia in segment II); anterior nephridia opening to the outside through separate pores on the dorsolateral surface of segment III; spermatheca in segment V, composed of three parts, a short muscular portion near the spermathecal pore, a middle tubular portion and a dorso-posterior, globose portion; testes in segments V and VI; vasa deferentia from segments V and VI joining the atrium in segment VI; no accessory sperm tube; alimentary canal straight, passing through the body near or along the mesial axis, somewhat expanded in segments I and II, strongly sacculated in segments III and IV, much narrowed in segments V and VI, slightly expanded in segment VII, narrowing from segment VII to the anal opening on the dorsal surface of the anterior half of segment X (In surface view the anus appears to open in the posterior half of segment IX, but sagittal sections show that the anal opening is between segments
IX and X and that the rectal portion of the alimentary canal is carried by segment X); caudal sucker ventral; smallest specimen examined 0.8 mm. in length; largest 3.1 mm. (preserved specimens).

Type: U.S.N.M. No. 17626 from White River, Irondale, near Andersonville, Ind., on Cambarus rusticus (Girard). Length 2.7 mm.

Previous locality records:
Ellis 1918:50—
2. Three miles up Potagannissing River, Drummond Island, Potagannissing Bay, Mich.

Ellis 1919:244—
1. White River, Irondale, near Anderson, Ind., on Cambarus rusticus.
2. White River, Noblesville, Ind., on C. rusticus.
5. Between Paoli and Wyandotte, Ind., on C. rusticus.

New locality records:
1. Champaign County, Ill., on C. virilis.
2. Indianapolis, Ind., on C. rusticus.
5. Galloway, Mo., on C. longidigitus.
8. Ozark, Mo., from Smallen Cave on C. setosus (cave crayfish).

Remarks: A large series of this form has been examined and all agree closely with the above description, the teeth variations all falling within the limits outlined above.

**Xironodrilus pulcherrimus** (Moore, 1894)


Description from Moore 1894:423-425:

“The beautiful transparency of the anterior segments which enables one to see with great distinctness the internal organs of that region suggested the name given to this species.

“Form rather stout, the body depressed, especially in the posterior
region. The segments increase regularly in width to the seventh, which is
the broadest; and behind which they rapidly narrow to the acetabulum.
Each post-cephalic segment consists of an anterior larger and a posterior
smaller annulus. The ventral surfaces of the eighth and ninth segments
are strongly flattened, and each bears on its extreme lateral margins a
cup-shaped adhesive organ, into the central depression of which a con-
spicuous gland opens. These are directed ventralward and doubtless
serve as accessory organs of attachment to aid the rather weak sucker.
Those on the eighth segment are usually the larger, but a considerable
range of variation is exhibited in this respect. The structures become
proportionally larger and more conspicuous in older individuals.

"The head is urn-shaped, slightly longer than broad in preserved
specimens, and its greatest width less than or just equal to that of the
first body segment. The breadth of the head varies greatly with the
degree of contraction of the specimen, but in the living individual always
appears narrow, and to form part of the generally even tapering outlines
of the body, never abruptly expanded as in B. instabilia. The oral region
is separated from the cephalic region by a deep constriction, which com-
pletely encircles the head. The mouth is enveloped by a pair (dorsal and
ventral) of distinct thick muscular lips, of which the dorsal one is the
larger and droops downward, partially enclosing the ventral lip. Each
presents a slight median emargination, but is otherwise entire. The lips
and head, as well as the sides of the principal annuli of the body, are
provided with a fringe of delicate hairs. Mouth opening nearly circular,
between the parted lips.

"The jaws are small and inconspicuous, in adult specimens less than
one-twelfth of the width of the head, and of a pale brown or amber color.
The rounded base bears three teeth, of which the larger lateral ones are
stout, curved, and divergent, while the smaller median one is straight and
sharp-pointed. The variations in the jaws involve frequent unsymmetrical
development of the teeth. The dorsal and ventral jaws are similar, and
both are fixed opposite to the constriction behind the lips, the teeth
being directed inward.

"The straight alimentary canal is strongly sacculated in the second,
third and fourth segments, behind which it is narrow, and direct in its
course to the anus, which opens on a slight papilla on the dorsal side of
the ninth segment.

"The greater part of the body cavity of the fifth and sixth segments
is filled with testicular cells in various stages of development; and the
glandular thickening of the skin of these segments renders the walls
conspicuously opaque. The two pairs of vasa deferentia open into the
nearly spherical atrium in the sixth segment. A conspicuous and broadly
pyriform spermatheca opens on the fifth segment. The ovaries and
accessory structures occupy the seventh. The anterior nephridia alternate in position, but open to the exterior by paired orifices in segment three. The posterior paired nephridia occupy the space on each side of the intestine in segment eight.

"This species is colorless and more or less translucent; the first four segments behind the head are remarkably clear and translucent, but behind this the body walls are rather opaque and the position of the internal organs obscured. The alimentary canal is throughout darkly colored, except within the head.

"Blood very pale red.

Length of mature individuals............ 6 mm.
Maximum breadth........................ 1.3 mm.
Width of jaws............................ .06 mm.
Diameter of acetabulum.................. .6 mm.

