

Freshwater Triclad (Turbellaria)
of North America,
VI: The Genus *Dendrocoelopsis*

ROMAN KENK

SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY • NUMBER 138

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ABSTRACT

Kenk, Roman. Freshwater Triclad (Turbellaria) of North America, VI: The Genus *Dendrocoelopsis*. *Smithsonian Contributions to Zoology*, number 138, 16 pages, 12 figures, 1973.—Five species of *Dendrocoelopsis* occur in North America, *D. vaginata* Hyman, *D. piriformis* Kenk, *D. alaskensis* Kenk, *D. hymanae* Kawakatsu, and *D. americana* [= *Sorocelis americana* Hyman]. *Dendrocoelopsis vaginata*, *D. piriformis*, and *D. americana* are described in detail. The taxonomic significance of multiple eyes in freshwater triclad is discussed.

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Freshwater Triclad (Turbellaria) of North America, VI: The Genus *Dendrocoelopsis*

Roman Kenk

Introduction

The genus *Dendrocoelopsis* was established by Kenk (1930:296) for a European species, *Dendrocoelum spinosipenis* Kenk (1925). The original definition of the genus was as follows: Dendrocoelidae without adenodactyl; penis with well-developed papilla, penis bulb not composed of two muscle layers separated by a glandular layer; oviducts uniting to a common terminal duct without embracing the bursa stalk; testicular zone extending to behind the copulatory apparatus; anterior end with subterminal true sucker; eyes not multiple.

This definition had to be modified as more species, undoubtedly close relatives of *D. spinosipenis*, were discovered and described. The genus *Amyadenium* de Beauchamp (1931:159) was merged with *Dendrocoelopsis* (Kenk, 1953:177), although some European workers still keep it separate. Today *Dendrocoelopsis* comprises some 14 species distributed over Europe, North America, and Asia. They show all transitions between highly developed adhesive organs and a lack of adhesive structures at the anterior end; the testicular zone may terminate at the level of the copulatory complex or extend to the tail end; and several species show a multiplicity of eyes while others have only two or are blind. Thus, the species placed today in the genus *Dendrocoelopsis* exhibit the following characters (cf. Hyman, 1935:338): Dendrocoelidae

without adenodactyl; penis with well-developed papilla, penis bulb of ordinary construction; oviducts uniting to a common oviduct without embracing the bursal stalk; eyes two, lacking, or multiple.

Dendrocoelopsis, thus described, can hardly be separated from the poorly defined Asiatic genus *Sorocelis*. The crucial distinction concerns the interpretation of the multiplicity of the eyes in the two genera. The use of the number and arrangement of the eyes for taxonomic purposes is of limited value (Kenk, 1930:152). Complete absence of eyes is generally correlated with ecological factors such as life in subterranean habitats or in deep lakes, while the occurrence of supernumerary or accessory eyes is observed frequently in two-eyed species of various genera of dendrocoelids and planariids. Such supernumerary eye spots may be of various size and structure, often confined to simple specks of eye pigment lacking any retinal or nervous elements. *Sorocelis* has what we may call a true, genetically determined, pluriocularity, while the multiple eyes of some *Dendrocoelopsis* species appear to be more closely related to accessory eyes. More evidence supporting this interpretation will be given in the section on *D. americana*.

The holotypes of the five North American species of *Dendrocoelopsis* are deposited in the American Museum of Natural History (AMNH) and the National Museum of Natural History, Smithsonian Institution (USNM: United States National Museum collections).

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I wish to express my thanks to Mr. Walter R. Brown, Dr. Kenneth M. Towe, and Mr. Charles R. Obermeyer II, all of the Smithsonian Institution, who kindly took the scanning electron photomicrograph and who performed the X-ray diffraction test and the X-ray concentration mapping on the spines of *D. americana*, respectively.

Dendrocoelopsis vaginata Hyman, 1935

FIGURES 1A, 2A, 3A, 4

Dendrocoelopsis vaginatus Hyman, 1935:339.

Dendrocoelopsis vaginata.—Kenk, 1953:177.

HOLOTYPE.—From shores of Flathead Lake, Montana, set of sagittal sections (AMNH 665).

