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A COMPARATIVE STUDY OF THE DIGESTIVE SYSTEMS OF
CAMBARINCOLA PHILADELPHICA (LEIDY, 1851) AND
XIRONODRILUS FORMOSUS (ELLIS, 1819) (ANNELIDA,
OLIGOCHAETA, BRANCHIOBDELLIDAE)

The Ohio State University, Ph.D., 1970
Zoology

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A COMPARATIVE STUDY OF THE DIGESTIVE SYSTEMS OF
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XIRONODRILUS FORMOSUS (ELLIS, 1819) (ANNELIDA,
OLIGOCHAETA, BRANCHIOBDELLIDAE)

DISSERTATION
Presented in Partial Fulfillment of the Requirements for
the Degree Doctor of Philosophy in the Graduate
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By
Bertha Orphe Richard, B.S., M.S.

The Ohio State University
1971

Approved by
Joseph Miller
Adviser
Department of Zoology
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VITA

October 13, 1938 .... Born, St. Martinville, Louisiana

1956 ............... High School Diploma; Carver High, Breaux Bridge, Louisiana

1959-1960 .......... Undergraduate Research Assistant in Botany, Southern University, Baton Rouge, Louisiana

1960 .................. B.S. Degree in Zoology, Southern University, Baton Rouge, Louisiana

1960-1962 .......... Zoology Teaching Assistant, The University of Wisconsin, Madison, Wisconsin

1962 .................. M.S. Degree in Zoology, The University of Wisconsin, Madison, Wisconsin

1962-1963 .......... Biology Instructor, Tuskegee Institute, Tuskegee Institute, Alabama

1963-1964 .......... Zoology Instructor; Southern University, Baton Rouge, Louisiana

1966 .................. Research Assistant in Physiological Chemistry, Research Center, The Ohio State University, Columbus, Ohio

1966-1967 .......... Anatomy and Physiology Instructor, Mt. Carmel School of Nursing, Columbus, Ohio

1967 .................. Teaching Associate, The Ohio State University, Columbus, Ohio

iii
<table>
<thead>
<tr>
<th>TABLE OF CONTENTS</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>ACKNOWLEDGEMENTS</td>
<td>ii</td>
</tr>
<tr>
<td>VITA</td>
<td>iii</td>
</tr>
<tr>
<td>LIST OF TABLES</td>
<td>vi</td>
</tr>
<tr>
<td>LIST OF FIGURES</td>
<td>vii</td>
</tr>
<tr>
<td>INTRODUCTION</td>
<td>1</td>
</tr>
<tr>
<td>THE BRANCHIOBDELLIDS (HISTORICAL REVIEW)</td>
<td>3</td>
</tr>
<tr>
<td>THE BRANCHIOBDELLIDS IN THIS STUDY</td>
<td>17</td>
</tr>
<tr>
<td>(DESCRIPTION AND DISTRIBUTION)</td>
<td></td>
</tr>
<tr>
<td>MATERIALS AND METHODS OF STUDY</td>
<td>29</td>
</tr>
<tr>
<td>THE MORPHOLOGY OF THE ALIMENTARY CANALS</td>
<td>35</td>
</tr>
<tr>
<td>Cambarincola philadelphica</td>
<td>35</td>
</tr>
<tr>
<td>Xironodrilus formosus</td>
<td>39</td>
</tr>
<tr>
<td>A SUMMARY OF THE MORPHOLOGY AND THE VASCULAR SYSTEM OF</td>
<td>42</td>
</tr>
<tr>
<td>THE BRANCHIOBDELLIDS</td>
<td></td>
</tr>
<tr>
<td>THE HISTOLOGY OF THE ALIMENTARY CANALS</td>
<td>45</td>
</tr>
<tr>
<td>Cambarincola philadelphica</td>
<td>45</td>
</tr>
<tr>
<td>Xironodrilus formosus</td>
<td>62</td>
</tr>
<tr>
<td>THE FOOD AND FEEDING MECHANISM</td>
<td>69</td>
</tr>
<tr>
<td>The Food</td>
<td>69</td>
</tr>
<tr>
<td>The Feeding Mechanism of Cambarincola philadelphica</td>
<td>71</td>
</tr>
<tr>
<td>DISCUSSION</td>
<td>75</td>
</tr>
<tr>
<td>SUMMARY</td>
<td>95</td>
</tr>
</tbody>
</table>

iv
<table>
<thead>
<tr>
<th>TABLE OF CONTENTS (Contd.)</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>LITERATURE CITED.</td>
<td>98</td>
</tr>
<tr>
<td>EXPLANATION OF FIGURES.</td>
<td>105</td>
</tr>
<tr>
<td>APPENDIX.</td>
<td>121</td>
</tr>
<tr>
<td>Table</td>
<td>Description</td>
</tr>
<tr>
<td>-------</td>
<td>-----------------------------------------------------------------------------</td>
</tr>
<tr>
<td>1</td>
<td>Locality records for <em>Cambarincola philadelphica</em></td>
</tr>
<tr>
<td>2</td>
<td>Locality records for <em>Xironodrilus formosus</em></td>
</tr>
<tr>
<td>3</td>
<td>The most characteristic features of the several regions of the alimentary canal of both <em>Cambarincola philadelphica</em> and <em>Xironodrilus formosus</em></td>
</tr>
</tbody>
</table>
# LIST OF FIGURES

<table>
<thead>
<tr>
<th>Figure</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td><em>Cambarincola philadelphica</em>, lateral views: a, entire animal; b, male reproductive system and spermatheca; c, dorso-lateral view of jaws; d, lateral view of jaws (After Hoffman, 1963).</td>
<td>106</td>
</tr>
<tr>
<td>2</td>
<td><em>Xironodrilus formosus</em>: a, dorsal view of entire animal; b, ventral view of male reproductive system; c, upper jaw; d, lower jaw (After Hobbs, et al, 1967).</td>
<td>106</td>
</tr>
<tr>
<td>3</td>
<td><em>Cambarincola philadelphica</em>, dorsal outline showing alimentary canal.</td>
<td>108</td>
</tr>
<tr>
<td>4</td>
<td><em>Xironodrilus formosus</em>, dorsal outline showing alimentary canal.</td>
<td>108</td>
</tr>
<tr>
<td>5</td>
<td>Mid-sagittal section of mouth, pharynx, esophagus, and anterior intestine of <em>Cambarincola philadelphica</em>.</td>
<td>110</td>
</tr>
<tr>
<td>6</td>
<td>Enlargement of the pharyngeal wall of <em>Cambarincola philadelphica</em>.</td>
<td>110</td>
</tr>
<tr>
<td>7</td>
<td>Mid-sagittal section of mouth, pharynx, esophagus and a portion of the anterior intestine of <em>Xironodrilus formosus</em>.</td>
<td>110</td>
</tr>
<tr>
<td>8</td>
<td>Sagittal section of the oral region, showing labial papillae in <em>Cambarincola philadelphica</em>.</td>
<td>112</td>
</tr>
<tr>
<td>9</td>
<td>Transverse section of the mouth, <em>Cambarincola philadelphica</em>.</td>
<td>112</td>
</tr>
<tr>
<td>10</td>
<td>Transverse section of the pharynx across the jaws, <em>Cambarincola philadelphica</em>.</td>
<td>112</td>
</tr>
</tbody>
</table>
LIST OF FIGURES (Contd.)

<table>
<thead>
<tr>
<th>Figure</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>11</td>
<td>Transverse section of the esophagus and &quot;heart&quot;, <em>Cambarincola philadelphica</em></td>
<td>112</td>
</tr>
<tr>
<td>12</td>
<td><em>Bdellodrilus illuminatus</em>, a diagram showing the vascular system (Modified from Moore, 1895).</td>
<td>114</td>
</tr>
<tr>
<td>13</td>
<td>Sagittal section showing the mid-intestine of <em>Xironodrilus formosus</em>.</td>
<td>116</td>
</tr>
<tr>
<td>14</td>
<td>Sagittal section showing the posterior intestine, rectum, and anus of <em>Cambarincola philadelphica</em>.</td>
<td>116</td>
</tr>
<tr>
<td>15</td>
<td>Transverse section of the anterior intestine of <em>Cambarincola philadelphica</em>.</td>
<td>116</td>
</tr>
<tr>
<td>16</td>
<td>Transverse section of the posterior intestine of <em>Cambarincola philadelphica</em>.</td>
<td>116</td>
</tr>
<tr>
<td>17</td>
<td>Transverse section of the intestine in segment seven showing ovum around the intestine, <em>Cambarincola philadelphica</em>.</td>
<td>118</td>
</tr>
<tr>
<td>18</td>
<td>Transverse section of <em>Cambarincola philadelphica</em> through segment nine, showing rectum, posterior sucker and associated structures.</td>
<td>118</td>
</tr>
<tr>
<td>19</td>
<td>Transverse section of <em>Xironodrilus formosus</em> through segment nine, showing rectum, posterior sucker, and associated glands and muscles.</td>
<td>118</td>
</tr>
<tr>
<td>20-26</td>
<td>The feeding movements of <em>Cambarincola philadelphica</em>.</td>
<td>120</td>
</tr>
<tr>
<td>27</td>
<td>A map showing the distribution of the branchiobdellids in North America and Mexico.</td>
<td>128</td>
</tr>
</tbody>
</table>
INTRODUCTION

The annelid worms of the oligochaete family Branchiobdellidae live as epizoites or ectoparasites on various holartic freshwater crustaceans, mostly members of the decapod family Astacidae. They are widely distributed in North America, South America, Europe, and most of Asia. In spite of their abundance and the ease with which they may be collected, the American branchiobdellids have received surprisingly little attention. As a result, fewer than a dozen detailed anatomical studies of even a single organ system have appeared in the literature (Holt, 1949). Among these, Moore's anatomical account of *Bdellodrilus illuminatus* (1895), Moore's account of the nephridial system of *B. illuminatus* (1897), and Holt's comparative study of the reproductive systems of *Xironogiton instabilius* and *Cambarincola philadelphica* (1949) are the most complete. Franzen (1962) briefly described the musculature of certain parts of the alimentary canal in his study of the morphology and histology of the muscle cells of the branchiobdellid, *Xironogiton instabilius*. However, as yet there is no detailed account of the histology and
function of the alimentary canal of the American branchiobdellids. The present investigation attempts to fill a part of this gap. The object of this study is (1) to compare the gross anatomy and histology of the digestive systems of Xironodrilus formosus and Cambarincola philadelphica; (2) to describe the feeding mechanism of Cambarincola philadelphica and the food of the two species, and (3) to offer clues as to the function of the various regions of the alimentary canal.
THE BRANCHIOBDELLIDS

The branchiobdellids comprise a family of annelid worms which live on the gills and exoskeleton of a few freshwater crustaceans, usually the crayfish. All known forms are ectoparasites or ectocommensals on freshwater crustaceans. None are known from marine or brackish waters; they have never been obtained in nature free from their crustacean hosts; they are known only from Holarctic area (with minor exceptions in the Neotropical), where their distribution corresponds in general to that of astacid crayfish (Holt, 1968).

Originally, the branchiobdellids were considered by their discoverer to be leeches (Odier, 1823). At a later period they were assigned to the oligochaetes (Vejdovsky, 1884; Michaelsen, 1909; Pierantoni, 1912; Stephenson, 1930; and Goodnight, 1940). Recently, after Franzen (1962) pointed out the hirudinean nature of their musculature, Holt (1965b) proposed that these epizoites constitute a distinctive order of clitellate annelids along with the Oligochaeta, Hirudinea, and Acanthobdellida. The branchiobdellids will be considered as oligochaetes in this investigation.
The body of the branchiobdellids is short, composed of only 15 segments. The first four segments form the head. There is no prostomium. The peristomium functions as an oral sucker and is set off from the remainder of the "head" by a sulcus (Holt, 1965b). The body (trunk) is composed of 11 segments. Each segment is subdivided, in leech-like fashion, by a constriction superficially similar to an intersegmental furrow, into an anterior prosomite and a posterior metasomite (Holt, 1965b). The last one or two segments form the caudal sucker. The branchiobdellids range in size from 1 mm. to 12 mm. in length. The body is cylindrical (terete) in most species, but members of the genera *Ankyrodrilus*, *Xironodrilus*, and *Xironogiton* are variously flattened dorsoventrally in body form (Hobbs, et al. 1967).

Goodnight (1940b) characterizes the family Branchiobdellidae as having "...the 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 the 5th or in the 5th and 6th segments; ovaries in the 7th segment; unpaired spermatheca in the 5th segment." Goodnight divided the family Branchiobdellidae into two subfamilies; (1) the Branchiobdellinae, having one pair of testes and
and male funnels located in the fifth segment, and (2) the Cambarincolinae, having two pairs of testes and male funnels located in the fifth and sixth segment. In these two subfamilies, there are sixteen known genera and approximately 80 species. Thirteen of the sixteen genera are known from North America. The two branchiobdellids in this investigation, *Cambarincola philadelphica* and *Xironodrilus formosus*, are in the subfamily Cambarincolinae.

The classification outlined below shows the relationship of the branchiobdellids to other annelid groups.