"Cocoons of this species are almost spherical and are borne on short stout stalks. Usually they are attached to the broad surfaces of the body, i.e., the sides of the carapace, inner faces of the anterior abdominal epimere, and the sternal face of the tail fin.

"Length of cocoon without stalk...... 46 mm.

"The adults are found attached almost anywhere on the exterior of the crayfish but more especially on the tergal surface."

Type: From Watauga Co., N. C., on Cambarus bartonii.

Previous locality records:
Moore 1894:425—
1. Watauga Co., N. C., on Cambarus bartonii.

Smallwood 1906:110—
1. Lake Clear, Franklin Co., N. Y.

Ellis 1919:246—
1. Trubies Run, a tributary of Buckhannon River, 7 miles above Buckhannon, W. Va., on C. obscursus.
2. Right Hand Fork of Chenowith Creek, Queens, W. Va., on C. obscursus.
5. Cheat River Bridge, Randolph County, W. Va., on C. bartonii carinirostris.
8. Indian Creek, Ranawha County, W. Va., on C. dubius.

New locality records:
1. Highlands, N. C., on C. bartonii.
2. Wilburton, Oklahoma, on C. longimanus.

Remarks: This description adequately describes all individuals examined with the exception of the tooth formula, which has greater varia-
tion than Moore realized. The first person to recognize this was Ellis (1919:247) who found that while the North Carolina material had the 3-3 tooth formula of Moore's description, the thirty-seven West Virginia worms had a formula varying from 4-4 to 5-5 with most individuals having a 5-4 formula. On the basis of this Ellis suggested that two subspecies might be represented but did not have enough material to be certain. The present writer has examined material from Highlands, North Carolina, and found the same 3-3 formula of Moore, but on the Oklahoma material the tooth formula was found to be 5-4 and 5-5. On this evidence the writer feels certain that two subspecies are actually represented, and he proposes the following names: *Xironodrilus pulcher- rimus pulcherrimus* (Moore, 1894) for the North Carolina worms with the 3-3 formula; and *Xironodrilus pulcherrimus dentatus* new subspecies for the form with the higher tooth formula as outlined above.

**GENUS BDELLODRILUS** Moore, 1895


*Bdellodrilus*, Stephenson 1930:801.

With the characteristics of the subfamily: spermatheca bifid; anterior nephridia opening to the outside through a single pore in the mid-dorsal line of segment III; no accessory sperm tube; a pair of clear large glands present in each of the nine postcephalic segments; no trunk appendages; penis eversible.

Type and only species: *Bdellodrilus illuminatus* (Moore, 1894).

*Bdellodrilus illuminatus* (Moore, 1894)


Description from Moore 1894:421-423:

"Body very slender in complete extension, but robust in contraction, tapering from the seventh segment very gently toward the head, and suddenly to the posterior sucker; terete in transverse section in all regions. Bi-annulation of segments very conspicuous throughout the entire length. Posterior sucker small and weak, on the same axis as the body segment. Head small, slender, and elongated; the post-oral part distinctly bi-annulate. Lips long and weak, of nearly equal size; ridged within by longitudinal folds. Mouth opening with its longest diameter transverse. No circumoral or other hairs have been detected in the adults of this species,
and in the young a single small bunch in the median region of each lip is all that is present.

"The jaws are remarkable, and although large, are inconspicuous on account of their transparency and lack of color. On the dorsal one, which is much the larger, a high median ridge is developed, which bears three strong teeth, the points of which are directed posteriorly (down the throat). The ventral jaw is shaped like a U each limb of which is bent out of the common plane into a boomerang shape. The angle of the boomerang on each side is uppermost and bears a very strong curved tooth, the two bounding a deep groove which accommodates the dorsal dentigerous ridge.

"The stomach is comparatively small, and behind it the evenly tubular intestine is thrown into loops, which become more obvious with the greater degree of contraction of the animal.

"In connection with the vascular system is developed a remarkable shallow sinus which covers almost the entire surface of the alimentary canal. This presents dorsal and ventral longitudinal enlargements into which the principal vascular trunks are received. The extensive vascular surface with the contained bright red blood thus presented gives the animals a delicate pinkish hue which distinguishes living individuals at a glance from the other species herein described.

"In each of the nine post-cephalic segments is a pair of peculiar translucent glandular bodies composed of large nucleated cells, and communicating with the exterior by slender ducts having ventro-lateral openings.

"The anterior two nephridia open into a gourd-shaped vesicle having an opening to the exterior in the mid-dorsal region of the major annulus of the third segment. The spermatheca is short, cylindrical and bifid; the penis-sac short-pedicled and spherical, and the atrium clavate and curved. The spermatheca, penis, ovaries, posterior paired nephridia and anus open respectively on the fifth, sixth, seventh, eighth, and ninth post-cephalic segments. Length of full grown individuals, 4 mm., maximum diameter (7th segment) 9 mm., diameter of acetabulum .35 mm."

Type: From Philadelphia, Pa., and Watauga Co., N. C., on Cambarus bartonii.

Previous locality records:
Moore 1894:421-423—
Allen 1933:119—
1. Durham, N. C.