The species was originally described from preserved specimens sent to Dr. Hyman by Dr. R. T. Young of the University of Montana, two of which were sexually mature. Kenk (1953) changed the ending of the specific name to *vaginata* to agree in gender with the feminine genus *Dendrocoelopsis*.

Sexually mature specimens are up to 21 mm long and 2.8 mm wide. The anterior end is truncate, the frontal margin, bearing the subterminal adhesive organ, in the quietly gliding animal is either slightly bulging or centrally retracted (Figures 1A, 2A). In locomotion this central portion is elevated somewhat above the substrate. The rounded corners of the head protrude gently laterally so that a slight narrowing or neck appears behind them. The margins of the body then diverge gradually for about one-fourth the body length, become parallel, and converge again in the region of the copulatory complex, forming a bluntly pointed posterior end.

The color of the animal in life is dark chocolate brown dorsally and a little lighter ventrally. A pair

of oval fields above the eyes, a spot at the mouth opening, and a circular field around the gonopore are free of pigment. Two indistinct lighter fields extend from the eyes toward the frontal margin, flanking the adhesive organ, and two short, light, longitudinal streaks parallel the body margins at the level of the neck. Occasionally a dark middorsal line is seen, beginning some distance behind the eyes and extending to the region of the pharynx, and a less distinct line, behind the pharynx to the posterior end. In her original description, Hyman (1935:339) reported that the species, collected in Montana, was white and, hence, without body pigment; in a later paper (1963:4) she stated that the dark color seen in another population, from Oregon, was due not to body pigment but to in-

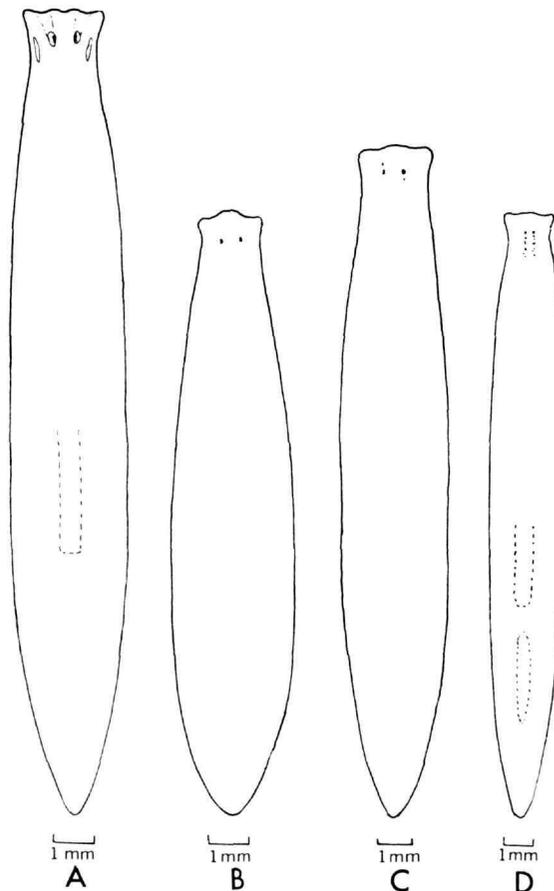


FIGURE 1.—Outline drawings of living specimens: A, *Dendrocoelopsis vaginata*; B, *D. piriformis*; C, *D. alaskensis*; D, *D. americana* from Brown Springs, Mt. Magazine, Arkansas.