Phylum - Annelida

Class - Archiannelida

Class - Polychaeta

Class - Hirudinea

Class - Oligochaeta

Order - Plesiopora

Family - Aelosomatidae

Family - Naididae

Family - Tubificidae

Family - Enchytraeidae

Order - Opisthopora

Family - Haplotaxidae

Family - Moniligastridae

Family - Glossoscolecidae

Family - Lumbricidae
Family - Megascolecidae

Family - Eudrilidae

Order - Prosopora

Family - Lumbriculidae

Family - Branchiobdellidae

Subfamily - Branchiobdellinae
- Genus - Branchiobdella

Subfamily - Cambarincolinae
- Genus - Cambarincola
- Genus - Ankyrodrilus
- Genus - Cirrodrilus
- Genus - Caridinophila
- Genus - Sathodrilus
- Genus - Cronodrilus
- Genus - Ceratodrilus
- Genus - Bdellodrilus
- Genus - Ellisodrilus
- Genus - Oedipardrilus
- Genus - Pterodrilus
- Genus - Xironogiton
- Genus - Xironodrilus
- Genus - Magmatadrilus
- Genus - Tettodrilus

Since the genital organs of the Branchiobdellidae are so much like those of the Lumbriculidae, Stephenson
(1930) believed that the branchiobdellids originated from the Lumbriculidae. Both families have the combined male ducts opening to the outside on the segment that contains the posterior pair of testes. "In many respects the Branchiobdellidae are only modified Lumbriculidae" (Goodnight, 1940b). Their relationships are shown in the accompanying diagram from Stephenson, 1930.

The worms have been variously described (1) as diatom feeders (Smallwood, 1906; Goodnight, 1940b), (2) as blood feeders (Stephenson, 1930; Yamaguchi, 1934), or (3) as parasites in the adult stage only (Bishop, 1968). Their food habit is far from settled. At present, they are
generally considered to be either commensals or facultative parasites. According to Holt (1965b), they are primarily grazers, cropping the abundant supply of detritus and epizoic flora and fauna carried by their hosts; however, some branchiobdellids live in the gill chambers of their host, apparently feeding on the blood obtained by clipping gill filaments. One species, *Cambarincola aliena*, seems to feed on the egg of its host, a cave isopod (Holt, 1963a). On the other hand, there is evidence that there is an absolute dependency of the egg and the encapsulated larva on the crayfish host (Young, 1966). According to Bishop (1968) the branchiobdellids are host independent as adults, as shown serologically, but parasitic during their developmental stages.

Host specificity is traditionally uncertain (Bishop, 1968; Ellis, 1919; Evans, 1939; and Goodnight, 1940b). The first significant contribution to host specificity was made by Goodnight (1940b) who, after reviewing the works of Ellis (1919) and Evans (1939) concluded that within the limits of the range of any branchiobdellid, any crayfish may serve as host. McManus (1960) found it surprising that the branchiobdellids should have the broad ecological ranges attributed to them, since Hobbs (1942) and Hobbs, et al. (1967) have shown that crayfish have restricted ecological tolerances within their range.
McManus' findings do not support the concept of host specificity, one species being confined to or being more prevalent on a single host species, even though two species of *Orconectes* appeared to be unsuitable hosts, while two species of *Cambarus* were about equally infested with the same species of branchiobdellids. The findings of Hobbs, et al., (1967) for the Mountain Lake, Virginia region agreed with Goodnight's conclusions (1940b). According to Hobbs, et al., (1967) there are instances of branchiobdellids known from only one host, but these are cases where the worm is known from only one or a few collections. They conclude from their study of over a hundred collections from a rather restricted area that "... the association from which it might appear that there is a 'preference' by a branchiobdellid species for one or another host species are surely to be interpreted as the consequence of the ecological relationships of the hosts and worms or as the product of the migration (distributional) patterns of the two." According to Holt, (1968) "...There is no strict host specificity among the branchiobdellids. Some species (e.g., *Cambarincola aliena*) may be confined to a single host because of specialized adaptations (feeding on isopod eggs in this case), but most species are limited in their occurrences within a geographical range by ecological factors that often appear to
be different from those influencing their host."

Most of the investigations on the branchiobdellids have been taxonomic. 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, Muller (1806) and Savigny (1809), mention them also, but not until 1823 was the first taxonomic description given. In that year Odier published in the Memoires de la Societe d'Historie Naturelle de Paris a very fine description of a common branchiobdellid of western Europe which he called Branchiobdella astaci. He believed it was a leech, closely related to the genus Hirudo.

No important work was published on the group for the next twenty years. In 1835 G. Henle reported an anatomical study in an article entitled "Über 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 a description of an American species which he called Astacobdella philadelphica. 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, 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*. This is the best general anatomical account yet published and the only one on an American species. Moore gave an excellent account of the nephridial system of *Bdellodrilus illuminatus* in 1897.

Schmidt pointed out in his papers (1902 and 1903) that the musculature of the branchiobdellids was more definitely similar to the Oligochaeta than to the Hirudinea.
Two years later (1905) Pierantoni gave 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 tetradora* from California and *B. digitata* from Japan. In the same year Smallwood gave an account of some observations on the life habits of some branchiobdellids in the neighborhood of Clear Lake, New York.

In 1912, Pierantoni published the first monograph on this group. He summarized the anatomy of branchiobdellids and showed that they are definitely oligochaetes. In this monograph, 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 tetradora* Pier., *B. americana* n. sp., *Bdellordilus pulcherrimus* Moore, *B. instabilus* Moore, *B. illuminatus* Moore, *B. philadelphica* (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 described a new species from Utah which he called *Ceratodrilus thysanosomus*. 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, 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 species; *Xironodrilus formosus*, *Xironogiton occidentalis*, *Xironogiton oregonensis*, *Pterodrilus mexicanus*, *Pterodrilus durbini*, *Cambarincola vitrea*, *Cambarincola chirocephala*, and *Cambarincola inversa*. In 1928, Alessandra gave an account of a new European species, *Branchiobdella italicca*.

Stephenson published a monograph on the Oligochaeta in 1930, in which he gave a lengthy discussion of the Branchiobdellidae, including as valid genera: *Branchiobdella*, *Cirrodrilus*, *Stephanodrilus*, *Bdellodrilus*, *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. In 1939, he reported four species: Cambarincola macrodonta, C. vitrea, C. chirocephala, and Bdellodrilus illuminatus.

In 1940, Goodnight published a monograph on the American branchiobdellids. He summarized all of the work done on this group, described several new species and included a taxonomic key. Subsequent to the appearance of his monograph, Goodnight published three additional short papers in which he described three new species of Cambarincola: Cambarincola floridana in 1941 from Florida, Cambarincola meyeri in 1942 from Kentucky, and Cambarincola macrocephala in 1943 from Idaho.

In 1947, the study of branchiobdellids was taken up by Perry C. Holt (Hoffman, 1963). In his master's thesis, published in 1949, Holt covered the comparative morphology of two species (Xironogiton instabilius and Cambarincola philadelphica) with respect to the male reproductive systems. Later, in his doctoral dissertation (1951), he covered the genera Xironodrilus and Pterodrilus in North America, with notes on other North American genera of the family Branchiobdellidae. In 1960, he published two papers (1960a and 1960b) on the taxonomy
and morphology of the genera 

Ceratodrilus and 

Ellisodrilus.


Holt and Berry, 1959, published a paper on the reactions of 

Xironodrilus formosus and Xironogiton instabilius to high temperature and low oxygen tension. Hoffman, one of Holt's students, revised the genus 

Cambarincola in 1963.

In recent years, several ecological studies have appeared. McManus (1960) worked on the distribution and host specificity of branchiobdellids. Young (1966) published a paper dealing with the nature of the association between the branchiobdellids and their host as well as certain aspects of their population dynamics. Blackford, (1968) studied certain aspects of the ecology and morphology of branchiobdellids found on the blue crab, 

Callinectes sapidius, which had been collected from fresh water in the New Orleans, La. area. This expanded the number of possible hosts for branchiobdellids to include a marine crab living in fresh water. Hobbs, et al., 1967, published a paper on the crayfishes and their epizootic ostracod and branchiobdellid associates of the Mountain Lake, Virginia region. For each species of these organisms, the taxonomic diagnosis, the range, and the distribution were presented. In 1968, Bishop performed an ecological study of the branchiobdellid commensals of some mid-western
Ontario crayfish. He investigated the population structure and attempted to elucidate the host-branchiobdellid relationship. He concluded that the branchiobdellids are host independent as adults, but host dependent in the immature stage.

Franzen, 1962, published notes on the histology of *Xironogiton instabilius* with special reference to its muscle cells. He pointed out that the musculature of *Xironogiton instabilius* consisted entirely of muscle cells of hirudinean type, and therefore he questioned their being classified as oligochaetes. Holt (1965b), in a paper on the systematic position of the Branchiobdellidae, reviewed the structure, distribution, and habits of the branchiobdellids, and added additional reasons to his previously expressed belief (Holt, 1963b) that this family should be elevated to ordinal rank.
THE BRANCHIOBDELLIDS IN THIS STUDY

Cambarincola philadelphica (Leidy, 1851)

SYNONYMS.-

Astacobdella philadelphica Leidy, 1851, Proc. Acad.
Nat. Sci. Philadelphia, 1851, p. 209.-Verrill,
688 (name only).

Branchiobdella philadelphica Moore, 1893, Proc.

Bdellodrilus philadelphicus Moore, 1895, Journ.

Cambarincola philadelphica Ellis, 1912, Proc. U. S.
S. Nat. Mus., vol. 48, p. 190.-Ellis, 1918, Trans.
American Microsc. Soc., vol. 37, p. 49; 1919,
1939, Journ. Parasitology, vol. 25, supp., p. 11
(abstract); 1940, Rep. Reelfoot Lake Biol.
Station, vol. 4, p. 171 (New York records); 1940,
Illinois Biol. Monogr., vol. 17, no. 3, p. 38
(records for N.C., Pa., W. Va., probably this


TYPE SPECIMENS.- Present whereabouts unknown.

DIAGNOSIS.- Hoffman (1963) stated:

"Peristomium divided into dorsal and ventral lobes, the dorsal larger and with four low marginal lobations; jaws relatively large and subrectangular in lateral aspect, the dorsal jaw usually a little larger than the ventral [and the dental formula 5/4 to 3/2]; male reproductive system moderate in size, filling from half to two-thirds of the coelom of one side of segment VI; bursa elongate, at least twice as long as broad, the penial sheath merging gradually into a fairly short ejaculatory duct; spermiducal gland slender and recurved ventrad, twice the diameter of prostrate, latter long and slender, reaching to ental end of spermiducal gland" (Figure 1).

DESCRIPTION.-Ellis (1919) stated:

"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. 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 Tilhance 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 - than the regular 5-4 type, showing that some variation does occur.

Hoffman (1963) described *Cambarincola philadelphica* from "typical" northeastern specimens as follows:

Body moderate to large in size, maximum length 5.0 mm. Proportions about normal for the genus, but anterior part of body less attenuated than in most species; segments IV to VIII of about equal diameter; prosomites about three times length of metasomites and of greater diameter, at least on anteriormost segments; caudal sucker small, its diameter less than that of segment I.

Head fairly large, as long as first three body segments, and its diameter equal to that of segment II; largest basally, narrowing slightly to base of peristomium which is set off by a distinct constriction and divided into two subequal halves. Dorsal half somewhat larger and longer than the ventral, and provided along its margin with four low rounded lobes (not visible in poorly preserved specimens, either macerated or shrunken), the ventral half with a median incision dividing it into two broad lobes. Peristomium not or but very slightly flared, generally continuing the head profile in lateral aspect.

Jaws massive, anisomorphic, heterodont, the dental formula 5-4 or 3-4, sometimes 3-2 in old specimens; dorsal jaw slightly larger than ventral, both, in lateral aspect, almost as high as long and thus subrectangular in appearance. Median tooth of dorsal jaw and paramedians of ventral larger than the lateral cusps but not to the extent seen in such species as *C. fallax, C. chirocephala,* and
Male reproductive system variable in size, usually occupying from one-half to two-thirds of the coelom of one side of the segment. Bursa typically elongate, at least twice as long as wide, most of the length being contributed by the atrium; penial sheath of normal size and proportions and confined to the ental third of the bursa. Ejaculatory duct broadest ectally, merging gradually into penial sheath; entally it becomes narrower and is rather short in total length. Spermiducal gland long and slender, curving cephalad and then abruptly ventrad, extending down as far as level of penial sheath, frequently with a small fairly distinct posterior deferent lobe visible near the ental end. Prostate long and slender, half the diameter of the spermiducal gland or less, but extending ventrad to the level of the ental end of the latter, with a small but distinct terminal bulb.

Spermatheca without specific peculiarities, consisting of the slender, elongate ectal duct extending about one-third the way up one side, a fusiform ental bulb, and a distinct, fairly large glandular ental process.

**DISTRIBUTION.**- Northeastern United States, from Wisconsin, south through the Appalachian system as far as South Carolina and Tennessee (Hoffman, 1963).

The host and branchiobdellid "associates" of *Cambarincola philadelphica* in the Mountain Lake, Virginia region was studied by Hobbs, et al. (1967). They found *Cambarincola philadelphica* on the following crayfish;

1. *Cambarus accumnatus*, 2. *Cambarus bartonii*, 3. *Cambarus carolinus*, 4. *Cambarus l. longulus* and *Cambarus sciotensis*. In other localities *Cambarincola philadelphica* was associated with *Astacus bartonii*, *Cambarus blandingii*,
C. diogenes, C. dubius, C. imminis, C. longiminus, C. neglectus, C. obscuris, C. propinquus, C. rusticus and C. virilis (See Table 1).

**Xironodrilus formosus** (Ellis, 1919)

**SYNONYMS.**


**TYPE SPECIMEN.**- Cat. No. 17626, U. S. Nat. Mus., body length 2.7 mm. White River, Irondale, near Anderson, Indiana, August, 1915. (M. M. Ellis) on *Cambarus rusticus* Girard (det. Faxon).

