

**AN EMENDED DESCRIPTION OF CAMBARINCOLA
MACRODONTA ELLIS, WITH REMARKS ON THE
DIAGNOSTIC CHARACTERS OF THE GENUS
(Oligochaeta: Branchiobdellidae)¹**

PERRY C. HOLT AND RICHARD L. HOFFMANN
*Virginia Polytechnic Institute
Blacksburg, Virginia*

In most phases of systematic biology the definition of species and higher groups usually passes through several stages of progressive refinement, as the structural bases of diagnosis tend to be drawn from more precise anatomical studies, particularly of the reproductive systems, and less from external body form. The utility of diagnostic criteria are thus subject to periodic re-evaluation, and since we have undertaken a study of the genus *Cambarincola*, looking forward to monographic treatment of the genus, it becomes desirable that we revise and add to the description of the species upon which the genus is founded, *Cambarincola macrodonta* Ellis.

This is particularly so in view of the history of our knowledge of the species. The original diagnosis (Ellis, 1912) consists of a rather long discussion of the general body form, the jaws, and the digestive tract, ending with the statement that "... its general anatomy, with the exceptions already made in the description, is practically the same as that of *Bdellodrilus illuminatus* (Moore)." Ellis's written description contains no mention of the reproductive systems, although a drawing which shows marked differences between *C. macrodonta* and *B. illuminatus* is included, and is actually the most valuable part of the account. The type material of the species was collected from *Cambarus diogenes* Girard at Boulder, Colorado. Ellis subsequently (1919) assigned considerable numbers of specimens to this species, including some from Texas, Louisiana, and Mississippi. These worms, which we have re-examined, are not conspecific with the typical Colorado material.

Bayliff (1929) attempted to discuss the anatomy of a branchiobdellid species which he regarded as *C. macrodonta*. As there is no indication given of the provenance of his material and his work is replete with obvious inaccuracies, we will not consider it further. Goodnight (1940, 1943) referred material from Illinois, Virginia, Arkansas, Missouri, Nebraska, Michigan, and Kansas to *C. macrodonta* and quoted Ellis' description, commenting only that "The above quotation describes very accurately this species which has little variation despite its large geographic

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range" (1940). We have not yet been able to restudy Goodnight's material, but we can assume from the analogy of Ellis's own misidentification of other species as *C. macrodonta* that Goodnight's determinations can be regarded as probably incorrect. It is now known that body form and jaw shape alone are not sufficient to distinguish species in this family.

One of us (Holt, 1949) has described the reproductive systems of a cambarincolid worm and has more recently (1953) pointed out the significance of features of the reproductive systems as taxonomic characters. The present study adds a description of these organs and a set of measurements to Ellis's original description of *C. macrodonta*. We have studied fourteen animals from Boulder, Black Wolf Creek, and Fort Collins, Colorado and the holotype in the United States National Museum.² A fluorite oil immersion objective, 40 X, N.A. 100, corrected to a working distance of 1.5 mm, was used for this work, measurements being made with a calibrated ocular micrometer and drawings with a camera lucida attachment.