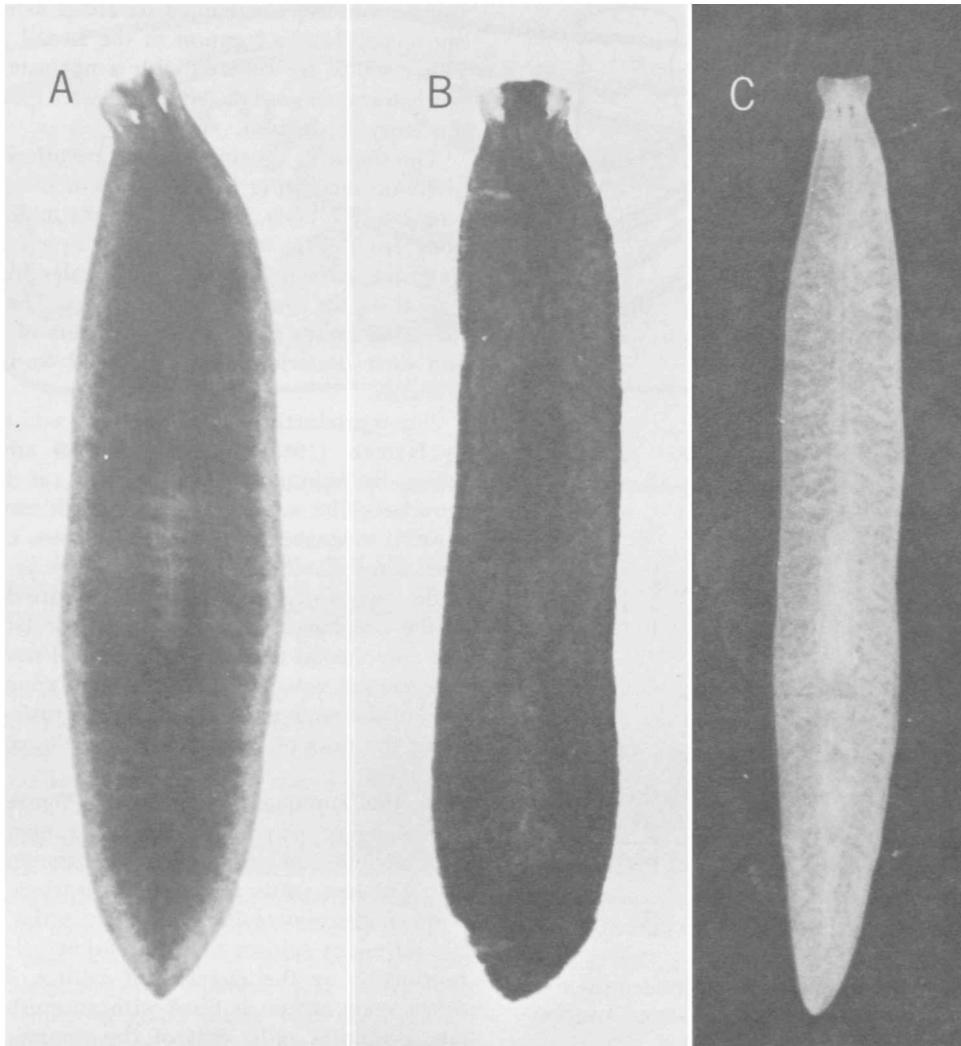


FIGURE 2.—Photographs of living animals: A, *Dendrocoelopsis vaginata* from Nigger Creek, Washington, $\times 9.6$; B, *D. ezensis* from Tomikawa-cho, Hokkaido, Japan, $\times 8.4$; C, *D. americana* from Brown Springs, Mt. Magazine, Arkansas, $\times 7.2$.

clusions in the cells of the gastrodermis, presumably originating from ingested food. It appears that Hyman had studied only preserved specimens. The pigment of *D. vaginata* is diffused in the mesenchymal tissue and is not the granular pigment confined to special mesenchymal cells that occurs in some other triclads and that can be identified in microscopic sections. Furthermore, it bleaches easily in preserved specimens and then cannot be recognized.

Live worms from both of Hyman's localities show clearly that the pigment is not confined to the intestinal system.

The two eyes are situated at a distance from each other equal to about one-third the width of the head and their distance from the frontal margin is slightly greater than that from the lateral margin.

The adhesive organ, located in the center of the frontal margin of the head, appears in the sections