**PARATYPES.**- Ten, Cat. No. 17627, U. S. Nat. Mus., and 10 others, collected with the type (Ellis, 1919).

**DIAGNOSIS.**- Hobbs, et al., (1967) stated:

Dental formula 4/3 to 6/5, teeth sub-equal in size with lateral teeth somewhat shorter than median ones; spermathecal duct distinct, bulb of spermatheca globose or cylindrical; spermiducal gland simple U-shaped tube, less than twice diameter of vasa deferentia; ejaculatory duct absent (Figure 2).

**DESCRIPTION.**- Ellis (1919) described *Xironodrilus formosus* as follows:
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; upper jaw usually type V, lower jaw type V or type VI; 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).

DISTRIBUTION.—*Xironodrilus formosus* is common in the glaciated areas of Ohio, Indiana, and Michigan; however, the range appears to be discontinuous. It occurs in a number of streams that flow into the Ohio River in Kentucky; Rolling Fork, Licking, Kentucky and Cumberland (Holt, 1969). In Tennessee it is known from the Duck and Caney Fork Rivers and small tributaries of the Cumberland; in Virginia, other than the New River, in the Powell and the upper reaches of the Roanoke and James Rivers (Holt, 1969).

In every locality in the Mountain Lake, Virginia
region that this worm occurred it was associated with the riffle-inhabiting *Cambarus* l. *longulus*, and may be ecologically restricted to much the same habitat (Hobbs, et al., 1967). According to previous locality records, *Xironodrilus formosus* was associated with *Cambarus bartonii, C. immunis, C. longidigitus, C. luteus, C. neglectus, C. propinquus, C. punctimonus, C. rusticus, C. setosus,* and *C. virilus* (See Table 2).
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The branchiobdellids used in this study were *Cambarincola philadelphica* (Leidy, 1851) and *Xironodrilus formosus* (Ellis, 1819). Approximately 900 worms were used in this study. One hundred sixty whole mount slides were made with a total of 640 specimens. Serial sections (sagittal, frontal, and transverse) of 40 worms (21 *Cambarincola* and 19 *Xironodrilus*) were made by the usual paraffin method; however, paraplast was used as the imbedding mass instead of paraffin. In addition, several hundred live worms were observed. In all, several thousand specimens were collected.

*Cambarincola philadelphica* was collected throughout the year, approximately once a month, for a period of two years. Even when the surface of the water was frozen, host crayfish were collected and their branchiobdellid "parasites" were removed. As expected, the number of worms per crayfish was considerably reduced during the winter months. Collections were taken from the Scioto River on the outskirts of Upper Arlington, Ohio in Griggs Dam Park. Most of the worms used were taken just below Griggs Dam on the Scioto River. The water at this location was shallow, clear, and slow
moving. The bottom was almost completely covered with rocks and boulders, between and under which the crayfish were found. The host crayfish in this vicinity was *Cambarus rusticus*. The branchiobdellids were found on the carapace, rostrum, chelipeds, pereiopod, uropod, telson, and around the eyes of the crayfish.

*Xironodrilus formosus* was collected at approximately three month intervals for about 18 months. Collections were taken from Big Darby Creek on the outskirts of West Jefferson, Ohio. These branchiobdellids were found also on the crayfish, *Cambarus rusticus*, but only in certain parts of the creek where there were swift riffles. They were attached to the chelipeds and the inside of the branchial chamber of the crayfish.

The crayfish were collected with a minnow seine, with a hand net, and with the hand. Upon collection, some of the crayfish (with branchiobdellids) were fixed in either A.F.A. fixing fluid (Lavdowsky's formula); 5% formalin; Bouin's Picro-formol; 85% ethyl alcohol; or Zenkers fixing reagent. Fixation was accomplished by placing one or two crayfish in a small jar that was half filled with the fixing reagent. Immediately after the crayfish were submerged, the branchiobdellids released their hold on the host, and fell to the bottom of the jar. The branchiobdellids were then removed from the jar and
preserved in 85% ethyl alcohol. This treatment caused the specimen to shrink somewhat and curl, but it proved satisfactory for gross anatomy and taxonomy. (This is the method that has been used by most investigators who have worked with branchiobdellids.)

Crayfish and their branchiobdellid parasites that were not fixed in the field were brought to the laboratory and fixed at a later date. They were maintained in the laboratory in 1 1/2 gallon aquaria. The bottom of the aquarium was partly covered with small rocks and stones, arranged so that the crayfish could crawl under and between them. These aquaria were tilted so that the height of the water (river water) in them ranged from about one inch at one end to approximately five inches at the other end. The river water was gradually replaced by tap water over a period of about a week. The crayfish and branchiobdellids were maintained in the laboratory for periods up to 6 months (with weekly changes of water and food).

Just prior to fixation of the worms that were being maintained on crayfish in the laboratory, the hosts were immersed in finger bowls containing cold water, 5-8 degrees centigrade. At this temperature, the branchiobdellids fell from the crayfish and attached to the bottom and sides of the finger bowl. This may have been caused
by the abrupt change in temperature from ambient room
temperature (23°C.) to 5°C. Branchiobdellids died within
30 minutes when left in water at 5°C.

The crayfish were removed from the finger bowl and
returned to the aquarium (This treatment had no apparent
effect on the crayfish). The cold water in the finger
bowl was replaced by a fixing reagent, either Bouin's
picro-formal, A.F.A., or Zenkers. With this method of
fixation, most of the branchiobdellids were almost
straight when they died, the "curling" or muscular con­
traction of the body wall being greatly reduced. The
worms that were to be sectioned were placed on a slide
(individually) in a drop of water and covered with a
cover glass. The water was drawn off on one side of the
cover glass with small pieces of filter paper while the
fixing reagent was gradually added to the opposite side
with a medicine dropper. When the worms appeared to be
completely relaxed, they were removed from the slide and
placed into a vial, containing the fixing reagent to
complete the fixation. After fixation, the worms were
preserved in 85% ethyl alcohol.

The whole mounts were stained with the following
stains: (1) Semichons; (2) Harris' hematoxylin and
eosin; (3) Borax-carmine; and (4) a solution of 4 drops
of Ehrlich's acid hematoxylin in 20 cc. of a saturated
aqueous solution of potassium alum (Goodnight, 1940b). Some specimens were mounted without staining. Specimens were cleared in either xylene, clove oil, phenol, or glycerin. Those cleared in xylene were mounted in balsam. The specimens cleared in glycerin, clove oil or phenol were examined, but were not prepared as permanent mounts.

For the serial sections, the branchiobdellids were imbedded in paraplast, and sectioned at 4 to 10 microns. Such sections were stained in either Borax-carmine, Delafield's hematoxylin and eosin, Harris' hematoxylin and eosin, Heidenhain's hematoxylin and eosin, or Mallory's triple stain. They were cleared in xylene and mounted in Canada balsam.

The slides were examined with a phase contrast binocular microscope. Most of the detailed histological study was done with the oil immersion objective, a total magnification of 1000 diameters.

Most of the drawings were made with the aid of a microprojector and a camera lucida; however, some of them, figures 6, 20-26, were drawn free hand.

For the study of the feeding mechanism, 10 branchiobdellids of the species *Cambarincola philadelphica* were removed from crayfish and placed in finger bowls. They were observed for an extended length of time with a binocular dissecting microscope. One or two specimens
were placed in a depression slide (with water) and viewed with the phase contrast microscope. Those fed on material in the water taken from the river and also on material from the exoskeleton of the crayfish.

Ten worms were starved for one, two, and three days, and then fed crayfish blood, crayfish branchial filaments and surrounding tissues, and pieces of crayfish appendages. Also, many branchiobdellids were observed from time to time on crayfish, maintained in the laboratory throughout the study.

For all measurements, the size range is listed first, followed by the mean measurement, which is placed in parenthesis. The mean measurements are based upon 4 to 6 measurements.
Cambarincola philadelphica

The size of the worms in this study was 2.4 - 2.9 mm. (2.7) in length and 0.2 - 0.5 mm. (0.4) in width, the latter measurements taken across segment 5. These measurements are based on extended specimens.

The alimentary canal of Cambarincola philadelphica extends from the anterior end of the head, the peristomial annulus, to the posterior part of segment nine (Fig. 3). (The conventional system of designating the first trunk segment as number one is used in this investigation.) The canal runs through the center of the body, slightly dorsal in some of the segments. It is distinguishable into five regions; oral, pharyngeal, esophageal, intestinal, and anal.

The mouth extends from the anterior end of the head to the two sclerotized jaws. It is surrounded by two very mobile lips, (one dorsal and one ventral) which are formed by the division of the peristomial annulus. The dorsal lip, being slightly longer than the ventral one, makes the mouth appear slightly subterminal. Labial
papillae are present on the inner margins of the lips. Fig. 8. The papillae vary from 11 to 13 in number in different individual specimens. They are best seen in whole mounts of specimens cleared in phenol. They measure 33 - 38 microns (36) in length and 13 - 15 (14) in width (Fig. 8). The oral cavity, posterior to the papillae, measures 44 - 48 microns (46) in length and 46 - 48 microns (48) in width. It is lined with a layer of cuticle that is continuous with the cuticle on the external surface of the lips.

The pharyngeal region, which begins with the sclerotized jaws, extends posteriorly to the anterior part of the first trunk segment. It measures 336 - 345 microns (346) in length and, at the widest point, 337 - 362 microns (353) in width. Like the oral cavity, pharyngeal lumen is lined with a delicate cuticle which gradually thins out and disappears where the transition from pharyngeal to esophageal region takes place. The wall of the pharynx is highly muscularized with numerous glands occurring between the muscle fibers (Fig. 5). When the longitudinal muscles contract, shortening the pharynx, two "diverticula" (one dorsal and one ventral) may be seen when viewed laterally; four lateral "diverticula" (two on each side) may be observed when viewed dorsally. These "diverticula" seem much smaller when
the head is extended. At the anterior end of the pharyngeal region, the two jaws (one ventral and one dorsal) appear to be solid sclerotized plates (Figs. 1 & 5). The dorsal jaw, slightly larger than the ventral one, has fine denticles or teeth (one large one in the center and two smaller ones on each side) (Fig. 1). The ventral jaw usually has four denticles (two large and two small). (Occasionally there are five denticles on the ventral jaw.) The denticles are located on the posterior edge of the jaws and extend posteriorly (Fig. 5). The combined size of the dorsal jaw and teeth is 25 - 28 microns (26) in length and 36 - 38 microns (38) in width; the ventral one is 22 - 25 microns (23) long and 32 - 35 microns (33) wide.

The esophageal region extends from the posterior end of the pharyngeal region to approximately the end of segment one (Fig. 3). It is distinguished from the pharynx, anteriorly, by the lack of cuticle on its inner surface and by the great reduction of the muscle tissue in its wall. The posterior boundary of the esophagus is not sharply defined, but may be distinguished from the intestine in that the outer wall of the esophagus is not covered with chlorogogue cells, and also in that its diameter is smaller than that of the intestine. The esophagus has a length of 61 - 63 microns (62) and a
diameter of 43 - 46 microns (44).

The intestinal region extends from the posterior end of segment one to the posterior end of segment nine (Fig. 3). It measures 670 - 692 microns (683) in length. The diameter of the intestine varies along its length. There is a gradual increase in its diameter from segment one to segment four (Fig. 3). (This corresponds to the gradual increase in the size of the worm in this area of the body.) From the posterior end of segment four to approximately the posterior end of segment seven, the diameter of the intestine is roughly one-half the diameter of the intestine in the anterior part of segment four. It enlarges slightly in segment eight, and gradually decreases again in segment nine, forming the rectum (Fig. 3). The peritoneum of the intestine is modified into chlorogogue cells, which characterize this region. These cells form a continuous layer from the anterior end of the intestine to the posterior end of segment six. They disappear in segment seven and reappear in segments eight and nine.

The anus is located at the posterior end of segment nine, opening to the outside on the middorsal surface. The anal opening appears as a transverse slit in extended live specimens. It is surrounded by two delicate, slightly lobulated lips.
Xironodrilus formosus

The specimens used in this study ranged from 1.7 mm. to 2.2 mm. in length (1.9 mm.) and when measured in segment five they ranged from 0.5 mm. to 0.6 mm. in width (0.5 mm.). The alimentary canal of this species extends from the anterior end of the peristomial annulus to the anterior half of segment ten. The length of the canal is 0.9 - 2.1 mm. (1.7). As in Cambarincola philadelphica, the canal runs through the mesial longitudinal axis, slightly dorsal in some of the segments. It, also, is distinguishable into oral, pharyngeal, esophageal, intestinal, and anal regions.

The morphology of the oral region is basically the same as that of Cambarincola philadelphica except for a few minor details; the labial papillae are fewer in number and smaller than those of C. philadelphica, measuring 27 - 30 microns (29) in length and 9 - 11 microns (10) in width. The oral cavity is 71 - 75 microns (74) in length and 99 - 104 microns (102) in width.

The general location and morphology of the pharyngeal region is very similar to that of Cambarincola philadelphica. The pharyngeal lumen is 309 - 318 microns (314) in length and 370 - 391 microns (385) in width. There are
nine to ten pharyngeal "diverticula"; two dorsal, one to two ventral, and six lateral (Fig. 4). The dorsal and ventral "diverticula" are located in the posterior part of the pharynx. Two of the lateral "diverticula" are located in the anterior half of the pharynx and four are in the posterior half. When the head is extended the "diverticula" are not very prominent since they are stretched, which reduces their depth.

The dental formula is expressed by two numbers, in which the first number represents the number of teeth on the dorsal jaw and the second number represents the number of teeth on the ventral jaw. The dental formula was 5-4 for most of the animals; however, (five 5-5 and one 6-5 were also observed). The size of the dorsal jaw is 35 - 38 microns (36) in length and 31 - 32 microns (29) in width.