New locality records:
1. Macoupin Co., Ill., on C. virilis.
2. Champaign Co., Ill., on C. blandinii acutus, C. virilis.

Remarks: This is an adequate description for the Illinois material examined.
GENUS STEPHANODRILUS Pierantoni, 1906

Stephanodrilus, Stephenson 1930:801.
Univ. 3(3):191-210.

With the characteristics of the subfamily: spermatheca simple, not bifid; no accessory sperm tube; anterior nephridia opening to the outside through separate pores in the dorsal half of segment III (except in St. koreanus); body cylindrical, not depressed, without body appendages.

Type species: Stephanodrilus sapporensis Pierantoni, 1906, from Japan.

Only known American species: Stephanodrilus obscurus new species.

*Stephanodrilus obscurus* new species

(Pl. I, Fig. 2; Pl. II, Fig. 6)

Description:

Length of worms examined varied from 2.0 mm. to 3.0 mm. Head subcylindrical, divided into three subequal portions by two constrictions; lips two, dorsal slightly longer than ventral, both entire but may have slightly wavy margin; dorsal and ventral jaws about 30 microns in diameter in a worm 2.5 mm. in length; dental formula 5-5 or 6-6 in material examined; dorsal jaw with the two outer teeth longer than median ones; ventral jaw similar to dorsal. Dorsal jaw may have a small denticle on the outer side of the two longer teeth.

Head diameter greater than segment I, about the same as segment II; segments increase regularly in diameter to segment VI or VII which is about 0.7 mm. in a worm 2.5 mm. long; diameter decreases to caudal sucker which is not especially large; major annulations of segments II to VII distinctly and visibly elevated over minor annulations. Gut relatively straight with sacculations in segments IV and VII.

Testes in V and VI, with a large male bursa in VI nearly filling the segment; spermatheca present in segment V, simple not bifid, enlarged in ventral portion. Anterior nephridia opening to the outside through separate pores in the dorsal half of segment III.

Holotype: From Fall River, Shasta County, California, on *Astacus nigrescens*.

Paratypes: From Fall River, Shasta County, California, on *Astacus nigrescens*.

Remarks: This is the first time this genus has been reported outside of the Japanese region and shows the close relation between the Oriental and Pacific-American faunas. This species differs from the previously described ones in the structure of the jaws and in the entire lips. All
other known forms of this genus have a peristomium divided into lobes which may be extended as digitiform appendages and have jaws provided with at least seven teeth. However these characters have been shown to be specific and not generic for other genera, and since this species otherwise agrees closely with the described forms of Stephanodrilus the writer feels that it is a member of that genus.

The holotype will be deposited in the United States National Museum and the paratypes in the collection of Dr. H. J. Van Cleave, of the University of Illinois, and in the collection of the writer.

GENUS TRIANNULATA new genus

With the characteristics of the subfamily; spermatheca simple not bifid; no accessory sperm tube; body cylindrical not flattened; head roughly triangular in shape with protruding lips; major annuli of most segments redvided to give the appearance of three annuli per segment; this is especially evident in the median segments and in moderately constricted specimens: anterior nephridia opening to the outside through separate pores in the dorsal half of segment III.

Type species: Triannulata magna new species.

KEY TO THE SPECIES OF THE GENUS TRIANNULATA
1. Lips entire except for a slight median emargination.................................
   Triannulata magna new species
2. Lips divided into lobes.................................Triannulata montana new species

Triannulata magna new species
(Pl. I, Fig. 4; Pl. II, Fig. 8)

Description:
Relatively large worms varying from 5.0 to 8.0 mm. in formalin fixed specimens. Head distinct from body, rounded, roughly triangular; lips two, dorsal slightly longer than ventral which has a slight median notch; lips narrower than head, so have a protruded appearance in side view: dorsal and ventral jaws similar, large, being 250 micra wide in a worm 5.0 mm. long; appearing as triangular blocks of chitin with a tooth at the apex, sides of the triangle not smooth but slightly undulating without definite teeth.

Head distinctly wider than segments I and II, about the same as segment III; segments distinct, increasing in width to segment VI or VII which is about 1.0 mm. in diameter in a worm 5.0 mm. long; segments then decreasing in diameter to the caudal sucker, which is large and prominent with large distinct glands; major annulations of most segments secondarily divided as discussed for genus; intestine relatively straight with sacculations in segments IV and VII.
Testes located in segments V and VI with rounded bursa in VI; spermatheca in V simple not bifid; anterior nephridia opening to the outside through separate pores in the dorsal half of segment III.

Holotype: From Naches, Wash., on Astacus sp.
Paratypes: From Naches, Wash., and Redmond, Wash., on Astacus sp.

Additional material: From St. Helens, Ore.; Cestsajo, Ore., on Astacus trowbridgii; Vernonia, Ore., on A. klamanthensis; Rogue River, Ore., on A klamanthensis.

Remarks: This species differs from Triannulata montana in the presence of entire lips and untoothed jaws while T. montana has lobed lips and toothed jaws.

The holotype will be deposited in the United States National Museum and the paratypes in the collection of Dr. H. J. Van Cleave, of the University of Illinois, and in the collection of the writer.