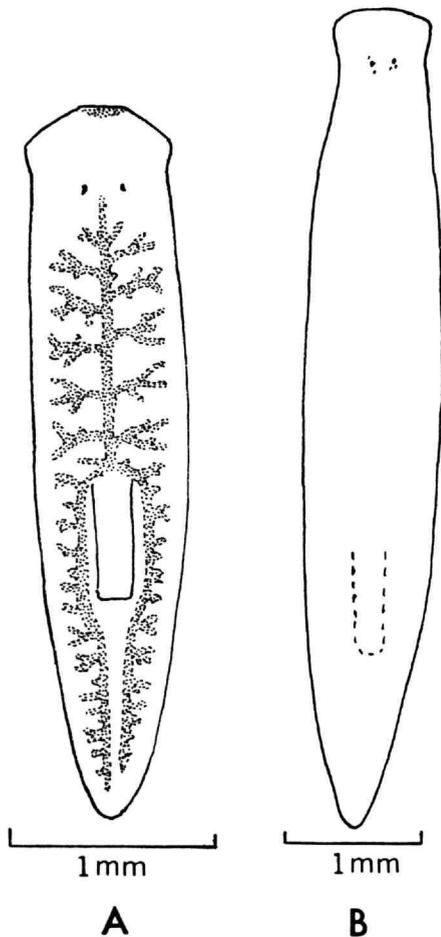


FIGURE 3.—Outline drawings of young (recently hatched) animals: A, *Dendrocoelopsis vaginata* from Yellow Bay Creek, Montana; B, *D. americana* from Brown Springs, Arkansas.

as a convex or concave field of infranucleate epithelium lacking cilia or rhabdites and perforated by numerous gland ducts filled with a granular, eosinophilic secretion. The cell bodies of these glands are scattered in the mesenchyme of the anterior third of the prepharyngeal region, predominantly dorsal to the intestinal branches. Muscle fibers attach to the adhesive area, chiefly extensions of the internal longitudinal layer of the ventral integumental musculature. The adhesive organ may be interpreted as a modification of the submarginal adhesive zone, which has a similar infranucleate and rhabdite-free epithelium. The organ and the zone are not con-

tinuous but are interrupted on either side at what appears to be the location of the lateral auricular lobes, which are covered with a nucleate, ciliated epithelium, in part lacking rhabdites, presumably a sensory epithelium.

The digestive system shows no peculiarities. The pharynx, measuring in length about one-sixth the length of the body, is inserted at the middle of the body length. Its internal muscle layer consists of intermingled longitudinal and circular fibers as is typical for the family Dendrocoelidae. The anterior intestinal ramus bears five to six pairs of branches and each posterior ramus about 12 to 14 lateral branches.

The reproductive system has been well described by Hyman (1935). The two ovaries are located below or behind the second pair of intestinal branches. The numerous, rather small testicles are ventral, arranged in longitudinal rows extending from some distance behind the ovaries to the level of the copulatory complex. Four rows are developed in the prepharyngeal region, one pair lateral and one pair medial to each of the ventral nerve cords. The medial rows terminate as they approach the level of the pharynx while the lateral rows continue along the sides of the pharynx and the copulatory apparatus.

In the copulatory apparatus (Figure 4) the genital atrium may be divided into a large anterior male atrium (*am*) and a smaller common atrium (*ac*), but frequently there is no constriction visible between the two cavities. Apparently the shape of the atrium is subject to deformation by muscular contraction at the moment of killing. The wall of the male atrium is lined with an epithelium of tall, glandular cells, that of the common atrium with a cuboidal epithelium. Below the lining of both divisions is a layer of circular muscle fibers, followed by a layer of longitudinal fibers.

The penis consists of a large spherical bulb and an elongated conical papilla. The bulb, which is formed by the usual concentric layers of muscle fibers, contains a voluminous cavity, the seminal vesicle (*vs*). The cavity is lined with a secretory epithelium and has villus-like extensions projecting inward. The cavity continues into the penis papilla as a narrower canal, the ejaculatory duct (*de*), running in the axis of the papilla and opening at its tip. The lining of this canal is a cuboidal epithelium. Below the flattened external epithelium of