The esophageal region is essentially the same as that of *Cambarincola philadelphica*. It has a length of 84 - 87 microns (85) and a width of 55 - 64 microns (61).

The intestinal region extends from the posterior end of segment one to the anterior end of segment ten. The length is 0.9 - 1.4 mm. (1.1). Like *Cambarincola philadelphica*, the diameter of the intestine gradually increases from segment one to segment four, but in *Xironodrilus formosus* it is more strongly sacculated. The
intestine is narrowed in segments five and six, slightly expanded in segment seven. It is gradually narrowed from segment seven to the anterior part of segment ten. The distribution of chlorogogue cells is about the same as that of *Cambarincola philadelphica*.

The anal opening is dorsal, between segments nine and ten. The morphology of the anal region is basically the same as that of *Cambarincola philadelphica*. 
A BRIEF SUMMARY OF THE MORPHOLOGY AND THE VASCULAR SYSTEM OF BRANCHIOBDELLIDS

Because of the close relationship of the vascular system to the digestive system, the topography of the vascular system of branchiobdellids will be summarized before describing the histology of the alimentary canal. This summary is based upon work by Moore on *Bdellodrilus illuminatus* and also on the two species, *Cambarincola philadelphica* and *Xironodrilus formosus*, described in the present study.

The vascular system of the Branchiobdellidae is known to consist of a dorsal vessel; a ventral vessel; six lateral vascular commisures, five in the anterior end of the worms and one in the posterior end; and the peri-enteric sinus (Fig. 12).

The peri-enteric blood sinus is highly developed in the branchiobdellids. It exists as a continuous space between the muscular and epithelial coats of the intestine, extending from the third to the eighth segment and forming at each end a system of passages and lacunae which have a retiform arrangement (Moore, 1895). Enlarged chambers exist here and there in the course of the sinus, and continuous enlargements extend along the
dorsal and ventral regions. According to Moore, the ventral or subintestinal enlargement remains throughout its entire length as strictly a part of the sinus, but the dorsal enlargement, which has a similar relationship posteriorly, begins to have the structure of a vessel in the fifth segment. The dorsal enlargement has more or less complete walls and rises above the level of the sinus, from which it may be entirely free for a short distance, but again opens into the sinus through a cleft. Perforating the septum between segments four and five, the dorsal enlargement becomes a distinct muscular tube, still imbedded amongst the chlorogogue cells. After increasing in diameter, the dorsal enlargement passes obliquely down the right side of the intestine with which it loses connection in the third segment (Moore, 1895). Here, it becomes a regularly pulsating tube, the "heart", which is thrown into a conspicuous loop. The heart lies to the right side of the esophagus, and in the first segment rises to a dorsal position, giving off the fifth pair of vascular arches. Afterwards, it continues anteriorly into the head as the dorsal trunk. From the dorsal trunk three delicate lateral trunks arise. They wind among the muscles of the pharynx and join the subneural vessel ventrally. After passing beneath the supra-esophageal ganglion, the dorsal vessel
terminates anteriorly bifurcating into a pair of trunks which arch through the lips and meet ventrally where they form the supra-neural blood vessel. Throughout its entire length the supra-neural blood vessel lies in contact with the dorsal side of the ventral nerve cord. In the seventh segment it gives off a pair of large ovarian vascular arches, which empty into the dorsal enlargement of the peri-enteric sinus (Fig. 12). The supra-neural vessel terminates in the tenth segment in a pair of large trunks, which arch around the intestine and pass forward, emptying into the dorsal region of the peri-enteric sinus, thus forming the beginning of the dorsal enlargement of the peri-enteric blood sinus.
THE HISTOLOGY OF THE ALIMENTARY CANAL

Cambarincola philadelphica

Histologically, the alimentary canal of Cambarincola philadelphica is divided into five regions; the oral, pharyngeal, esophageal, intestinal and anal.

The wall of the canal consists, typically, of three layers: an outer peritoneal layer; a muscular coat of longitudinal and circular fibers; and an inner epithelium (endothelium) with either ciliated or non-ciliated cells.

Oral Region - In sagittal section the oral cavity is surrounded dorsally and ventrally by the lips and laterally by the labial papillae (Fig. 8). The external and internal surfaces of the lips and the external surface of the papillae are lined with a delicate cuticle. In live or unstained specimens, the cuticle is colorless, transparent, and appears to be homogeneous. With Mallory's triple stain preparations, the cuticle stains blue and appears to be a clear, hyalin substance. The cuticle of the oral cavity is about the same thickness (0.94 microns) as the cuticle of the epidermis. Many granules are seen on the cuticle, in the oral cavity and just outside the lips (Fig. 5).
These granules, undoubtedly are mucous granules since they stain blue with Mallory's triple stain and red with mucicarmine. Beneath the cuticle is a layer of low columnar epithelium which lies upon a very thin basement membrane. The epithelium is interspersed by numerous glands. The musculature has an irregular arrangement and will be considered later in association with the dorsal and ventral lips.

As seen in sagittal section, the dorsal lip is slightly longer and thicker than the ventral lip (Fig. 5). Externally, the epithelium of the dorsal lip is composed of low columnar cells with large centrally located nuclei. The cell membranes of these cells are somewhat indistinct. Between some of these cells, the ductules of unicellular glands open to the exterior. These glands are located just beneath the epithelial cells. These gland cells are round or oval with large round nuclei and dark staining nucleoli. Beneath the anterior surface of the dorsal lip similar glands are found. Most of these are composed of four cells which can be seen in sagittal section (Fig. 5). Also, beneath the anterior surface of the dorsal lip, one may observe a large conspicuous gland which stains redish orange with Mallory's triple stain (Fig. 5). This gland is approximately 6 cell layers deep, an estimate obtained
by counting the number of nuclei from the surface to the base of the gland. (The cell boundaries are indistinct). The cytoplasm and nucleoplasm stains redish orange with Mallory's triple stain. In both parts of the cell, numerous dark staining granules are found. The base of this gland appears to be attached to a muscle fiber, which extends diagonally from the base of the gland to the dorsal and posterior part of the dorsal lip (Fig. 5).

When viewed in sagittal section, the inner surface of the dorsal lip appears to be thrown into folds (Fig. 5). The epithelium of this area appears to be almost cuboidal, with a few unicellular glands. Just anterior to the jaws, there is a group of multicellular glands similar to the ones on the external surface. These are probably salivary glands. In Bdellodrilus illuminatus these glands are more highly developed than in the worms of the present investigation.

The central part of the dorsal lip contains the bases or bodies of the glands, together with a few muscle fibers that originate at the jaw pads. These fibers, originating dorsally, extend diagonally across the lip to its anterior surface. There are also a few circular muscles near the basal membrane of the epidermis (Fig. 5).

The histology of the ventral lip is very similar to that described above for the dorsal lip. The outer
epidermis is made up of low columnar cells. Beneath these cells is a very thin basement membrane. Below the basement membrane, a few circular muscle fibers, and both unicellular and multicellular glands are found in the center of the ventral lip. Near the base of the lip, radial muscle fibers extend anteriorly from the base of the jaw pad (Fig. 5). The anterior epithelium of the ventral lip has a few redish orange glands similar to the one described above on the dorsal lip. The inner surface of the ventral lip is thrown into folds also. Just inward from the redish orange glands, the epithelium of the anterior part of the internal surface of the lip is very thin, measuring approximately two microns, appearing to consist of a thin layer of simple squamous epithelium; however, its cellular structure is obscure. On the posterior part of the inner surface of the ventral lip the cells appear to be cuboidal epithelium, or very low columnar, measuring approximately 5 microns in thickness. A group of glands open into the oral cavity just anterior to the jaws. These glands are located ventral and opposite to the glands of the dorsal lip. The glands of both dorsal and ventral lips appear to have the same structure (Fig. 5).

In sagittal section, labial papillae are seen between the two lips (Fig. 8). Superficially, these papillae
look very much like the cirri found in *Amphioxus*. The surface of the papillae is lined with a cuticle of the same relatively thickness as the dorsal and ventral lips. Beneath the cuticle, the labial papillae are made up of closely packed round to oval cells with granular cytoplasm, clear round nuclei, each of which contains a nucleolus which stains red with Mallory's triple stain. Some of the cells of the papillae have large clear vacuoles. Posterior to the labial papillae, 5-6 bands of muscle fibers extend dorso ventrally. These muscle bands are the circular muscles of the jaw pad (Fig. 8).

A transverse section (Fig. 9) in the oral region shows the following layers, in the order of their occurance from the lining of the oral cavity to the outer epidermis: (1) the cuticle with mucous granules dispersed unevenly; (2) the epithelium which has a width of from 12 to 9 microns in the mid-dorsal and mid-ventral parts respectively. It tapers progressively to a width of 4 - 5 microns (4) laterally; (3) a very thin, transparent basement membrane; (4) one to two layers of circular muscle; (5) a few radiating muscle fibers extending outward from the circular muscles and epithelium to the epidermal cells. These fibers have large granular nuclei, located near their attachment to the circular muscles; (6) a thin peritoneum which surrounds the circular
muscles; (7) both unicellular and multicellular glands (mentioned above) which are seen in the body cavity. The outer body wall is composed of an outer circular and a longitudinal muscle layer, epithelium and glandular tissue, and an outer cuticle.

**Pharyngeal Region** - The histology of the pharyngeal region is similar throughout, with the exception of the region of the jaws and the region of transition into the esophagus posteriorly. These two regions will be considered separately.

In sagittal section the pharyngeal region is found to be thrown into many tiny folds and two pairs of "diverticula" (Fig. 5). It is lined with a cuticle of the same relative thickness as that found in the oral cavity. The epithelium beneath the cuticle has a complicated and obscured structure. It ranges from 3 to 4 microns in thickness. The cell boundaries are seldom clearly distinguishable. The protoplasm of most of the cells stains orange with Mallory’s triple stain. There are a few cells that remain clear, having a highly granular protoplasm. Large radially arranged muscle fibers are attached to certain epithelial cells, which have developed numerous supporting fibrils or tonofibrillae (Figs. 5 and 6). (Moore, 1895, made similar observations in *Bdellodrilus illuminatus*.) Each muscle fiber is
attached to an epithelial cell provided with fibrils. Such epithelial cells alternate with epithelial cells lacking these supporting elements. The supporting fibrils spread radially at the periphery of the epithelial cells, thus running somewhat parallel to the cuticular surface (Fig. 6). The number of fibrils in each epithelial cell is large, being estimated by Franzen (1963) to approximate 50 per cell in Xironogiton instabilia. The nuclei of these cells that have supporting fibrils are hard to see while the nuclei of the alternating epithelial cells are large and round.

Just inside the epithelial cells that do not have fibrils, and thus alternating with the radial muscles fibers, is a layer of circular muscle. The cells of the circular muscle layer have a regular arrangement (Figs. 5 and 6). In sagittal section they appear round, each with a round nucleus and a bright red nucleolus when stained with Mallory's triple stain. The diameter of these fibers is 4 - 5 microns. Outward, from the layer of circular muscle, several multicellular glands are found between the radial muscles (Fig. 6).

At their outer ends, the radial muscle fibers often separate into two branches. These branches are interwoven into the longitudinal muscle layer of the body wall and attached to the epidermis (Figs. 5 and 6).
radial muscles have a corticle layer of radially arranged myofibrils, within which is a medullary portion of granular, undifferentiated cytoplasm. The nucleus is situated more or less in the center of the granular cytoplasm. It is oval in shape with a large nucleolus which stains red with Mallory's triple stain (Fig. 6).

At the anterior end of the pharyngeal region, dorsal and ventral evaginations of the epithelium and cuticle are found. On the inner walls of these evaginated pockets, the jaws (described earlier) are molded. The jaws are bounded dorsally and ventrally by thick muscular pads, the jaw pads (Fig. 5). In sagittal section the pads appear roughly oval in shape. Both jaw pads consist of several oval shaped muscle cells closely stacked upon each other. These are circular muscles which apparently bring the jaws together when contracted (Fig. 5). Other muscles around this circular mass act as retractor and protractors of the two jaws. The protractor muscles consist of dorso-ventral fibers derived from the anterior face of the muscular jaw pads. They insert on the cuticle of the evaginations (Fig. 5). The retractor muscles are very large fibers which originate posterior to the jaw on the longitudinal muscle layer of the body wall. They pass obliquely forward and insert,
in the case of the dorsal jaw, directly on the posterior part of the jaw plate. In the case of the ventral jaw, they insert immediately behind the jaw, into the epithelium and cuticle (Fig. 5).

A transverse section cut across the jaw pads shows that the muscular apparatus is composed of two (a dorsal and a ventral) half discs, each consisting of about four semi-circular muscular fibers piled upon one another. The two half discs meet laterally (Fig. 10). The radial muscles in this part of the pharynx have a regular arrangement. In a transverse section of the pharynx, they resemble the spokes of a wagon wheel. The epithelium is thickened in the mid-dorsal and mid-ventral areas, beneath the jaws and teeth.

In the posterior part of the pharynx certain gradual changes in the histology become apparent (Fig. 5). The cuticle lining this part of the alimentary canal becomes thinner and gradually disappears in the anterior part of the first cephalic segment (segment 1). On the other hand, the epithelial layer increases in thickness and the cells have nuclei that stain bright red with Mallory's triple stain. The circular muscle fibers gradually increase in diameter from 5 microns in the anterior half of the pharynx to 15 microns in this posterior region, then gradually decrease in diameter. The number of radial
muscles gradually decrease also in this region.