Triannulata montana new species

(Pl. I, Fig. 1; Pl. II, Fig. 7)

Description:
Body cylindrical and relatively large, up to 5.0 mm. in the material examined; major annuli secondarily divided as described above, head large and distinct; peristomium divided into twelve lobes (four dorsal, four ventral, and four lateral) which may be extended into tentacular appendages, dorsal longer than ventral or lateral; jaws large, 250 mica in diameter in a worm 5.0 mm. long; jaws with a dental formula of 7-5, each with a longer median tooth and smaller lateral ones; head diameter greater than segment I or II. about the same as segment III; segments increasing slightly to segment VI or VII which are about 1.25 mm. in diameter in a worm 5.0 mm. long; segments then decreasing to the caudal sucker which is fairly prominent with well developed glands; segments distinct; intestine relatively straight with sacculations in segments IV and VII.

Testes present in segments V and VI with bursa in VI; spermatheca in segment V simple not bifid; anterior nephridia opening to the outside through separate pores in the dorsal half of segment III.

Holotype: From Kalami River, Wash., on Astacus sp.
Paratypes: From North Fork of the Clearwater River near Bovill, Idaho, and from the Kalami River, Wash., between Centralia and Chihaliso, on Astacus sp.

Remarks: This species is very similar in appearance to Triannulata magna but differs greatly in the structure of the jaws and in the lobed peristomium. Triannulata montana has toothed jaws while T. magna has untoothed jaws; T. magna has entire lips rather than the lobed lips of T. montana.
The holotype will be deposited in the United States National Museum and the paratypes in the collection of Dr. H. J. Van Cleave, of the University of Illinois, and in the collection of the writer.

GENUS PTERODRILUS Moore, 1895

Pterodrilus, Stephenson 1930:801.

With the characteristics of the subfamily: spermatheca tubular not bífid; anterior nephridia opening to the outside through a common pore in the dorsal portion of segment III; body cylindrical, not depressed; head not distinct; blunt cylindrical appendages present along the median dorsal line of the body.

Type species: Pterodrilus alcicornus Moore, 1895.

KEY TO THE SPECIES OF THE GENUS PTERODRILUS

1. (a) Segments VII and VIII with funnel-shaped enlargements of the dorsal portions; funnel of VIII excavated dorsally so its dorsal margin bears two small “horns”..............................Pterodrilus durbini Ellis, 1919
   (b) Without these funnel-shaped enlargements as described under (a).........2
2. (a) Dorsal appendages on segment VII only........................................
   ...........................................................Pterodrilus mexicanus Ellis, 1919
   (b) Dorsal appendages on more than one segment.................................3
3. (a) Dorsal appendages on segments II to VIII, inclusive....................Pterodrilus distichus Moore, 1895
   (b) Dorsal appendages on segments III, IV, V, and VIII.....................Pterodrilus alcicornus Moore, 1895

Pterodrilus alcicornus Moore, 1895


Description from Moore 1895a:450-453.

"In this species, which is described from sections and specimens mounted entire, the body is terete throughout, or owing to the increase in thickness of the dorsal walls of the major annuli, appears somewhat compressed at these points. The somites VI, VII, and VIII are of about equal diameter, those anterior and posterior to them tapering respectively toward the head and caudal disks. Bi-annulation of the body somites is very marked. The head is rather slender, and consists of a circum-oral annulus divided into thick entire dorsal and ventral lips, and two similar post-oral rings. The caudal sucker is a muscular disk of simple form, and about the diameter of the first post-cephalic somite; its axis coincides with that of the body somites.

"Dorsal organs are highly developed in this species on post-cephalic
somites III, IV, V, and VIII. Somites VI and VII, and in less degree, II also, exhibit slight dorsal thickenings, of the body musculature. On the dorsum of the major annulus of somite III the body walls rise into a high compressed transverse ridge or plate, which fades out on the sides of the somite, and is produced laterally into a conspicuous, forwardly projecting trilobed wing, the anterior division of which flares outward and extends far forward over somite II, usually ending in a slightly bifid expansion. The remaining lobes are simple and conical tines, which project upward and slightly outward. The two wings flare so strongly that the distance between their apices is about 1½ times the diameter of the somite. Their shape is very strongly suggestive of the antlers of a young moose, hence the name given to the species. The generic name was also suggested by this species, in which the dorsal organs have a wing-like aspect not seen in the other species.

"The dorsal appendage of the VIIIth somite is also highly developed, and similar to the one just described. Its lateral wings, however, are less conspicuous, and are directed posteriorly instead of anteriorly, and also flare outward more conspicuously. The whole organ is strongly concave behind, while that on the third somite is similarly concave before. A small gland, closely resembling a ciliated gland, is sometimes present (in two out of three series of sections) embedded in the base of the organ on each side. On the IVth and Vth somites the appendages are less highly developed, but are similar, the low dorsal ridges bearing on each side a pair of slender and simple cylindrical processes.