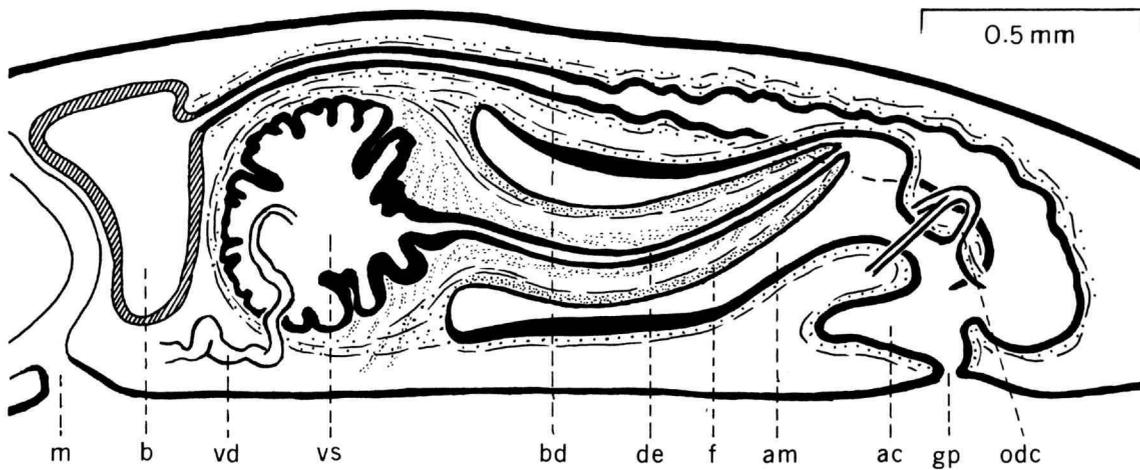


FIGURE 4.—Copulatory apparatus in sagittal section of *Dendrocoelopsis vaginata* (after Kenk, 1972). [Abbreviations used in figures: *a*=genital atrium, *ac*=common atrium, *am*=male atrium, *b*=copulatory bursa, *bd*=bursal duct or stalk, *bp*=penis bulb, *de*=ejaculatory duct, *f*=fibrous layer, *gl*=gland ducts, *gp*=gonopore, *m*=mouth, *odc*=common oviduct, *ph*=pharynx, *pp*=penis papilla, *sv*=false seminal vesicle or spermiductal vesicle, *vd*=vas deferens, *vlc*=common vas deferens, *vs*=seminal vesicle.]

the penial papilla is a thick layer of fine circular fibers which do not stain like muscle fibers, the fibrous layer (*f*); presumably this is of an elastic nature and seems to impart a certain rigidity to the papilla. This layer is followed by a sheet of longitudinal muscles which in part attach to the fibrous layer. The two sperm ducts or vasa deferentia (*vd*), which at the sides of the pharynx had enlarged to form the tortuous false seminal vesicles or spermiductal vesicles, approach the penis bulb, enter it from the sides, and open separately into the seminal vesicle. Numerous gland ducts, with a granular, faintly eosinophilic secretion, penetrate the penis bulb from the surrounding mesenchyme and empty into the posterior part of the seminal vesicle and the ejaculatory duct.

The two oviducts or ovovitelline ducts converge toward the midline and unite in the space between the atrium and the bursal stalk to form a common oviduct (*odc*) which opens into the atrium at the transition between the male and common atria. The terminal parts of the paired oviducts and the common oviduct receive many outlets of strongly eosinophilic glands, the so-called shell glands.

The sac-shaped copulatory bursa (*b*) is well-developed. Its outlet or stalk (*bd*) originates from its

posterior wall, first ascends dorsally, proceeds above the penis and the genital atrium in the midline or somewhat to the right side, and finally bends ventrally to open into the atrium close to the genital aperture (*gp*). In its proximal part, above the penis, the duct is rather narrow and smooth, but it progressively widens distally, and is thrown into irregular folds. Its muscular coat consists of interlaced circular and longitudinal fibers and gradually increases in thickness toward its posterior opening.

Dendrocoelopsis vaginata is an inhabitant of cool streams and lakes in some of the northwestern states. So far it is known only from a few localities, but it will probably be found to be more widely distributed upon further collecting. The following are the records that have come to my attention:

MONTANA. GALLATIN COUNTY: (1) Spring north of Belgrade, in outlet crossing the county road about 4 miles north of junction with U. S. Highway 10. 2 September 1967: water almost stagnant, with much vegetation, temperature 10.4° C, pH 7.5; 5 immature specimens under stones. (2) Tributary of Thompson Creek, crossing county road north of Belgrade, 4.3 miles from junction with U. S. Highway 10. 2 September 1967: water with fast current, 10.8° C, pH 7.6; about 15 specimens under stones, 5 of them mature. 4 September 1967: 10 specimens of various sizes, 4 of them mature, under stones. 4 June 1970: 14.0° C, 4 specimens under stones, 2 of them mature (*Polycelis* sp. also occurs in this