**Esophageal Region** - In sagittal section, the epithelial lining of the esophagus appears to be thrown into longitudinal folds which tend to narrow the diameter of the lumen (Fig. 5). There is no cuticular lining. The epithelium here is taller than that found in the mouth and the pharynx. The cells in this region have a granular cytoplasm and oval nuclei located near the base of the cells.

The cell boundaries are ill defined. Some cells have round, and often have bulbous, extensions which project into the lumen (Fig. 5). Beneath the epithelium, a thin sheet of circular muscle is found which is surrounded by longitudinal muscle.

In cross section, the esophagus is roughly oval in shape, the widest diameter being later (Fig. 11). The cavity or lumen of the esophagus is comparatively small. The epithelium is thrown into folds, especially laterally. A few rings of circular muscle fibers, seen just outside the epithelium, blend in with each successive muscular septum, where they derive additional fibers from the septum. The circular muscles are surrounded by a longitudinal muscle layer. These muscles are enclosed within a thin sheath of peritoneum measuring approximately one micron in thickness. This sheath is separated
from the muscles in the mid-ventral and mid-dorsal regions. In the dorsal wall of the esophagus, a few circular muscle fibers line the peritoneum (inside). These constitute the "heart" (Fig. 11).

**Intestinal Region** - In a sagittal section near the midline of the worm, the histology of the intestine in segments two, three and four is basically the same (Fig. 5). (In the present paper, the intestine in segments two, three and four will be referred to as the anterior intestine; in segments five, six and seven, the mid-intestine; and in segments eight and nine, the posterior intestine.) The epithelium of the anterior intestine is columnar, being one to two cell layers thick. The cells bordering the lumen of the intestine project inward, especially near some of the septa where they form valve-like papillae. Two types of epithelial cells are apparent; those staining light blue and those staining red with Mallory's triple stain. The cells with blue granular cytoplasm are more numerous (Figs. 5 and 15). A few of the blue-staining cells also contain small yellow globules. All of the blue-staining cells have round to oval shaped nuclei which contain a few granules and one bright orange or red nucleolus. These cells are variously shaped; most of them are rectangular with the nucleus near the basement membrane; however, some are
oval, and a few are round. Scattered among these epithelial cells, are red stained cells that are roughly goblet-shaped (Figs. 5 and 15). The detailed structure of these cells is unclear. When the nucleus is visible, it has the same general appearance as that of the cells described above; however, in these cells the cytoplasm stains red instead of blue. The red staining substance evidently is a secretion since it appears in the intestinal lumen directly opposite goblet-shaped cells that have emptied their contents.

The end of the epithelial cells that lies farthest from the lumen lies against a thin basement membrane.

Between the basement membrane and the muscular layer, a small continuous cavity is seen in segments three and four. This cavity is the peri-enteric blood sinus (Fig. 5). It has an average width of 2 microns. It has no apparent walls of its own; but appears to be surrounded by the basement membrane on one side, and the longitudinal muscle layer, on the other (Fig. 5). The basement membrane measures approximately 0.5 microns in width; the muscular layer measures approximately 0.9 microns in width. These two limiting membranes of the sinus are thrown into folds, giving the sinus a "zig zag" appearance (Fig. 15). Several thin fibrils extend across the sinus in the anterior part of segment three.
The muscle of the gut wall appears to be predominantly longitudinal in sagittal sections. The circular muscle layer appears to be absent except at or near the septa. Here several large circular fibers are seen. They appear to be continuous with the septal musculature (Fig. 13).

Surrounding these muscle layers, and enveloping the intestine is a layer of chlorogogue cells. This chlorogogue tissue is a modification of the peritoneum. At the septa it is replaced by the large circular muscle fibers described above. The size of the chlorogogue cells varies along the length of the intestine. These cells also have different shapes, most being oval to rectangular. They are either flattened or bulging, depending upon the degree of contraction of the intestinal musculature. The cytoplasm of the chlorogogue cells is highly granular. Small clear globules or vacuoles are present in some of these cells. The nuclei are oval in shape and are located near the outer border of the cells (Fig. 5). The nucleus contains a slightly granular nucleoplasm and a large bright red nucleolus when stained with Mallory's triple stain. Certain cells which have the same characters as the chlorogogue cells are seen free in the coelom, occurring in groups of two and three cells. Groups of such cells were observed also either
inside or on the outer surface of the nephridia.

In a transverse section through the anterior intestine, in segment four, the following structures are seen (Fig. 15). The lumen is partially filled with mucous granules. It is lined by large columnar epithelial cells with large oval nuclei located near the thin basement membrane. Between the basement membrane and the muscular layer, the blood sinus is continuous, all around the intestine. It has mid-dorsal and mid-ventral enlargements. The muscles which form the outer wall of the sinus appear to consist of both circular and longitudinal fibers.

In segments five, six and seven, the diameter of the intestine is reduced, forming the mid-intestine. The reproductive organs occupy most of these segments. The epithelium, for the most part, looks like that described above for the anterior intestine. However, the height of the cells gradually decreases as the posterior end of segment seven is approached. In this region, the number of red staining goblet shaped cells is reduced; however, there are numerous masses of red secretory granules in the lumen of the intestine opposite goblet cells that appear to be emptied of their contents. The remains of diatoms and small animals are also to be seen in the lumen, surrounded by secretory
granules which stain blue with Mallory's triple stain.

In segments six and seven, the lumen of the intestine is almost filled with mucous. Here, also, many cells of the inner epithelium, with large clear vacuoles, have apparently emptied their content.

The musculature of the mid-intestine does not differ from that described above for the anterior intestine.

The chlorogogue tissue in segments five and six has an irregular arrangement (Fig. 14). Generally, the size and the number of cells decreases gradually as the posterior end of segment six is approached. There are small areas where the cells are absent and small areas where they are very large. In segment seven, the chlorogogue tissue is replaced by a flat or thin layer of cells, the peritoneum (Fig. 14). The ovum (in some specimens two ova) lies next to the intestinal wall. The ovum appears to lie next to the muscular wall of the blood sinus (Fig. 17). In some specimens, an ovum is seen to almost completely surround the intestine. In segments eight and nine the chlorogogue tissue reappears (Fig. 14).

In a section across the posterior part of segment seven the inner epithelial lining appears to be ciliated. Here, the blood sinus is continuous all around the intestine, with dorsal and ventral enlargements. The
muscular layer is thin. There are no chlorogogue cells in this segment. An ovum partially surrounds the sinus, in contact with its wall in certain places. A peritoneum is not apparent (Fig. 17).

In a transverse section across segment eight, the lumen appears practically devoid of mucous. In this region, the cells are ciliated columnar epithelium. The blood sinus all around the intestine has little outpockets. These outpockets become larger as the posterior end is approached. At the posterior end of segment eight, or at the anterior end of segment nine, the sinus is separated into compartments by fibrils running across it (Fig. 16). In this region the chlorogogue cells are present.

In the region of the rectum and anus, in the posterior part of segment nine, the height of the epithelium gradually decreases to a thin squamous-like layer which is best observed in sagittal section. The posterior end of the rectum and the anus is lined with a thin cuticle. In this region the thickness of the circular muscle layer increases, forming a sphincter (Fig. 14).

In a transverse section through the region of the rectum, the lumen is comparatively small, being nearly obliterated by the folds of the epithelium (Fig. 18). A
continuous sheet of circular muscle surrounds the epithelium. There are two pairs of muscle bands lateral to the intestine, which extend dorso-ventrally. The chlorogogue tissue is absent. There is also a group of glands, situated dorso-laterally to the rectum, which have cells that appear somewhat similar to the chlorogogue cells, except they are larger and the nuclei are not so clearly defined. According to Moore, 1895, these are acetabular glands. (The branchiobdellids have a posterior sucker, which is an acetabulum.)
**Xironodrilus formosus**

The histology of the alimentary canal of *Xironodrilus formosus* is essentially the same as that of *Cambarincola philadelphica*. The five morphological regions also are similarly distinguishable histologically. The detailed structure of the wall of the alimentary canal appears generally either more highly developed or better differentiated than that of *Cambarincola philadelphica*.

**Oral Region** - In a sagittal view, one observes that the oral cavity is surrounded by two lips (dorsal and ventral) as in *Cambarincola philadelphica*. The internal and external surfaces of both lips are lined with a thin sheath of cuticle which is covered in many places with granules, apparently mucous. Mucous granules occur, also, in the oral cavity and outside the epidermis of the lips. Similar granules are found in the epithelial cells which are located immediately below the cuticle. The epithelium of the outer surface of the lip appears to be cuboidal, while the cells of the oral cavity appear to be squamous epithelium. The glands beneath the anterior surface of the lips are not so prominent as those of *Cambarincola philadelphica*. On the posterior lining of the oral cavity, there are four well developed multicellular glands, two ventral and two dorsal (Fig. 7).
The dorsal lip, like that of *Cambarincola philadelphica*, is thicker and longer than the ventral lip. The tissue of the dorsal lip of *Xironodrilus formosus* seems more developed and compacted than the ventral lip. Muscle fibers, radiating out from the region of the jaw pads, attach to the epithelium of the dorsal lip (Fig. 7). A few radial fibers also extend from the ventral jaw pad. There also are a few thin fibers extending from the ventral to the dorsal surface of the ventral lip.

The labial papillae, so well developed in *Cambarincola philadephica*, are not so prominent here in *Xironodrilus formosus*. In a sagittal section, lateral to the midline, one may observe that the lateral wall of the oral cavity is thrown into folds. Four evaginations are prominent on each side. The surface of the papillae is lined with a thin cuticle. The internal structure of these papillae, or evaginations, appears to be glandular; however, their structure is not very clear. The cells of this glandular tissue contain cytoplasm with fine granules and nuclei with prominent nucleoli. The cell boundaries are obscure. The circular muscles of the jaw pad are visible a short distance posterior to the labial papillae.

**Pharyngeal Region** - In a sagittal section, the pharyngeal walls appear to be rather straight, without
infoldings, except for two pairs of invaginations at the posterior end (Fig. 7). The cavity of the pharynx is lined with a thin sheath of cuticle which gradually becomes thinner as the posterior end is approached. The pharyngeal tissue is basically the same as that of *Cambarincola philadelphica*. The cell boundaries are more clearly distinguishable, especially those of the muscle tissue. The epithelio-muscular tissue described previously in *Cambarincola philadelphica* is also present here; however, the radial muscles branch at the ends which insert on the epithelium of the pharynx, giving an illusion of an increase in the number of muscles (Fig. 7). The circular muscle fibers, just outside the epithelium appear to be oval in shape in sagittal section. A thin layer of longitudinal muscle is present dorsally and ventrally just outside the circular muscle fibers. This layer originates at the junction of the head and segment one and seems to insert on the jaw pads.

The structure of the jaw and jaw pads are basically the same as that of *Cambarincola philadelphica*.

In the posterior part of the pharynx the cuticle becomes thinner, disappearing in the anterior third of segment one. The circular muscle fibers of the pharyngeal wall increase in size as the posterior end of the head is approached, then rapidly decreases in size at the
posterior end of the pharynx. The increase is greater on the dorsal side than on the ventral side. The radial muscles of the pharynx extend posteriorly as far as the junction of the head and first body segment (Fig. 7).

**Esophageal Region** - The histology of this region does not differ from that of *Cambarincola* in any important detail. The epithelial cells are a little taller than those of the pharynx. In sagittal section, the epithelium is thrown into deep folds. The epithelium is columnar, some of the cells having bulb-like extensions which project into the lumen. The cells have granular cytoplasm and round nuclei located near the basement membrane (Fig. 7). The muscular tissue is similar to *Cambarincola philadelphica*. The lumen of the esophagus in *Xironodrilus formosus* is comparably larger in diameter than that of *Cambarincola philadelphica*.

**Intestinal Region** - The histology of the intestinal region differs only slightly from that of *Cambarincola philadelphica* (Fig. 7). In most of the specimens examined, there has been an accumulation of mucous in the lumen. This is especially true for the intestine in segments four, five, and six where a lot of partially decomposed digested food is also present. In most parts of the intestine, the epithelium has a brush-like border on the free edge of the cell. This appears to be an accumulation of a secretory product (Fig. 13). This
product stains red with mucicarmine stain; therefore, it probably is mucous that has been secreted. These cells have round nuclei, located near the basement membrane. The goblet shaped cells, so conspicuous in *Cambarincola philadelphica*, are very sparse here. There are, however, many epithelial cells that are practically devoid of protoplasm. In segments six, seven, and eight, the endothelial cells are ciliated (Fig. 13). In segments eight and nine there is much infolding of the endothelial lining, almost obliterating the lumen of the intestine.

The muscular structure and arrangement of the intestine of *Xironodrilus formosus* is about the same as that of *Cambarincola philadelphica*.

The structure of the blood sinus does not differ in any important detail from *Cambarincola philadelphica*, except that it begins in the posterior part of segment two while the sinus in *C. philadelphica* begins in segment three.

The chlorogogue tissue begins in segment two. It is continuous to segment six, but is absent in segment seven, appearing again in segment eight as mentioned previously. The chlorogogue cells have many more clear globules or vacuoles than the cells in *C. philadelphica*. These cells look like adipose tissue. The chlorogogue cells in segment three also were in contact with the
nephridia, as they were in _Cambarincola philadelphica_. They are absent in the posterior part of segment nine, the rectal region.

In a cross section of the rectum, one may observe that the epithelium is thrown into deep folds which extend into the lumen. The circular muscle of the rectum is prominent around the epithelium. Two pairs of muscle bands are seen lateral to the rectum, extending from the dorsal to the ventral surface of the body (Fig. 19).