"The transverse dorsal ridges are built up chiefly of short, thick, longitudinal muscle fibres, which extend between the anterior and the posterior covering of hypodermis. Spaces partly filled with a connective tissue network are observable among the fibres, and a similar more extensive space . . . separates the muscles of the dorsal organ from the longitudinal muscles of the body walls. A few vertical muscle fibres, are also developed in the lateral margins of the ridges. Over this firm muscular basis the hypodermis, with the circular muscle layer, extends, and this alone, with a core of loose, spongy tissue, probably derived from the subdermal connective tissue, forms the terminal processes and lobes. . . . In the formation of these dorsal appendages from the body walls, it would seem that the loose fold of hypodermis and circular muscle fibres that rises freely from the longitudinal muscle fibres is pinched up, as it were, at several points, from which the skin and connective tissue underlying it proliferate to form the marginal processes, while the space remaining becomes filled, save for a few narrow clefts, with muscle fibres that proliferate from the ends of the longitudinal muscle fibres of the body walls at the points where these meet the hypodermis.

"The alimentary canal is enlarged to form a saccular stomach in the
four anterior body somites, while posteriorly it is narrow and tubular, and, with the exception of a slight transverse loop in the VIIth and VIIIth somites, proceeds directly to the anus on the dorsum of somite X.

"The jaws are small, measuring 0.02 mm. in breadth. They are of similar form, being quadridentate, with a median pair of long, sharply-conical, widely-separated, and divergent teeth, bent at a nearly right angle from the plane of the somewhat quadrangular basal plate. In extreme lateral positions are a pair of inconspicuous blunt teeth. When in position the basal plates are fixed in the cuticle of the pharynx, and the points of the teeth of the two jaws cross in the pharyngeal lumen.

"The spermatheca lies in the Vth somite to the left of the intestine. Its lower half is narrow and cylindrical, its upper abruptly expanded.

"The copulatory bursa is rather thin walled, and with the penis is capable of complete invagination. The penis sheath is relatively short, and exhibits no muscular atrial enlargement at the upper end. The glandular atrium is short, nearly spherical, and thick walled. It receives the vasae deferentiae, which are of the usual form. In the mounted specimen from which figure it was drawn, the atrium was twisted so that in the figure the anterior end is directed posteriorly.

"The common opening of the anterior pair of nephridia is located on the dorsum of the major annulus of somite III, immediate posterior to the dorsal appendage.

"The largest examples found among about a dozen specimens measure about 1 mm. in length."

Type: From Johns River, Watauga Co., N. C., on *Cambarus acuminatus*.

Previous locality records:
Moore 1895a:453—
I. Johns River, Watauga Co., N. C., on *Cambarus acuminatus*.

Remarks: This species has not been encountered in the present study.

*Pterodrilus distichus* Moore, 1895


Description from Moore 1895a:453-454:

"Dorsal appendages are present on post-cephalic somites II to VIII inclusive, and are much simpler than in *P. alcicornus*. The dorsal ridges are not compressed and plate-like, and are similar on all the somites. On somites II to VII each bears a pair of bluntly pointed cylindrical lateral appendages, while somite VIII bears two pairs, they become somewhat larger anteriorly.

"These appendages contain no longitudinal muscle fibres, and the
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ridges on which they rest are largely formed .... of a muscular network derived from the circular fibres.

"In somites VII and VIII a complete transverse loop is developed on the intestine, which is otherwise as in P. alcicornus. The jaws are also very similar, but differ in the shorter median pair of teeth, and the stouter form of the basal plate ....

"The spermatheca is slender and clavate, and regularly tapers from blind end to mouth. It lies to the left of the intestine. The copulatory bursa is nearly spherical, with thin muscular walls, and larger bursal glands than P. alcicornus. Its inner surface is thrown into deep ridges, among which the penis lies. The whole structure when evaginated is shaped not unlike a mushroom, and resembles the corresponding parts of Bdellodrilus philadelphicus. The glandular atrium is remarkable in being divided by a deep cleft into two similar lobes, the structure being flattened in a plane perpendicular to this cleft, giving the organ a shape much resembling the conventionalized heart. The penis sheath is short, and lacks a sacular dilation.

"The anterior nephridial pore is on the crest of the ridge of the IIIrd somite. In other respects this species resembles P. alcicornus.

"The largest example .... from among upwards of fifty specimens measured 1.5 mm. in length, the usual size being about 1 mm."

Type: From western New York on Cambarus bartonii.

Previous locality records:
Moore 1895a:454—
1. Western New York on Cambarus bartonii.

Ellis 1919:254—
1. Oxford, Ohio, host not given.
2. Cedar Point, Ohio, host not given.

New locality records:
1. Oakwood, Ill., on C. propinquus.

Remarks: The local material of this species examined agreed closely with Moore's description.