locality). (3) Tributary of Gallatin River, opening into the river above the bridge on U. S. Highway 10, 5.3 road miles northwest of Belgrade. 2 September 1967: water fast, clear, 16.6° C, pH 8.8; 2 *Dendrocoelopsis* under stones, one of them mature. LAKE COUNTY: (1) Along shore of Flathead Lake and in tributary of the lake, type-locality of *D. vaginata* (Hyman, 1935:344). (2) Yellow Bay Creek, about 10 yards from the mouth of the creek in Flathead Lake (possibly the same locality as that mentioned by Hyman). 10 August 1969: several specimens collected by Mr. Frank P. Crowley and shipped to me alive [*Polycelis coronata coronata* (Girard) also present]. MISSOULA COUNTY: Greenough Park, Missoula, feeder spring and creek for Rattlesnake Creek (1 mile from Clark Fork River). 21 May 1968: water slightly muddy, 10° C, 8 specimens collected by Mr. F. P. Crowley, most of them sexually mature.

OREGON. MULTNOMAH COUNTY: Woodbury Spring in Crystal Springs area of Eastmoreland District of Portland, one-half block south of Holgate on 28th Avenue. 12 September 1967: water almost stagnant, clear, 11.2° C, pH 6.3; many *D. vaginata* taken on liver bait, both young and mature (the spring contains also *Phagocata oregonensis* Hyman and *Polycelis* sp.). This is possibly the same locality as that mentioned by Hyman (1963:1).

WASHINGTON. WHITMAN COUNTY: Nigger Creek, 18 miles south of Cheney. 1 August 1970, 5 *D. vaginata* collected by Mrs. Virginia Erickson and sent to me alive, one of them mature.

Sexually mature specimens of *D. vaginata* were taken in the field at all seasons, when collections were made, from March to September; no data are available for the winter months. It is possible that the species breeds the year round. No indications of asexual reproduction were observed. The temperature of the water varied from 10° to 16.6° C, with an average of 12.2° C (6 measurements), the pH from 6.3 to 8.8. Further observations on the physico-chemical parameters of the habitats are lacking.

Specimens were kept in the laboratory in cold-water cultures (14° C) for several months, fed beef liver or *Tubifex* worms, but could not be maintained indefinitely. Three cocoons were deposited in the aquaria, all within the first weeks after the collections. The cocoons were unstalked, spherical, with a diameter of 1.6 to 1.8 mm, attached to the substrate by a copious amount of colorless jelly. Two cocoons hatched several weeks after deposition and yielded seven and five young. They were of different sizes, the largest being about 3.5 mm long and 0.7 mm wide. They showed the adhesive organ as a transverse, opaque field in the center of the frontal margin (Figure 3A). On both sides of the organ the margin sloped backward to the region of the feebly developed rounded auricles, behind

which a slight constriction or neck was visible. The young were initially pigmentless, white, but had acquired body pigment by the time they were four weeks old.

The three pigmented species of the genus *Dendrocoelopsis*, i.e., *D. vaginata*, *D. piriformis* Kenk (1953) from Alaska, and *D. ezensis* Ichikawa and Okugawa (1958) from Hokkaido, Japan, resemble each other rather closely in their external appearance. *Dendrocoelopsis vaginata* may be distinguished from *D. piriformis* by having a slightly different outline of the body, the lateral margins running parallel when the animal is gliding quietly, while in *D. piriformis* the greatest width is in the last third of the body. Furthermore, the pigmentation of the two species is different, *D. vaginata* lacking the accumulation of dark pigment between the eyes and on the sides of the adhesive organ and not showing any pattern of longitudinal stripes, such as are seen frequently in *D. piriformis*. *Dendrocoelopsis ezensis* (Figure 2B), which in its pigmentation appears to be close to *D. vaginata*, has the eyes set farther apart (about one-half the width of the head) than *D. vaginata*. Anatomically the three species may be separated by the location of the testes: in *D. vaginata* they are ventral, extending to the copulatory apparatus; in *D. piriformis*, dorsal, extending to the posterior end; and in *D. ezensis*, ventral and dorsal, extending to the posterior end of the body. The anatomy of the penis also furnishes good distinguishing characteristics: *D. piriformis* lacks a fibrous layer in the wall of the penis papilla; and *D. ezensis* has a plug-shaped penis papilla and a thick muscular layer surrounding the seminal vesicle and the ejaculatory duct.