The epithelium of the anus is reduced in height and it also is lined by a thin cuticle. The circular muscles are prominent.

The most characteristic features of the several regions of the alimentary canals of both branchiobdellids are summarized in Table 3.
Table 3. The Characteristic Features of the Alimentary Canal of Cambarincola philadelphica and Xironodrilus formosus

+ Indicates feature is present. ++ Indicates the degree of development of muscles & No. of Glands

<table>
<thead>
<tr>
<th>Region of Alimentary Canal</th>
<th>Cuticle Present</th>
<th>Type of Epithelium</th>
<th>Ciliated Epithelium</th>
<th>Glands (Multicellular)</th>
<th>Intrinsic Muscle</th>
<th>Radial Muscle or Others</th>
<th>Peritoneum</th>
<th>Chlorogogue Tissue</th>
<th>Peri Enteric Sinus Present</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mouth</td>
<td>+</td>
<td>Squamous</td>
<td>-</td>
<td>++</td>
<td>+</td>
<td>Radial</td>
<td>+</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Pharynx</td>
<td>+</td>
<td>Columnar (Low)</td>
<td>-</td>
<td>++</td>
<td>++</td>
<td>Radial Protractor</td>
<td>+</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Esophagus</td>
<td>-</td>
<td>Columnar</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>-</td>
<td>+</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Anterior Intestine Seg 2,3,4</td>
<td>-</td>
<td>Columnar</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>Mid Intestine in Segment 5,6</td>
<td>-</td>
<td>Columnar</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>-</td>
<td>+</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>Intestine in Segment 7</td>
<td>-</td>
<td>Columnar</td>
<td>+</td>
<td>-</td>
<td>+</td>
<td>-</td>
<td>+</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>Posterior Intestine Seg. 8,9</td>
<td>-</td>
<td>Columnar</td>
<td>+</td>
<td>-</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Rectum</td>
<td>+</td>
<td>Low</td>
<td>-</td>
<td>++</td>
<td>-</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Anus</td>
<td>+</td>
<td>Squamous</td>
<td>-</td>
<td>+</td>
<td>++</td>
<td>-</td>
<td>?</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>
THE FOOD AND FEEDING MECHANISM

The Food

The study of the natural food of the branchiobdellids in this investigation is based upon the food content of the gut of stained and unstained whole mounts and sagittal sections. A variety of algae and protozoa were found. The diatoms were especially numerous. A few small crustacea occasionally were found also. Some of these organisms were partially digested.

In the gut of most branchiobdellids, small oval cells, larger rod shaped, and spindle shaped cells were found. Their size ranges, shapes, and structures matched that of blood cells taken from live crayfish. Twenty specimens of *Cambarincola philadelphica* were picked randomly from the collection of prepared whole mount slides, 12 of which were found to have crayfish blood cells in their intestine. Twenty specimens of *Xironodrilus formosus* also were randomly picked. Sixteen of those had crayfish blood cells in their alimentary canals.

Specimens of *Cambarincola philadelphica* were removed from their crayfish hosts, placed in tap water, and starved for one, two, and three days. They were fed
crayfish blood, crayfish appendages, and crayfish branchial tissue. When drops of crayfish blood were added to the water near the specimens, feeding activity was initiated. On the other hand, branchiobdellids responded negatively to branchial tissue by moving away from it, even when this tissue was placed next to the mouth. When the chelipeds were placed into the dish, the branchiobdellids moved toward these structures and attached to the exoskeleton. The branchiobdellids then fed on the exposed muscles at the broken joints. Sometimes they pulled violently on the muscle fibers, tearing off small pieces, and sometimes they appeared to merely suck the fibers but did not remove them. They also appeared to be feeding on material on the exoskeleton of the cheliped.

At the time the crayfish were collected, the branchiobdellids were found more often on the appendages, rostrum, or in the soft tissue around the eye. On several crayfish in the laboratory, branchiobdellids were seen in the soft tissue around the eye and they appeared to be exhibiting feeding movements similar to the feeding movements exhibited when they ate the exposed muscle cells. There is a possibility that the branchiobdellids are able to draw blood from the soft parts of the crayfish body, as around the eyes and
between the joints. When the tissue in the above areas was punctured with a small pin, crayfish blood immediately oozed out. Therefore, it is possible that branchiobdellids can obtain crayfish blood by puncturing the soft tissue with their teeth.

The Feeding Mechanism

There are a few morphological details of the mouth parts of the branchiobdellids of this study that are seen on live specimens but that are barely visible on fixed specimens. On live specimens of *Cambarincola philadelphica*, one can observe that the anterior edge of the dorsal lip is divided into four lobes. The anterior and lateral edges of the dorsal lip contain many short bristles. The anterior edge of the ventral lip is divided into two lobes. The labial papillae, which are visible only on the lateral surfaces of fixed specimens, are present all around the inner surfaces of the lips (Fig. 23).

The movements of the branchiobdellids vary. They move around from place to place in hirudinean fashion. When the posterior sucker is attached, a wave of circular contraction sweeps over the branchiobdellid, and the body is lengthened and extended forward. The anterior sucker then attaches (mostly with the ventral lip), and the posterior sucker releases. A wave of
longitudinal contractions occurs, shortening the animal and moving the posterior sucker forward. This is repeated. They also swim in leech-like fashion, with vertical undulations. The worms often attach by the posterior sucker and rotate the body in all directions. The above motions occur about half of the time if the worms are not disturbed. If they are disturbed, as in moving the dish or directing bright light toward the dish, these movements increase. They tend to move away from the light, indicating that they apparently are negatively phototactic. At such times the branchiobdellids do not appear to exhibit any feeding motions. At other times the worms remain almost motionless. They may attach by the posterior sucker to the bottom of a container or to a part of a crayfish exoskeleton. At such times, the body of the branchiobdellid is relaxed with its head in contact with the surface, upon which it is feeding. At this time feeding occurs.

The feeding motions are sequential, some movements are rapid while others are slow. They may be divided into the following steps:

1. the lateral sweeping movement of the head;
2. the extension of the lips;
3. the retraction of the lips;
4. the extension and closure of the lips;
5. the chewing motion; and
the swallowing motion.

All of these steps are not always present or apparent.

When the worm is feeding, its head is resting on the surface, usually ventral side down, but sometimes the lateral or dorsal side is in contact with the surface. It moves the head slowly from side to side over the surface of the crayfish. When the motion stops, the lips are extended. (The pharynx is extended only very slightly.) This extension is usually very brief, but the lips may remain extended for about 15 seconds. The lips are then slowly retracted. While retracting, the lips flare out and the mouth is wide open (Fig. 22). The teeth on both jaws are oriented dorso-ventrally (Fig. 23). (The teeth normally point posteriorly.) At this time the teeth are separated, the mouth remains retracted for a few seconds after which the lips are quickly extended and closed (Fig. 24). The dorsal jaw and teeth are protracted and retracted very quickly (Figs. 25a & b). In retracting, the teeth of the dorsal jaw, interdigitate with the teeth of the ventral jaw, in a shearing action. This is immediately followed by the movement of the material, mostly fluid, down the pharynx into the esophagus (Fig. 26). Because of the pulsation of the "heart" and peri-enteric sinus, the transport of the swallowed material cannot be followed
beyond the esophagus. The pulsation of the heart and peri-enteric sinus moves the blood in an anterior direction on the dorsal side of the alimentary canal. This gives the illusion of reverse peristalsis.

In the intervals between the feeding movements described above, there are violent contractions of the muscles of the body wall. In one specimen this occurred about every 10 seconds. There are also jerking movements of the head that initiate a wave of contraction along the body wall in a posterior direction. This occurs every 2 or 3 seconds.

The five steps in feeding described above were observed when the worms were either in river water (with microorganisms present); on portions of the exoskeleton of the crayfish; or in tap water, to which crayfish blood had been added. When the branchiobdellids came in contact with exposed muscle tissue or soft tissue at joints, the lips flared out and pieces of tissue were torn off with the teeth. In some instances, as mentioned before, the branchiobdellids appeared to suck only the muscle ends.
DISCUSSION

Oral Region

The anatomy of the oral region of the two branchiobdellids in this study is essentially the same. The anatomy differs also in only a few minor details as indicated in the observations that were made. The labial papillae are well developed in Cambarincola philadelphica, but poorly developed in Xironodrilus formosus. The development of the labial papillae has varied also in previous studies on other species. In Bdellodrilus illuminatus, the labial papillae are absent, with only a few faint ridges indicating a slight tendency toward their development, while in Branchiobdella, labial papillae are highly developed (Moore, 1895). How the labial papillae function in the branchiobdellids is not known. The writer's opinion is that they may either help in the transport of food material into the mouth, as do the labial palps of some molluscs, or perhaps they help prevent back flow of material in the mouth when the lips are extended just before swallowing. On the other hand, they seem to have a glandular structure; therefore, they may be involved in secretion, either associated with the
adhesion of the sucker or with the movement of food down the pharynx.

The numerous unicellular and multicellular glands found in the epidermis of the lips of the two species were also found in *Bdellodrilus illuminatus* (Moore, 1895). How these two types of head glands function has not been determined; but the behavior of the animals suggest that the glands may secrete a sticky fluid which probably either helps the lips function as adhesive organs or in attaching their cocoons or both. According to Moore, 1895, the multicellular glands just anterior to the ventral and dorsal jaw function as salivary glands. In the specimens of the present study, these glands are not as well developed as they are in *Bdellodrilus illuminatus*. In *Bdellodrilus illuminatus* the salivary gland fills up the basal portion of the upper lip, but differs in appearance from any of the glands described in this study. In *Bdellodrilus illuminatus*, it is developed from a tubular invagination of the oral epithelium, just in front of the upper jaw. In the adult, it consists of a single stratum of coarsely granular pyramidal cells, opening into a short tubular duct.

The lining of the buccal cavity of the branchiobdellids is basically similar to that of other oligochaetes. The epithelium, mostly columnar, is lined with a thin
cuticle. There are no cilia in the oral cavity. The epithelium of the buccal cavity of the earthworm is composed of cylindrical cells without cilia and with a heavy cuticle (Gurwitsch, 1901). However, a dorsal diverticulum of the cavity is lined by ciliated epithelial cells.

The buccal cavity which apparently aids in the taking in of food, is protrusible in many earthworms and in other annelids (Andrews, 1959). The branchiobdellids in this study also protract their lips in feeding. The lips take an active part in locomotion and in feeding. The circular muscle fibers continue unchanged from the pharynx to the anterior surface of the lips. The longitudinal muscles partly continue, but they break up into delicate dorso-ventral and radiating fibers, which constitute the chief musculature of the lips.

In the gnathobdellids, which lack a proboscis, the gross anatomy of the oral region is very similar to that of the branchiobdellids of this investigation. The mouth of these leeches is also located in an anterior sucker and is flanked by upper and lower lips. Just within the oral cavity of these leeches there are three large oval blade-like jaws, each bearing a large number of small teeth. The three jaws are arranged in a triangle, one dorsal and two lateral. The branchiobdellids also have jaws and teeth, but they are located in
the anterior part of the pharynx instead of the mouth and they only have two jaws with teeth. The presence of the anterior and posterior suckers, jaws, and dorsal anal opening suggest that the branchiobdellids are closely related to the leeches or that the two groups probably had a common origin. According to Stephenson (1930) the family Branchiobdellidae is an offshoot from the family Lumbriculidae and the Hirudinea is an offshoot from the Branchiobdellidae.

Pharyngeal Region

The morphology and histology of the pharynx of the branchiobdellids in this study are essentially the same. The musculature of *Xironodrilus formosus* seemed more highly developed than *Cambarincola philadelphica*, but probably this only appears to be the case because the heads are shaped differently. The head of *Xironodrilus formosus* is dorso-ventrally flatten while that of *Cambarincola philadelphica* is cylindrical. The anatomy of the pharynx of *Bdellodrilus illuminatus* (Moore, 1895) and *Xironogiton instabilia* (Franzen, 1962) is also very similar to the worms in this study. In the four worms mentioned above, the pharynx is distinguished by the great development of muscular tissue, and doubtless functions in the capacity of a suction bulb.
According to Moore, 1895, this suction bulb increases the flow of blood from the wounded tissue of the host. The structure of the pharynx is similar throughout except at its anterior and posterior ends as indicated in the observations.

The pharynx, including the diverticula, is lined throughout with a thin cuticle. The epithelial cells are columnar and non-ciliated. The epithelium in the pharynx of the Lumbricidae consists of columnar cells, also, but in the pharynx proper, patches of these cells bear cilia while other patches of them are covered with cuticle. In the dorsal diverticulum of the earthworm, the cells are uniformly provided with cilia which have conspicuous deeply staining basal granules (Andrews, 1959). As was shown by that author, a peculiar feature of the cells of the dorsal diverticulum of the earthworm's pharynx is the presence within them of long fibrillar structures, apparently of a supporting nature. Certain epithelial cells in the pharynx of the branchiobdellids also have developed numerous supporting fibrils which are attached to the "proximal" ends of the large radial muscles of the pharynx (Fig. 6). The pharynx functions as a suction bulb, as mentioned previously, and the epithelium on its inner surface is subjected to stretching when food is present. The supporting fibrils
give the epithelium a certain firmness. In the specimens of this study, there were some epithelial cells in the pharynx that did not contain supporting elements of this type. These cells alternated with those containing the fibrils. The cell boundaries of all of the epithelial cells were obscure. Franzen (1962) also found that the boundaries of the epithelial cells in the pharynx of *Xironogiton instabilius* were obscure. He concluded that this is a tendency toward a formation of a syncytium. This "tendency" seems to occur in most of the epithelial tissue in the present study.