_Pterodrilus durbinii_ Ellis, 1919


Description from Ellis 1919:254-255:

"Body rather short and thick, size small; width of the head scarcely equaling the width of segment I; body segments increasing rapidly in diameter from segment I to segment VII; segment VII (sometimes segment VI) the wide segment of the body; at least 10 body segments visible in side view; major and minor annulations of segment I of about
the same diameter, the major annulation, however, being about twice the length of the minor annulation; major annulations of segments II, III, and IV conspicuously elevated laterally and dorsally, forming ruffle-like bands around the anterior halves of each of these three segments; minor annulation of segment V almost obliterated, major annulation of segment V elevated dorsally and laterally into a midsegmental crest which almost encircles the segment; major annulation of segment VI low, the minor annulation elevated into an encircling segmental crest; major annulation in segment VII elevated and expanded into a funnel-shaped collar which encircles it and stands free from it except at the junction of the segment proper and the collar, the bell of the funnel being directed cephalad: minor annulation of segment VII low; major annulation of segment VIII elevated and expanded into a funnel-shaped collar like that on segment VII, except that the funnel of segment VIII is directed posteriorly, its bell opening caudad and standing free above the low minor annulation of segment VIII; dorsal margin of the funnel-shaped collar of segment VIII excavated in the mid-dorsal line, so that the margin of the funnel shows two distinct "horns" when seen from front or rear; segments IX and X low, small, and regular; head not exceeding the first two body segments in length, divided into three rather equal thirds by two indistinct grooves: lips two, the upper the longer, both slightly emarginate in the median line; oral bristles present; dental formula 5-4: . . . . major pharyngeal diverticula two, one dorsal and one ventral; alimentary canal straight, maximum enlargement in segment IV; testes in segments V and VI; vasa deferentia from segments V and VI meeting in segment VI; no accessory sperm tube; spermatheca simple and tubular; caudal sucker large, termino-ventral; its diameter equalling or exceeding the greatest diameter of the head; largest specimen examined 2.0 mm. in length."

Type: U.S.N.M. No. 17655 from White River, Irondale, near Irondale, near Anderson, Ind., on *Cambarus rusticus* Girard.

Previous locality records:
Ellis 1918:50—
2. Three miles up Potagannissing River, Drummond Island, Potagannissing Bay, Mich., on *C. virilis*.
4. Little Cass Island, head of Detour Passage, Mich., on *C. virilis*.
5. Churchville Point, head of Lake George, 46° 31' N, Mich., on *C. virilis*.
6. Winona Slips, Bay City, Saginaw Bay, Mich., on *C. virilis*.
Ellis 1919:254—
1. Anderson, Ind., on *Cambarus rusticus*.

Remarks: The single specimen examined agreed closely with Ellis' description.
Pterodrilus mexicanus Ellis, 1919


Description from Ellis 1919:254:

“The type-specimen was unique, and, unfortunately poorly preserved. Consequently but a brief diagnosis can be given. General body form similar to Pterodrilus distichus Moore; no dorsal processes on segments II to VII, inclusive; segment VIII bearing a simple four-horned appendage like that on the same segment of P. distichus; dental formula 5-4; . . . . As far as the internal anatomy could be traced in a whole mount of this poorly preserved specimen, the organs resembled those of P. distichus Moore and P. durbinii, new species.”

Type: U.S.N.M. No. 17654 from Mirador, Vera Cruz, Mexico, on Cambarus mexicanus Erichson. Length 1.0 mm.

Previous locality records:
Ellis, 1919:254—
1. Mirador, Vera Cruz, Mexico.

Remarks: This form needs further study but unfortunately no specimens were available to the writer.

GENUS CIRRODRILUS Pierantoni, 1905


Ceratodrilus and Cirrodrilus, Stephenson 1930:800-801.


With the characteristics of the subfamily; spermatheca simple, not bifid; no accessory sperm tube; anterior nephridia opening to the outside through separate pores in the dorsal half of segment III; penis eversible; body cylindrical, not depressed; with body appendages in the form of pointed bands extending transversely across the dorsal surface.

Type species: Cirrodrilus cirratus Pierantoni, 1905, from Japan.

Only known American species: Cirrodrilus thysanosonus (Hall, 1914).

Remarks: Hall differentiated Ceratodrilus from Cirrodrilus on the basis of the dorsal appendages because Pierantoni had described Cirrodrilus as having ventral appendages. However Yamaguchi (1932a: 362-365) collected material and found that Pierantoni’s specimen was nothing but a poorly preserved worm which he had incorrectly oriented. Yamaguchi (1932a:364-365) summarizes his evidence as follows:

The specimen, on which Pierantoni based his description, was, as he indicated in a poor state of preservation, and could not be used for the investigation of its internal anatomy.
...the main difference between Pierantoni's and my specimens lies in the position of the trunk appendages, while the other characters accord generally with each other.

Before entering upon the discussion of the question the following fact is noticeable. In my specimens, those fixed with Zenker's solution or sublimate-alcohol almost retain the structure of living condition, while those fixed with dilute alcohol are considerably deformed and bear remarkable resemblances to Pierantoni's specimen in pyriform head which lacks the membranous margin and obscuresness of the lamellar ridge and the annulations of the trunk.

In regard to the difference in number of the head appendages between Pierantoni's specimen and my own, I am of the opinion that his specimen is abnormal or damaged.

The position of the trunk appendages in his specimen, the most distinguishable character of all, seems to me to be doubtful. In his paper no description of the anus, spermathecal pore and male pore is given. Therefore, it must be depended only upon the head in distinguishing the dorsal and ventral surfaces of the worm.

Furthermore, in the figure, the neck is very narrow and the annulations of the anterior part of the trunk obscure. Thus it seems to me possible that in his specimen the head was twisted on account of ill-preservation.

On the basis of the above evidence it seems to the writer that Pierantoni's Cirrodrilus and Hall's Ceratodrilus are one and the same genus.