Cambarincola macrodonta Ellis

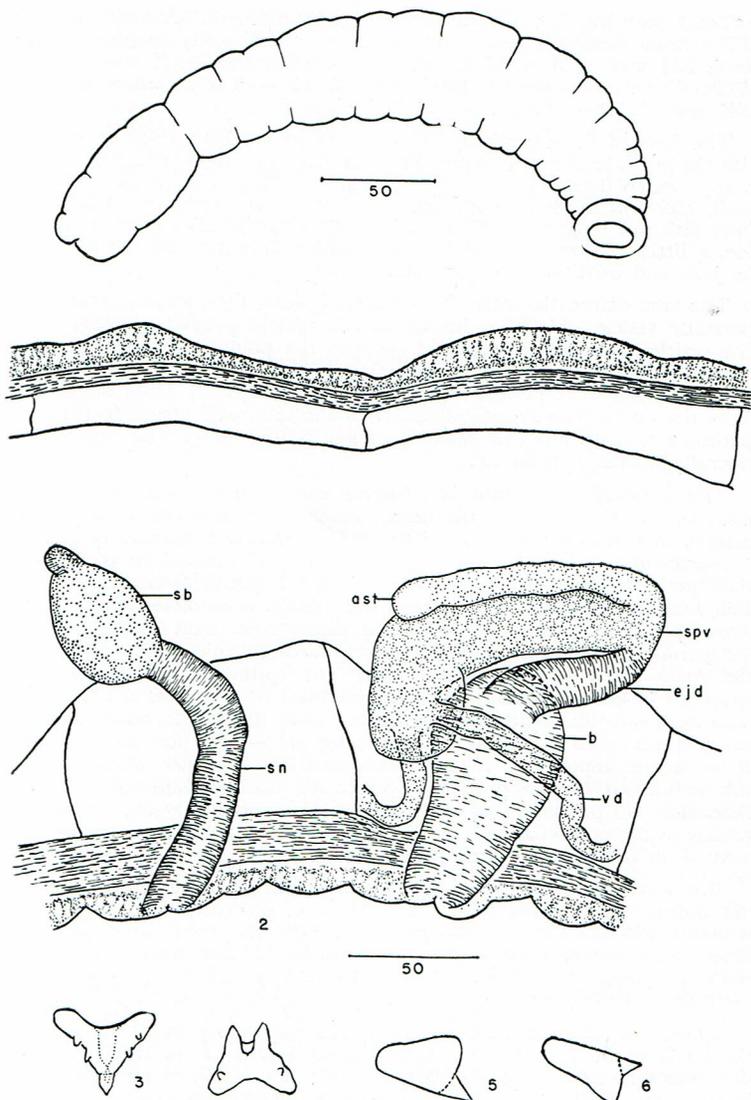
Figures 1-6

Cambarincola macrodonta Ellis, 1912, Proc. U. S. Nat. Mus., 42: 481, figs. 1-5; 1919, Proc. U. S. Nat. Mus., 55: 251 (Colorado records only). — Hall, 1914, Proc. U. S. Nat. Mus., 48: 190 (name only).—Goodnight, 1940, Ill. Biol. Monogr., 13 (3): 31 (description only, localities not applicable).
Type specimen. — U. S. Nat. Mus. No. 53794, from Boulder, Colorado, on *Cambarus diogenes* Girard.

Diagnosis. — Head elongate; lips entire; body slender, smooth in outline (fig. 1); upper jaw heavy, triangular, bearing five teeth, the median tooth much larger than the lateral ones (fig. 3); lower jaw bearing four teeth of which the median two are more prominent, subequal in size to upper jaw. Bursa pyriform, its length less than half the body diameter; spermatheca normally lying horizontally above bursa, its proximal, anterior end bent ventrad; accessory sperm tube slender, ending at or about the ventrad bending of the spermatheca, with a bulb-like proximal portion. Spermatheca with long spermathecal duct, bulb ovoid produced proximally into a short sac-like projection (fig. 2).

Description. — *Cambarincola macrodonta* is probably to be considered a medium sized member of the genus. The general appearance of the animal is that of a relatively slender worm with a smooth body outline, the head only slightly greater in diameter than the first body segment and slightly longer than usual for the family. The least body diameter is that of the sucker, the greatest occurs at segments V and VI, which are subequal. At present, body size and proportions cannot be used exclusively to characterize a species: there are not enough comparative data and no standardized way of making measurements has been established. Anticipating, however, the possibility of resolving these difficulties in the near future, we present the following body measurements of the fourteen specimens examined. The first dimension cited is the average for the series, the parenthetically enclosed figures are the extremes.

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EXPLANATION OF FIGURES

Legend. — *Ast*, accessory sperm tube; *b*, bursa; *ejd*, ejaculatory duct; *sb*, bulb of spermatheca; *sn*, spermathecal duct; *spv*, spermatic vesicle; *vd*, vas deferens.

Fig. 1. *Cambarincola macrodonta* in lateral view.

Fig. 2. Reproductive systems of *C. macrodonta* in lateral view.

Fig. 3. Upper jaw of *C. macrodonta* (after Ellis).

Fig. 4. Lower jaw of *C. macrodonta* (after Ellis).

Fig. 5. Upper jaw of *C. macrodonta* in lateral view.

Fig. 6. Lower jaw of *C. macrodonta* in lateral view.

Total body length, 3.33 mm (2.8 — 4.0); head length, 0.562 mm (0.493 — 0.636); head diameter, 0.400 mm (0.318 — 0.549); body length (without head), 2.77 mm (2.31 — 3.37); greatest body diameter, 0.573 mm (0.409 — 0.572); diameter segment I, 0.375 mm (0.334 — 0.517); sucker diameter, 0.345 mm (0.318 — 0.437).

The jaws of *C. macrodonta* are of the type we have come to associate with the genus in the strict sense. They are dark structures, relatively massive in appearance (figs. 3-6); the upper jaw bears a large median tooth and two small lateral denticles on each side; the lower jaw terminates in a median sinus with two large paramedian teeth and a single smaller denticle on each side, a little removed from the margin. Ellis's drawings and description of the jaws and dentition are adequate.

The vasa deferentia enter, from opposite sides, the proximal end of the spermatic vesicle which lies in the antero-ventral portion of segment VI. The vesicle is somewhat expanded between the points of entry of the vasa deferentia and runs dorsad to about the dorsal border of the bursa. At this point it is bent posteriorad and runs longitudinally alongside the gut above the bursa. The average diameter of the spermatic vesicle in the seven specimens measured is 71.7 microns (range 62.0 — 82.0). The organ has a generally slender appearance.