The musculature of the pharynx of the branchiobdellids is very similar to that of other oligochaetes and Hirudinea. It includes both longitudinal and circular fibers as well as a rich supply of radial fibers, which extend from the epithelium of the pharynx to the body wall. The circular muscles constrict the pharynx while the radial muscles together with the longitudinal muscles obviously dilate the pharynx. In some leeches, and probably in some of the branchiobdellids, the pump-like activity of the pharynx is used in sucking blood from the host.

The histology of the muscles of the pharynx and other parts of the branchiobdellids in this study closely resembles the hirudinean musculature. The muscle cells
are cylindrical, having a completely closed cortical layer of myofibrils and a medullary portion of granular, undifferentiated cytoplasm. Moore's drawings (1895) of the muscle cells in the pharynx of *Bdellodrilus illuminatus* clearly show a close resemblance to the cells of the pharyngeal muscles of the two species in this study. Franzen, 1962, made similar observations in *Xironogiton instabiluis*. The presence of hirudinean muscle cells is another morphological character that probably separates the Branchiobdellidae and Hirudinea from their primitive progenitors within the Lumbriculidae. Franzen questions the branchiobdellids being classified as oligochaetes because of the histology of the muscle cell. Holt (1963b) suggests they be elevated to ordinal rank.

Several glandular masses are developed in the pharyngeal region of the head. These are irregularly shaped and occupy the spaces between the radial muscles, outside the circular muscles of the pharynx. How these glands function or what they secrete has not been thoroughly investigated, but this study shows that the cells of some of the glands have granules that stain red with mucicarmine. Therefore, a logical assumption is that one of the secretions of these glands is mucous. The pharyngeal glands of the Lumbricidae are also mainly mucous-producers, the mucous probably lubricating the
food. In Hirudo, unicellular glands of the pharynx secrete an anti-coagulant, huridin, into the blood which is drawn in as food.

**Esophageal Region**

The structure of the esophageal region of the two branchiobdellids in this study is essentially the same. The esophagus is a rather short portion of the alimentary canal located in the posterior part of the first trunk segment. The anatomy is similar throughout, not being modified at different levels as a stomach, a crop, or a gizzard. The crop and gizzard are commonly found in terrestrial oligochaetes (Barnes, 1967). The gizzard, which is used in grinding food particles is lined with a cuticle and is very muscular. This latter author states "...that the gizzard represents an adaptation to terrestrial feeding is indicated by the very great size reduction of the gizzard in those earthworms that have returned to an aquatic environment or at least to wet boggy soils". In the branchiobdellids, the jaw and teeth in the pharynx are somewhat analogous to the gizzard of the lumbricids in that both structures are associated with mechanical digestion. The teeth of *Cambarincola philadelphica* are used in cutting off pieces of crayfish muscle, breaking it into smaller pieces.
In the aquatic naïdids, the esophagus is dilated posteriorly, forming a stomach. However, the manner in which this type of "stomach" functions is not known. Histologically, it appears to be very similar to the intestine (Barnes, 1967). At the level of the stomach the chlorogogue cells begin to appear. The stomach of the naïdids is similar to the anterior part of the intestine of the branchiobdellids. In the branchiobdellids of this study, the esophagus and anterior intestine have essentially the same structure; however, the intestine has a larger lumen and also has chlorogogue cells.

In the aquatic oligochaetes, the esophagus is generally ciliated, but this is not so in earthworms (Dales, 1967) or in the branchiobdellids of this study. In the family Lumbricidae, there are specialized outpushings of the esophagus, known as calciferous glands, which often have a complicated detailed structure, and in which the epithelium is thrown into radially arranged lamellae. The general conclusions seem to be that these calciferous glands act as regulators in getting rid of excess calcium (Myot, 1857 and Robertson, 1935). The esophagus of the branchiobdellids is lined by an epithelium of non-ciliated columnar cells, most of which appear to be secreting mucous.
Intestinal Region

The intestine is the longest and widest portion of the alimentary canal in the branchiobdellids. As in the lumbricids, the intestine of branchiobdellids has a yellowish color, due to the chlorogogue cells which cover it. The intestine bulges segmentally and constricts intersegmentally. This sacculation is very marked in segments two, three, and four. The wall of the intestine consists of four layers as do other portions: the epithelium; the longitudinal muscle layer; the circular muscle layer; and the peritoneum, which is modified as the chlorogogue layer.

Epithelium - From segments two to the anterior part of segment seven, the epithelium appears to have almost the same structure in both species of the worms that were studied. Two types of cells are recognized; those staining light blue and those staining red with Mallory's triple stain. The opinion of the present writer is that the light blue cells are nonglandular absorptive cells while the red cells are secretory cells.

The blue staining cells have a fine granular cytoplasm. The granules do not appear to be mucous granules because of their small size. In some of these cells small yellow globules are found which may be some form of absorbed material. The oval nucleus and nucleolus are
clearly seen. The shape of these cells varies from rectangular to round or oval. Stephenson, 1930, describes the absorptive cells of the earthworm's intestine as follows:

The non-glandular or ciliated cells are yellow in color, slender, compressed between the glandular cells and hence, of somewhat variable shape; according to Willem and Minne they owe their yellow color to a number of extremely small granules.

Sneider, 1908, states that the epithelial cells which have an absorptive function in earthworms, bear cilia in all parts except the typhlosole. He describes the nuclei as oval, usually with a small nucleolus.

In the branchiobdellids those epithelial cells of the intestine which appear red when stained with Mallory's triple stain exhibit conspicuous evidences of secretion. Red granules, assumed to be secretory, are seen in the cytoplasm of these cells and also in the lumen of the intestine directly opposite "empty" spaces in the epithelium. The nucleus of these cells appears to be similar to that of the absorptive cells which stain blue. The nucleus can only be seen in cells which do not have many secretory granules.

In segments six and seven, the number of red staining cells is gradually reduced. Other cells, which stain blue, in this region secrete mucous which is mixed
with food in the lumen.

In segments seven and eight, the epithelium is ciliated. The cilia are rather long and undoubtedly aid in the transport of food in this region. These cells do not appear to be secretory, probably functioning chiefly in absorption.

The lining of the rectum is composed of nonciliated columnar epithelial cells. Most of the cells in this region appear to be active in the secretion of mucous which undoubtedly lubricates, helping the movement of the feces toward the anus. In the rectal region of the intestine, the height of the epithelium gradually decreases as the anus is approached. The epithelium of the anus and proctodeal part of the rectum is lined with a thin sheath of cuticle.

In the branchiobdellids of this study, as in other oligochaetes and polychaetes, the intestine is the principal site of digestion and absorption. The intestinal epithelium consists of secretory and absorptive cells. Undoubtedly, soluable food materials diffuse into blood sinuses that lie between the mucosal epithelium and the intestinal muscles.

Peri-enteric Sinus - The peri-enteric sinus, or alimentary plexus, is situated between the epithelium and the muscular layers of the intestinal wall of
branchiobdellids. Voigt (1888) described the walls of the gut sinus of *Branchiobdella varians*. According to him, a nucleated basement membrane, lying on the gut epithelium is bathed by blood. The inner-most layer of the outer wall of the sinus is likewise a nucleated connective tissue membrane. This connective tissue membrane did not appear to be present in the worms of this study. Voigt (1888) further states that the sinus is covered by a layer of chlorogogue cells, under which is found the coats of longitudinal and circular muscles. Livanow (1904) found that the circular muscles lie outside the longitudinal muscle layer with their cell bodies lying among the chlorogogue cells. "Under the circular muscle coat is the basement membrane of the peritoneum, and inside this membrane lie the longitudinal muscle fibers projecting into the sinus" (Livanow, 1904). Bilek, 1908, who examined *Branchiobdella parasita*, found that the layers of the gut wall are as follows: "...chlorogogen cells; a coat of circular muscles; longitudinal muscle fibers; a skeletal membrane, the blood sinus; another skeletal membrane; the gut epithelium."

According to Hanson, 1948, the wall of the dorsal vessel has the same layers as the sinus, and also possesses vasotheial cells. These vasotheial cells, however, do not lie on the skeletal membrane, but, according to Bilek,
are separated from the rest of the wall and are situated around the heart body. Bilek considered that the blood is situated between the coats of the wall, and that the true lumen of the vessel is a small space between the heart body and its covering of vasotheelial cells. Bilek considered the sinus to be intraendodermal, although he described a skeletal membrane lying in the gut epithelium. Moore (1895) states that the gut sinus is located between the epithelium and muscular layers of the intestine of Bdellodrilus illuminatus, and the present study shows that this is true also for Cambarincola philadelphica and Xironodrilus formosus except in segment seven. In segment seven, the ovary and developing ova practically fill the whole segment. The chlorogogue tissue is absent, and therefore, the ova come in very close contact with the blood sinus. In this segment, the muscle layers appear to be either greatly reduced or absent.

The musculature of the intestine consists of a layer of inner longitudinal and a layer of outer circular muscle fibers. In sagittal sections the musculature appears to be composed of only longitudinal fibers except at the septa where large circular muscle fibers are seen in association with the septa. In branchiobdellids, observed while living, the muscles of the intestine appear
to move blood anteriorly in the peri-enteric sinus, toward the heart, and the contraction of the body wall seems to transport the food posteriorly. When the worms are feeding there are twitch-like contractions of the body and also slow waves of contraction along the body wall in a posterior direction. According to Hanson, 1948, the contents of the alimentary canal in aquatic oligochaetes are not moved along by peristaltic contractions of its wall as they are in other animals, but the activity of the musculature actually tends to hinder their movements towards the anus. The gut epithelium of aquatic annelids is ciliated, and the cilia undoubtedly transport the food posteriorly while the muscles, in species with a sinus, aid in the transport of blood anteriorly. It is also possible that the contraction of the longitudinal and circular muscles of the body wall also help to transport the content of the alimentary canal toward the anus.

Chlorogogue Tissue - As stated previously, the chlorogogue cells are found on the outer surface of the intestine except in segment seven and in the rectal region of segment nine. Their distribution is relatively the same in the two organisms in this study.

According to Stephenson (1930), the modification of the peritoneum into chlorogogue tissue in oligochaetes
takes place (a) on the intestine, in regions where there is an absorptive vascular network in the gut-wall (in confirmation of this observation, chlorogogue cells are absent over the pharynx, esophagus and rectum of the branchiobdellids in this study); (b) on the dorsal vessel over an extent corresponding to that of the chlorogogue cells of the gut; (c) on the vessels that convey blood from the intestinal network to the dorsal vessel; and (d) often also on the initial portion of the vessels which are given off from the dorsal vessel. This modification of the peritoneum into chlorogogue cells was observed in the organisms of this study.

The most obvious character of the chlorogogue cell is the presence of yellowish globules. According to Stephenson, 1930, these globules are chlorogosomes, semi-liquid elastic globules. In the chlorogogue cells, the chlorogosomes are formed from the blood of the intestinal network and other vessels.

Exactly how the chlorogogue cells function is still not fully determined. According to Schneider, 1896, and Liebman, 1927, the chlorogogue cells function chiefly in the storage of fat and protein which they give off to the coelomic fluid, and hence, through the coelomocytes or wandering cells, to the tissues. Liebman, 1931, found that the chlorogogue cells contain
spheres and granules which consist of protein or of pro-
tein and fat. When a cell is "ripe", that is, when the
fat is abundant, the nucleus undergoes amitotic divisions
and the fat-containing portion of the cell constricts
off with one of the nuclei. He further contends that
such constricted portions are distributed through the
body fluid to other regions, probably serving as nourish-
ing elements. "The chlorogogue cells contribute their
fat for the egg yolk, for the cells of the clitellum and
for pigment" (Liebman, 1931). These coelomocytes were
observed in the branchiobdellids in this study. They
were frequently associated with the nephridia. According
to Moore, 1897, the chlorogogue cells give up a part of
their load of waste substances to the freely circulating
coelomic corpuscles, thus partly freeing the waste
matter which they hold. The products of disintegration
(the coelomic corpuscles) are continuously drawn into the
nephridial current, passing into the nephrostome, and
from time to time expelled from the nephridiopore.

A possible explanation for the absence of chlorogogue
cells in segment seven in the worms in the present study
is given by Bell, 1943. He showed that an increase in
the size of the developing egg in the earthworm occurs
at the time that the chlorogogue cells are denuded from
the wall of the gut. By observation of living worms, he
found that the egg is tightly attached, at this time, to the chlorogogue tissue. Microscopically, Bell found the chlorogogue cells embedded in the wall of the eggs, and it seemed certain to him that the cytoplasm and granules of the chlorogogue cells were elaborated into yolk material.

The Food and the Feeding Mechanism

The food of the branchiobdellids in this study consisted of algae, protozoa, very small multicellular aquatic animals, crayfish muscle tissue, and crayfish blood. All of these organisms and tissues were found in the alimentary canal of Cambarincola philadelphica and Xironodrilus formosus. In nature, the small organisms are usually found on the exoskeleton of the crayfish. In other words, the crayfish carry a supply of food, eaten by the branchiobdellids, on their exoskeletons. In the laboratory, the feeding activities of C. philadelphica were observed either on the crayfish or on a portion of its appendages. The chelipeds were more frequently used. When the chelipeds were placed in a dish near the branchiobdellids, the latter almost immediately attached to them and exhibited the feeding movements already described. This same reaction was observed with the branchiobdellids that were starved for
one, two, and three days, and also those that were not starved. The apparent withdrawal of food for a period of one to three days did not show any significant results or differences in the branchiobdellid's feeding behavior.