Dendrocoelopsis piriformis Kenk, 1953

FIGURES 1B, 5

Dendrocoelopsis piriformis Kenk, 1953:174.

HOLOTYPE.—From Moose Creek, on Glen Highway, Alaska, near mile-post 186, set of sagittal sections (USNM 22334).

Since the original description (Kenk, 1953), the species has been collected in a number of arctic lakes in Alaska and western Canada by C. Holmquist (1967a, 1967b). The following description is based on these three publications.

The species is up to 16 mm long and about 3

mm wide. The head is truncate, with a bulge on the frontal margin corresponding to the position of the subterminal adhesive or grasping organ, and a pair of rounded auricles which project slightly laterally (Figure 1b). Behind the head the lateral margins gradually diverge to reach the greatest width at the beginning of the last third of the body. The pigmentation is very variable even within the same population. The dorsal side may be almost uniformly brown or brownish gray, or may appear somewhat spotted; there is often a dark median stripe which may be flanked by a pair of lateral longitudinal stripes. The area between the eyes is very dark and the pigment extends toward the frontal margin along both sides of the adhesive organ. The periocular spaces and a rounded field above the adhesive organ are free of pigment. A pair of indistinct, light-colored streaks, presumably the auricular sense organs, may be seen on the lateral margins of the head. The ventral side is gray.

There are normally two eyes, a little more than one-third the width of the head apart and nearer to the lateral margins than to the frontal margin. Accessory or supernumerary eyes may occur on one or on both sides.

The adhesive organ is similar to that of *D. vaginata*. It consists of a subterminal adhesive field perforated by numerous gland ducts filled with an eosinophilic secretion, and of muscle fibers, presumably serving as retractors.

The ovaries, situated at the level of the second pair of intestinal branches, show no peculiarities. The numerous testes are dorsal, forming a pair of broad bands extending from the level of the ovaries to the posterior end.

The copulatory apparatus (Figure 5) generally resembles that of *D. vaginata*. The genital aperture (*gp*) leads directly into the male atrium (*am*) as there is no common atrium developed. The penis consists of a rounded muscular bulb and an elongated, conical or finger-shaped papilla. The bulb contains a large cavity, the seminal vesicle (*vs*), the walls of which form villus-like processes projecting into the lumen. From this cavity a smooth, narrow ejaculatory duct (*de*) proceeds into the penis papilla and opens at its tip. The penis bulb has, as is usual, concentric layers of interlaced muscle fibers in its peripheral part and a parenchymal zone surrounding the seminal vesicle. The penis papilla is covered by a cuboidal epithelium

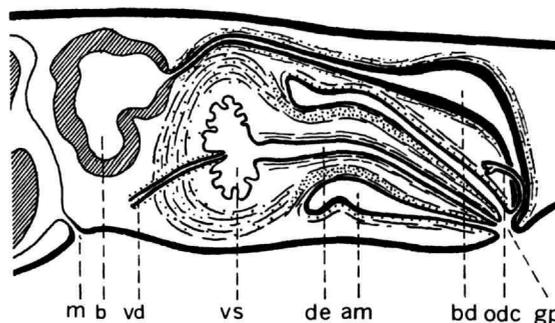


FIGURE 5.—Copulatory apparatus in sagittal section of *Dendrocoelopsis piriformis* (after Kenk, 1953), $\times 49$. [See Figure 4 for abbreviations.]

below which is a muscular zone consisting of several layers; first, a thin longitudinal layer developed chiefly in the proximal (anterior) part of the papilla, followed by a strong sheet of circular fibers and, finally, a second, internal, longitudinal layer. An elastic fibrous layer, such as is developed in *D. vaginata*, is lacking in *D. piriformis*. The ejaculatory duct has a coat of longitudinal fibers.

The two vasa deferentia (*vd*) enter the penis bulb anterolaterally and open into the bulbar lumen separately, but close together, each on a short conical papilla.