The accessory sperm tube is a blindly ending diverticulum of the spermatic vesicle. It arises from the distal end of the vesicle and its lumen discharges, in common with that of the vesicle, into the ejaculatory duct. In *C. macrodonta* it is a slender organ averaging 31 microns in diameter in nine specimens (range 25 — 37 microns); in all specimens studied it is less than half the diameter of the spermatic vesicle. A notable feature of the accessory sperm tube is its histological distinctness. Holt (1949) described the spermatic vesicle of *C. philadelphica* as having a thin muscle layer which also encloses the accessory sperm tube. The epithelium of the former is composed of tall columnar, basophilic glandular cells; that of the latter of a vacuolated cuboidal epithelium. Whether these differences reflect different secretory functions or not — they probably do — they are more certainly of taxonomic importance. No sectioned material of *C. macrodonta* is available to us, but the study of Ellis's unstained material indicates that these differences are present in *C. macrodonta*. More specifically the clear homogeneity of the epithelial cells of the accessory sperm tube is in marked contrast to the denser, more granular epithelium of the spermatic vesicle.

One final feature of the accessory sperm tube must be noted: the bulb-like nature of its closed proximal end. In *C. philadelphica* this bulb-like structure was described as composed of "a layer [enclosed in the peritoneal sheath and muscle coat] of thin, flat epithelial cells with dense, deeply staining cytoplasm" (Holt, 1949). Again, the unstained specimens of *C. macrodonta* correspond to similarly prepared specimens of *C. philadelphica*.

There is nothing remarkable about the ejaculatory duct, the penis, or the bursa of *C. macrodonta*. These structures differ from those previously described for *C. philadelphica* (Moore, 1895; Holt, 1949) in size and possibly in only statistically detectable differences in proportions, if at all. We present the following measurements of these organs, giving the number of specimens measured in parentheses, the average, and then the extremes, likewise in parentheses.

Ejaculatory duct diameter (5), 47 microns (41 — 51); bursa length (6), 209 microns (174 — 246); bursa diameter (8), 124 microns (103 — 154).

In unstained whole mounts there are no obvious features of any taxonomic significance associated with the ovaries in segment VII. The spermatheca in segment V, however, is quite distinct (fig. 2). Its uniqueness consists of the long spermathecal duct and a small sac-like projection of the proximal end of the bulb.

Holt (1949) failed to note that the spermatheca of *C. philadelphica*, and other members of the genus, may properly be described as composed of two parts, overlooking the distal duct or stalk, which is a more muscular and narrower outlet duct. In part this was owing to the relative shortness of the spermathecal duct in *C. philadelphica* and in part because of the fact that it insensibly widens into the spermathecal bulb in that species. In *C. macrodonta* the length of the spermathecal duct is much greater, as much as a third of the body diameter. The exact length cannot readily be measured, since the duct bends laterad from the median pore and then dorsad alongside the gut before entering the enlarged bulb of the spermatheca. The duct averages 54 microns in diameter in eight specimens (range 33 — 99). The bulb is an expanded flattened structure and difficult to measure. It averages 76 microns in eight specimens (range 51 — 139). The histology of the spermatheca appears to correspond to that previously described for *C. philadelphica* (Holt, 1949).

Other details of the reproductive systems are not readily studied in whole mounts and any distinguishing features that may be associated with the sperm funnels, efferent ducts, vasa deferentia, etc., if they exist, would not constitute feasible taxonomic characters. Our study of other aspects of the anatomy of *C. macrodonta* has been limited to confirming the presence of the median dorsal opening of the common nephridiopore on segment III.

In perhaps the majority of invertebrate groups, the form of the reproductive systems has become increasingly recognized as the most satisfactory basis for classification. That this condition should hold likewise in the Branchiobdellidae is therefore not as surprising as the failure in practice to group species on the basis of recognized similarities in reproductive systems. As a consequence, the utilization of body form, jaw shape, surface ornamentation and superficial segmentation has resulted in some remotely related forms being juxtaposed and close relatives thrown into different groups. The generic diagnosis which Ellis stipulated for *Cambarincola* was entirely sufficient to embrace the two species, *macrodonta* and *philadelphica*, which he originally referred to it, but it was not based upon a natural and delimiting assemblage of characters and the genus has become something of a dumping ground for all branchiobdellids lacking some remarkable external characters or other. With the increasing number of species that are being recognized in our work, it seems important that some limitations be imposed upon the flexibility of the generic concept. The material studied thus far, including hundreds of some species, shows conclusively that the general shape and size of the reproductive tracts is fairly constant and characteristic of a given species over a geographic range that is reasonably compact and understandable. The definition of species which we propose abolishes the idea of continent wide distributions such as Goodnight's records (e.g., Vera Cruz, North Dakota, Michigan, North Carolina, New York) of "*Cambarincola philadelphica*" would indicate.