*Cambarincola philadelphica* is normally found on the appendages, on the rostrum, and in the sub-rostral region around the eye stalk. Around the eye stalk and at the joints of the appendages of the crayfish the exoskeleton is rather soft. The findings in the present research indicate that the branchiobdellids, of the species, *C. philadelphica*, actually puncture the soft tissues around the joints with their teeth and feed on the blood that oozes out. This is what they appear to be doing when they are near these soft areas of the host. Since the blood cells of the crayfish have been found in the gut of these branchiobdellids, and since they react negatively to branchial tissue of the host and positively to the soft tissue of the exoskeleton, it seems highly probable that these branchiobdellids feed on muscles and blood of the crayfish. Similar observations have been made by various investigators who have worked on other species of branchiobdellids. According to Stephenson, 1930,

"...the jaws of the adult branchiobdellids are used to
break the skin of the host in order to suck the blood."
Hall, 1915, found striated muscles in the intestine of adult branchiobdellids; Moore, 1895, found crayfish blood in the gut of *Bdellodrilus illuminatus*. However, many investigators feel that the branchiobdellids do not feed on crayfish blood or crayfish tissue, but merely feed on the flora and fauna carried by this "host". (Goodnight, 1940b; Smallwood, 1906, and Holt, 1965b). Before any conclusions concerning the food habits of the branchiobdellids can be reached, a more extensive study of the food habits of many different species is needed. Even then, the writer believes it will be found that in this group of animals, as in most other groups, divergent evolution has taken place, and the feeding habits or nutrition of these animals will vary.
SUMMARY

A comparative study was made of the morphology and histology of the alimentary canals of *Cambarincola philadelphica* and *Xironodrilus formosus*. The structure of the two canals appears to be essentially the same.

The walls of the alimentary canals of these two species consist typically of three layers: (1) an outer peritoneum, which becomes modified as chlorogogue tissue in the intestinal region; (2) a muscular coat of longitudinal and circular muscle layers; and (3) an inner epithelium (endothelium) composed of columnar cells resting upon a very delicate basement membrane.

The alimentary canals of both worms can be divided into five regions; oral, pharyngeal, esophageal, intestinal, and anal.

The Oral Region - The oral region is located in the peristomial annulus, between two very mobile lips, one dorsal and one ventral. The epithelium of the oral cavity, composed of low columnar cells and various glands, is lined by a thin cuticle.

The Pharyngeal Region - The pharyngeal region extends from the sclerotized jaws, located in the pharynx, to the anterior part of the first trunk segment. The wall of the
pharynx is highly muscular with numerous glands occurring between the muscle fibers. The epithelium of the pharynx is composed of low columnar cells, some of which are modified into epithelio-muscular tissue. The lumen is lined with a thin cuticle.

The Esophageal Region - The esophagus is located in the posterior part of the 1st trunk segment. It is characterized by tall columnar epithelium, the lack of cuticle, and by a great reduction of muscle tissue in its wall.

The Intestinal Region - The intestine extends from the posterior end of segment one to the posterior end of segment nine. It is characterized by a covering tissue of chlorogogue cells and also a peri-enteric blood sinus. The epithelium, which is columnar, is ciliated at the posterior end.

The Anal Region - The anus is located at the posterior end of segment nine. It opens to the outside on the mid-dorsal surface. The opening appears as a transverse slit, surrounded by two lobulated lips.

The topography of the vascular system of branchiobdellids is summarized since a part of this system, the peri-enteric sinus, is located in the wall of the intestine. Different interpretations of the structure of this sinus are presented.
The structure of the chlorogogue cells is presented. Possible explanations of how these cells function in food storage and excretion is discussed.

The food and the feeding mechanism are presented. The food of *Cambarincola philadelphica* and *Xironodrilus formosus*, as seen in the alimentary canal, consists of algae, protozoa, small multicellular animals, crayfish muscle and crayfish blood. Food ingestion in *Cambarincola philadelphica* has been described. The lips are the "food collecting" apparatus. The jaws and teeth are used in cutting off pieces of crayfish tissue in the soft areas of the exoskeleton, such as the regions around the eye and between joints.

Based only on the anatomy and histology of the different regions of the alimentary canal, clues as to their function are presented: the oral and pharyngeal regions are associated with food gathering and ingestion; the esophagus probably only with transport; the intestine functions in absorption and secretion; and the anal region in defecation.
LITERATURE CITED


Hanson, J. 1948. The transport of food through the alimentary canal of aquatic annelids. Quart. J. Micr. Soc. 89:47-51.


Salensky, W. 1885. Développement de Branchiobdella Arch. de Biol. tom. 6 fasc. 1:1.


______ 1908. Histologische praktikum der tiere, Jena.


EXPLANATION OF FIGURES

Figure

1. **Cambarincola philadelphica**, lateral views:
   a, entire animal; b, male reproductive system and spermatheca; c, dorso-lateral view of jaw; d, lateral view of jaws. (After Hoffman, 1963).

2. **Xironodrilus formosus**: a, dorsal view of entire animal; b, ventral view of male reproductive system; c, upper jaw; d, lower jaw. (After Hobbs, et al., 1967.)

Abbreviations

b - bursa
d - dentine
ed - ejaculatory duct
fu- funnel
pr - prostate
sg - spermiducal gland
sp - spermatheca
EXPLANATION OF FIGURES

Figure

3. Cambarincola philadelphica; dorsal outline showing alimentary canal. X10.

4. Xironodrilus formosus; dorsal view showing alimentary canal. X10.

Abbreviations

A - anus
AG - acetubular gland
A INT - anterior intestine
ES - esophagus
J - jaws
M - mouth
M INT - mid-intestine
O - ovum
OV - ovary
PH - pharynx
P INT - posterior intestine
R - rectum
T - testes
EXPLANATION OF FIGURES

Figure

5. Mid-sagittal section of mouth, pharynx, esophagus and anterior intestine of Cambarincola philadelphica. Bouin's, Mallory's triple stain X1000


7. Mid-sagittal section of mouth, pharynx, esophagus and a portion of the anterior intestine of Xironodrilus formosus. Bouin's, Harris' hematoxylin and eosin. X1000.

Abbreviations

BC - "blue" epithelial cell
CHL - chlorogogue cell
CM - circular muscle
CU - cuticle
DJ - dorsal jaw
EM - Epithelio-muscular tissue
ES - esophagus
INT - intestine
J - jaw
JP - jaw pad
LM - longitudinal muscle
M - mouth
MUG - mucous granule
NUC - nucleus
OG - oral gland
P - peritoneum
PH - pharynx
PHD - pharyngeal diverticular
PHG - pharyngeal gland
PIS - peri-enteric sinus
PM - protractor muscle
RC - "Red" epithelium cell
REM - Retractor muscle
RM - radial muscle
SEP - secretory product
SG - salivary gland
TF - tonofibrils
UG - unicellular gland
VL - ventral lip
EXPLANATION OF FIGURES

Figure

8. Sagittal section of the oral region showing the labial papillae, Cambarincola philadelphica. Bouin's, Mallory's triple stain. X200.


Abbreviations

CM - circular muscle   LM - longitudinal muscle
CU - cuticle           LP - labial papillae
DJ - dorsal jaw        M - mouth
DL - dorsal lip        P - peritoneum
EP - epithelium        PHG - pharyngeal gland
ES - esophagus         RM - radial muscle
H - "Heart"            VL - ventral lip
JP - jaw pad
EXPLANATION OF FIGURES

Figure

12. *Bdellodrilus illuminatus*, a diagram showing the vascular system. (Modified from Moore, 1895.)

Abbreviations

DT - dorsal trunk
H - "heart"
LVC - lateral vascular commisure
O - ovum
OV - ovary
PIS - peri-enteric sinus
SNV - supra-neural vessel
VNC - ventral nerve cord
EXPLANATION OF FIGURES

Figure

13. Sagittal section showing the mid-intestine, *Xironodrilus formosus*. Bouin's, Harris' hematoxylin and eosin. X1000.

14. Sagittal section showing the posterior intestine, rectum and anus of *Cambarincola philadelphica*. Zenkers, Mallory's triple stain. X1000.

15. Transverse section of anterior intestine of *Cambarincola philadelphica*. Bouin's, Mallory's triple stain. X1000.

16. Transverse section of posterior intestine of *Cambarincola philadelphica*. Bouin's, Heidenhuin's hematoxylin and eosin. X1000.

Abbreviations

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Description</th>
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<td>anus</td>
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<tr>
<td>BB</td>
<td>brush border</td>
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<tr>
<td>BC</td>
<td>&quot;blue&quot; epithelial cell</td>
</tr>
<tr>
<td>CHL</td>
<td>chlorogogue cell</td>
</tr>
<tr>
<td>CIL</td>
<td>cilia</td>
</tr>
<tr>
<td>CM</td>
<td>circular muscle</td>
</tr>
<tr>
<td>CU</td>
<td>cuticle</td>
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<td>DE</td>
<td>dorsal enlargement</td>
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<td>FI</td>
<td>fibril</td>
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<td>peritoneum</td>
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<td>PIS</td>
<td>peri-enteric sinus</td>
</tr>
<tr>
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<td>rectum</td>
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<td>sphincter</td>
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<td>VE</td>
<td>ventral enlargement</td>
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</table>
EXPLANATION OF FIGURES

Figure

17. Transverse section of intestine in segment seven showing ovum around the intestine, Cambarincola philadelphia. Lavdowsky's A.F.A. Harris' hematoxylin and eosin. X1000.

18. Transverse section of Cambarincola philadelphia through segment nine, showing rectum, posterior sucker and associated structures. Zenkers, Mallory's triple stain. X1000.

19. Transverse section of Xironodrilus formosus in segment nine, showing the rectum, posterior sucker and associated glands and muscles. Bouin's, Mallory's triple stain. X1000.

Abbreviations

AC(PS) - acetabulum
ACG - acetabular gland
CM - circular muscle
DVM - dorso-ventral muscle
EP - epithelium
LM - longitudinal muscle
MU - muscle

NUC - nucleus
0 - ovum
PS - posterior sucker
PIS - peri-enteric sinus
R - rectum
VBV - ventral blood vessel
VNC - ventral nerve cord
EXPLANATION OF FIGURES

Figure

20 - 26 illustrates the feeding movements of Cambarincola philadelphica. All figures were sketched in the dorsal view except Figure 23. X60.

20. Normal position of lips (Step 1).
21. Extension of lips (Step 2).
22. Retraction of lips (Step 3).
23. Retraction of lips, infacing view (Step 3).
24. Extension and closure of lips (Step 4).
25a. Protraction of dorsal jaw (Step 5).
25b. Retraction of dorsal jaw (Step 5).
26. Swallowing (Step 6).

Abbreviations

DJ - dorsal jaw
DL - dorsal lip
F - food
LP - labial papillae
M - mouth
PH - pharynx
VJ - ventral jaw
GEOGRAPHICAL DISTRIBUTION OF BRANCHIOBDELLIDS
IN NORTH AMERICA

The genera and species of branchiobdellids that have been described and their known geographical distributions are listed below. A map which shows the distribution of branchiobdellids in the United States, Canada, and Mexico is included at the end of the list (Fig. 27). The numbers on the map correspond to the numbers in the list.
<table>
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<th>Geographical Distribution</th>
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Virginia

16. *Cambarincola vitrea*  
Alabama  
Arkansas  
Colorado  
Florida  
Georgia  
Illinois  
Indiana  
Kansas  
Kentucky  
Louisiana  
Michigan  
Minnesota  
Mississippi  
Missouri  
New York  
North Dakota  
Oklahoma  
South Dakota  
Texas  
Wisconsin  
Wyoming  
Canada

17. *Cambarincola osceola*  
Florida  
Georgia  
North Carolina  
South Carolina  
Virginia

18. *Cambarincola ingens*  
North Carolina  
Tennessee  
Virginia  
West Virginia  
Wisconsin  
Canada

19. *Cambarincola philadelphica*  
Florida  
Illinois  
Indiana  
Kentucky  
Maryland  
Michigan  
Minnesota  
Missouri  
New York  
North Carolina  
North Dakota  
Ohio
20. *Cambarincola chirocephala*

- Florida
- Illinois
- Indiana
- Iowa
- Kansas
- Kentucky
- Missouri
- New York
- North Dakota
- Pennsylvania
- Tennessee
- Virginia
- Canada

21. *Cambarincola macrodonta*

- Arkansas
- Colorado
- Illinois
- Kentucky
- Louisiana
- Mississippi
- Missouri
- Nevada
- New Mexico
- South Dakota
- Texas
- Virginia

22. *Cambarincola meyeri*

- Kentucky

23. *Cambarincola fallax*

- Georgia
- New York
- North Carolina
- Tennessee
- Virginia
- West Virginia

24. *Cambarincola holostoma*

- Virginia

25. *Cambarincola heterognatha*

- Kentucky
- North Carolina
- Tennessee
- Virginia
- West Virginia
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<tr>
<td>50</td>
<td><em>Branchiobdella hexadonta</em></td>
<td>Europe</td>
</tr>
<tr>
<td>51</td>
<td><em>Cambarincola okadai</em></td>
<td>Japan</td>
</tr>
<tr>
<td>52</td>
<td><em>Cirrodrilus cirratus</em></td>
<td>Japan</td>
</tr>
<tr>
<td>53</td>
<td><em>Stephenodrilus sapporensis</em></td>
<td>Japan</td>
</tr>
<tr>
<td>54</td>
<td><em>Stephenodrilus japonicus</em></td>
<td>Japan</td>
</tr>
</tbody>
</table>
EXPLANATION OF FIGURES

Figure

27. The distribution of the branchiobdellids in North America and Mexico. The numbers on the map correspond to the numbers on the list on the preceding pages.