*Cirrodrilus thysanosomus* (Hall, 1914)


Description:

Head distinct from body; peristomium bilobed, each lobe fringed with four or five papillae; body of relatively uniform diameter throughout although slightly greater in segment VI or VII. Hall (1914:191) gives the following measurements which agree rather well with my material: "Length 2 to 2.6 mm.; maximum head diameter, 400 micra; maximum body diameter 660 micra; maximum sucker diameter, 360 micra. Maximum length of cirriform appendages of head, about 180 micra." Anterior dorsal portion of head with a membranous border deeply incised to form four tentacular appendages: first seven trunk segments have dorsal appendages, extending from the lateral border in a pointed band, the number of points varying from 6 to 8 but usually being 6.

Testes present in segments V and VI with male bursa in VI; without accessory sperm tube; spermatheca in V cylindrical or flask-shaped, simple; penis eversible.

Dorsal and ventral jaws slightly dissimilar with a 7-6 dental formula; teeth of comparatively uniform size. Intestine relatively straight with several sacculations with an anus in the mid-dorsal line of segment X.

Type: U.S.N.M. No. 17708 from streams of the Great Basin, Salt Lake City Utah.
Previous locality records:
Hall 1914:191:
1. Salt Lake City, Utah.

New locality records:
1. Burley, Idaho, on Astacus gambelii.
3. Evanston (Bear River), Wyo., on A. gambelii.

Nomina Nuda

Three species mentioned in the literature have been either incompletely described or remain wholly without description, and since none of these has been recognized under the International Code, these names must be regarded as nomina nuda.

*Bdellodrilus manus* Moore, 1895

Moore (1895a:454): "*Pterodrilus distichus* was found in great numbers with *Bdellodrilus philadelphicus, B. manus* n.s." He never described this form or differentiated it in any way.

*Branchiobdella chilensis*

Moquin-Tandon (1846:300): "Branchiobdelle . . . . Gay, lettre à M. de Blainv., Institut., 1936 mars 28.—'Hab. le Chili, aux environs de Santiago, sur les branchies d'une écrevisse (Gay).'"

*Branchiobdella auriculae*

Moquin-Tandon (1846:301): "Branchiobdelle . . . . Gay, lettre à M. de Blainv., Institut., 1936 mars 28.—'Hab. le Chili, trouvée dans la poche pulmonaire de l'Auricula Dombeii (Gay).'"

IX. BIOLOGY

Host Specificity

Ellis (1919) found nearly every form of branchiobdellid that he studied from sufficient number of specimens on a great number of different species of crayfish. Evans (1939) found the species of those worms he studied in Champaign County on all forms of crayfish encountered. The writer's work confirms this, and by adding many new host records for previously described species practically proves that there is no host specificity. For example, *Cambarincola philadelphica* has been found on a great number of crayfish, including *Cambarus bartonii, C. obscurus, C. dubius, C. latimanus, C. rusticus, C. diogenes, C. virilis, C. propinquus, and C. blandingii acutus*. In short, within the limits of the range of any branchiobdellid any crayfish may serve as host.
Food Habits

Dorner (1865) from observations on European forms believed the food of branchiobdellids was largely the blood of crayfish. Smallwood (1906) thought that Xironogiton instabilis and Bdellodrilus illuminatus did not feed on the crayfish since their intestine was filled with algae. Hall (1914) believed young animals to be non-parasitic but adults to be parasitic in their food habits. Yamaguchi (1934) thought the gill-inhabiting species fed on the blood of the host, but the others did not.

After examining a large number of specimens containing food in their intestine, the writer has come to the conclusion that in most forms diatoms are the favorite food during all stages of their life. Other things were found, as parts of very small insect larvae, algae, and in many cases immature individuals of the same species. In many instances worms were found with the gut fairly extended with small diatoms. As a result the writer concludes that while some species may occasionally take food from their host, in general most forms are non-parasitic and feed largely on diatoms. If some are parasitic they are probably only facultative parasites.

Longitudinal Distribution of Branchiobdellids in a Stream

"Spotty" field collecting at various places gave the impression that the distribution of these worms in a stream was independent of size or drainage area. In order to check this hypothesis, Spanish Needle Creek, a stream about twenty miles long, was selected and crayfish were collected from source to mouth. Collections were also made at several points in Macoupin Creek, to which Spanish Needle Creek is a tributary.

Spanish Needle Creek is located in the central part of Macoupin County, Illinois. This stream has a sand and rock bottom throughout its entire course and has water in it almost to its source even during the driest months of the year. The creek has the typical invertebrate fauna of a central Illinois stream, including large numbers of dytiscid, gynnid, and hydrophilid beetles; corixid, notonectid, and gerrid bugs, amphipods (Gammarus), and isopods (Asellus).

The first station for collecting was near the source. Here the water was less than a foot deep and the stream was very narrow with low banks. In this place were found large numbers of the crayfish Cambarus virilis and C. blandingii acutus, all possessing in great numbers Cambarincola macrodonta.