The original diagnosis of the genus was given by Ellis (1912: 481) as follows:

"This genus is easily distinguished from *Bdellodrilus* Moore by the noneversible penis, by the simple spermatheca, by the large accessory tube connected with the male reproductive organs in segment 6, and by the absence of the conspicuous, clear, paired, segmental glands in the first nine postcephalic segments. It is separated from *Branchiobdella* Odier by the single, median dorsal, pulsate papilla carrying the single common opening of the anterior nephridia, by the possession of two pairs of testes and vasa deferentia, and by the dis-similar dental plates."

This diagnosis was quite sufficient to separate the genus, as known to Ellis, from the other two genera named. It proved inadequate for later work, however, and Goodnight (1940: 30) presented a somewhat modified definition:

"With the characteristics of the subfamily; spermatheca simple, not bifid; accessory sperm tube present; bursa but not penis ever-sible; anterior nephridia opening to the outside through a common pore situated on a median dorsal papilla; body cylindrical, not flattened; without body appendages."

Goodnight's emendations provided a distinction between *Cambarincola* and *Pterodrilus*, but the allowance for morphological variations in internal structure in the above diagnoses has not been adhered to in practice. We believe that at least two distinct genera are represented in the four species of his "subgenus *Cambarincola*" and at the same time have serious doubt that the presence or absence of peristomial lobes or tentacles constitutes a valid subgeneric character. The following generic diagnosis is one which we think defines the limits of a group of closely related species, all of which adhere closely to the same general plan of the male reproductive system and differ among themselves in details of size, shape, jaw structure, and relative size and shape of the reproductive organs.

Genus CAMBARINCOLA Ellis

Cambarincola Ellis, 1912, Proc. U. S. Nat. Mus., 42:481; 1919, Proc. U. S. Nat. Mus., 48: 190. —Goodnight, 1940, Ill. Biol. Monogr., 17 (3): 30.

Type species — *Cambarincola macrodonta* Ellis, by original designation.

Diagnosis. — Branchiobdellidae with the following characteristics: Terete, body without specialized projections; jaws large and massive, subtriangular in dorsal aspect, the upper jaw with a large median tooth and usually smaller denticles on each side, the lower jaw with a median sinus and two large paramedian teeth. Anterior nephridia opening through a common median dorsal papilla on segment III.

Male reproductive system: bursa subpyriform to obcordate, becoming broadest proximally, capable of being everted; a distinct cone-shaped penis enclosed in the proximal portion of the bursa, non-eversible, but carried outside the body by the eversion of the bursa; ejaculatory duct present, normally about half as long as the bursa, with strong muscular walls; spermatic vesicle present, usually as long as or longer than the bursa and with the proximal end directed cephaloventrad; an accessory sperm tube present, its origin adjacent to the commisure of the ejaculatory duct and spermatic vesicle, its length variable, but never less than half as long as the spermatic

vesicle and always less than half its diameter, terminating proximally in a thin-walled, bulbous structure.

Female reproductive system: spermatheca with a more or less elongate outlet duct, enlarging proximally into a differentiated bulbar structure, never branched.

Species.—

- C. macrodonta* Ellis, 1912, Boulder, Colo.
- C. philadelphia* (Leidy), 1851, Philadelphia, Pa.
- C. vitrea* Ellis, 1919, Douglas Lake, Mich.
- C. inversa* Ellis, 1919, Eugene, Oregon
- C. chirocephala* Ellis, 1919, Rolla, Missouri
- C. okadai* Yamaguchi, 1933, Lake Chuzenji, Nikko, Japan
- C. elevata* Goodnight, 1940, Leaf River, Illinois
- C. floridana* Goodnight, 1941, Taylor Co., Florida
- C. meyeri* Goodnight, 1942, Raven's Creek, Lexington, Kentucky
- C. macrocephala* Goodnight, 1943, Polecat Creek, Teton Co., Wyoming
- C. gracilis* Robinson, 1954, Whitman College, Walla Walla, Washington
- C. branchiophila* Holt, 1954, Giles Co., Virginia
- C. macbaini* Holt, 1955, Boyd Co., Kentucky

The species listed above have been assigned to the genus *Cambarincola*. In view of the foregoing remarks, we simply list them with their type localities and say nothing as to their final disposition.

Summary. — *Cambarincola macrodonta* Ellis, 1912, is re-described on the basis of Ellis's material. The reproductive systems are described for the first time and drawings are presented. Additional measurements of body proportions and the reproductive systems are given. The status of the genus *Cambarincola* is discussed and an emended diagnosis is attempted.

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