Station 2, about 1 1/2 miles down stream, had a much greater volume of water. The creek here was about 1 1/2 feet deep and steep banks were beginning to form. Here again were found Cambarus virilis and C. blandingii acutus, all having large numbers of Cambarincola macrodonta.
Station 3, about the median portion of the stream, was very rocky, with numerous rapids. The water averaged about 2-3 feet deep with many holes which were much deeper. At this point the stream was very wide, and steep high banks were formed. Nearby a fairly large tributary entered. Although the character of the stream had changed greatly, *Cambarus virilis* was found to harbor *Cambarincola macrodonta* in about the same numbers.

The water at Station 4, near the mouth of the stream, was about 4 feet deep with many deeper holes. It had a smooth sand bottom. Here around the roots of trees that extended into the water, *C. virilis* again was found in great numbers, still harboring *Cambarincola macrodonta*.

Station 5 was at the mouth of the stream where it flowed into Macoupin Creek. Here the water was 5-6 feet deep but the crayfish collected carried the same worms. A few collections were made in Macoupin Creek itself, and the worms were found to be of the same species as was found in Spanish Needle Creek.

This study seemed to confirm the tentative conclusion that the distribution of branchiobdellids in a stream is independent of size and drainage area.

**X. CONCLUSIONS**

So far as is known, there are nine genera and twenty-one species of Branchiobdellidae in North America. These are:

- *Branchiobdella tetradonta*
- *Branchiobdella americana*
- *Cambarincola elevata*
- *Cambarincola inversa*
- *Cambarincola vitrea*
- *Cambarincola macrodonta*
- *Cambarincola chirocephala*
- *Cambarincola philadelphica*
- *Xironogiton occidentalis*
- *Xironogiton instabilis*
- *Xironodrilus formosus*
- *Xironodrilus pulcherrimus*
- *Bdellodrilus illuminatus*
- *Stephanodrilus obscurus*
- *Triannulata magna*
- *Triannulata montana*
- *Pterodrilus durbinii*
- *Pterodrilus mexicanus*
- *Pterodrilus distichus*
- *Pterodrilus alcicornus*
- *Cirrodrilus thysanosomus*

The family is divided into two subfamilies, Branchiobdellinae with one pair of testes and Cambarincolinae with two pairs of testes.

One new genus, *Triannulata*, is recognized and defined.

The generic name *Ceratodrilus* Hall. 1914, is believed to be a synonym of *Cirrodrilus* Pierantoni, 1905.

The genus *Cambarincola* is found to be divisible into two subgenera, *Cambarincola* and *Coronata*.
Cambarincola elevata, Stephanodrilus obscurus, Triannulata magna, and Triannulata montana are described as new species.

Xironogiton oregonensis Ellis is considered to be a western subspecies of Xironogiton instabilis (Moore).

Xironodrilus pulcherrimus is found to be divisible into two subspecies due to differences in jaws. These are called Xironodrilus pulcherrimus pulcherrimus and Xironodrilus pulcherrimus dentatus.

The presence of an accessory sperm tube, the number of anterior nephridial openings, the general shape of the body, the presence and shape of appendages, and gross morphological structures, as clear glands of Bdellodrilus, etc., are considered to be of generic importance.

Keys are provided for the identification of all known North American species.

Branchiobdellids have little if any host specificity.

Branchiobdellids apparently are distributed in a stream independent of size of stream or drainage area.

The food of branchiobdellids consists principally of diatoms.

The west coast fauna was found to be closely related to the Oriental fauna. The genera Cirrodrilus and Stephanodrilus are common to both faunas. Stephanodrilus has been first reported from North America in the present work.

A great deal of additional work needs to be done, as whole regions of the United States are unknown so far as this group is concerned and no complete life history has been worked out for these forms.
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Lankester, E. R.

Leidy, J.

Lemoine, V.

Michaelson, W.
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Stephenson, J.

Tannreuther, G. W.

Vallot.

Vejdovsky, F.

Verrill, A. E.

Voigt, W.

Voinow, D. O.

Ward, H. B., and Whipple, G. C.

Whitman, C. O.

Yamaguchi, H.
PLATE I

Each line represents 0.02 mm.
(All figures drawn with camera lucida.)

Fig. 1.—Jaws of *Triannulata montana* new species.
Fig. 2.—Jaws of *Stephanodrilus obscurus* new species.
Fig. 3.—Jaws of *Cambarincola elevata* new species.
Fig. 4.—Jaws of *Triannulata magna* new species.
PLATE II
Each line represents 0.5 mm.
(All figures drawn with Eddinger projector)

Fig. 5.—Lateral view of Cambarincola elevata new species.
Fig. 6.—Lateral view of Stephanodrilus obscurus new species.
Fig. 7.—Dorsal view of Triannulata montana new species.
Fig. 8.—Dorsal view of Triannulata magna new species.

Abbreviations: A—anus. AC—accessory sperm tube. B—male bursa.
PLATE III
(Figures modified from various sources)
Fig. 9.—Lateral outline of Bdellodrilus Moore.
Fig. 10.—Lateral outline of Cambarincola Ellis.
Fig. 11.—Ventral outline of Xironodrilus Ellis.
Fig. 12.—Dorsal outline of Cirrodrilus Pierantoni.
Fig. 13.—Ventral outline of Xironogiton Ellis.
Fig. 14.—Lateral outline of Pterodrilus Moore.