The two oviducts approach the midline at the level of the copulatory complex, the right one passing between the wall of the male atrium and the outlet of the copulatory bursa. They unite to a common oviduct (*odc*) which empties into the atrium from the dorsal side close to the gonopore.

The copulatory bursa (*b*) is a lobate sac lined with a tall secretory epithelium. Its outlet or duct (*bd*) runs posteriorly above the penis bulb and the male atrium. Its anterior part is a rather narrow canal, but it widens gradually in the posterior half, curving ventrally and opening into the atrium (or almost independent of it) very close to the gonopore. Both parts of the duct have a muscle coat consisting of intermingled circular and longitudinal fibers.

Holmquist (1967a:456) reports that the cocoons of *D. piriformis*, collected in the field, are round, brown to almost black, and have a diameter of 1–3 mm.

Dendrocoelopsis piriformis has been collected by Kenk in four lakes and two streams in subarctic

Alaska, by P. F. Scholander in a lake near Umiat on the Arctic Slope of Alaska (Kenk, 1953:178), and by C. Holmquist (1967a:454–455 and table 1) in 21 lakes in arctic Alaska, both north and south of the Brooks Range, in the arctic sections of Yukon Territory, and in the Mackenzie District of Northwest Territories of Canada.

Dendrocoelopsis piriformis is a eurythermic species living in lakes and their outlets under a considerable variety of environmental conditions. Physicochemical measurements of some parameters of its habitats were furnished by Holmquist (1967a; table 1). The temperature range at the time of the collections was between 5.5° and 15.5° C in arctic localities and between 11.5° and 26.6° C in subarctic habitats (Kenk, 1958:178). The values of pH (not measured in the field) varied between 7.0 and 9.2. Other parameters measured were: Cl⁻, 1.78–26.6 mg/liter; CaCO₃, 16.1–114.8 mg/l; and conductivity, 12–277 micromho (at 25° C). The worms were collected at depths of 0–15 m. Holmquist (1967a:455) points out that very shallow lakes that freeze solid in winter contain no triclad.

The reproduction of the species is presumably only sexual, by egg capsules, as no evidence of fission has been observed. The species has not been kept in laboratory cultures and little is known about its food habits. It probably feeds on a variety of aquatic invertebrates, for Holmquist (1967a:463) has identified remains of copepods in its gut. This observation is of interest as it may explain the presence of cestode plerocercoids in some of her specimens.

TAXONOMIC POSITION.—By its external appearance, as well as its anatomical characters, *D. piriformis* is, without doubt, closely related to *D. vaginata* and to the Japanese *D. ezensis*. The differences between the three species have been discussed in the section on *D. vaginata*.

Dendrocoelopsis alaskensis Kenk, 1953

FIGURES 1C, 6

Dendrocoelopsis alaskensis Kenk, 1953:178.

HOLOTYPE.—From creek crossing Elliot Highway, Alaska, at milepost 31, set of sagittal serial sections (USNM 22335).

The original description of this species was based on the study of only a few specimens, none of

which was at full sexual maturity. Through the courtesy of Dr. Robert L. Rausch of the Arctic Health Research Center at College, Alaska, I received several additional samples of the species, only one of which had the reproductive system developed but not fully differentiated. The following description is taken chiefly from the original publication.

The largest specimen measured was 20 mm long and 4 mm wide (Figure 1c). The anterior end is truncate, with a convex frontal margin and rounded auricular lobes which protrude both anteriorly and laterally, causing a slight narrowing of the lateral margins to appear behind them. There is no adhesive organ visible in live specimens. The body is unpigmented, white. The two principal eyes are about one-third the width of the head apart and the distance of each eye from the frontal margin is equal to, or slightly longer than, the distance from the lateral margin. Supernumerary eyes may appear either anterior or posterior to the principal eyes.

As no fully mature animal could be studied, the description of the reproductive system must be considered to be preliminary, lacking definite morphological and histological details. The testes are predominantly ventral, but individual follicles may be located in the mesenchymal "septa" between the intestinal branches farther toward the dorsal side. The testicular band on either side extends posteriorly to the level of the copulatory complex. The ovaries are situated below the third or fourth pair of intestinal branches. The copulatory organs (Figure 6), though not in their final shape, show the essential characteristics of the genus *Dendro-*

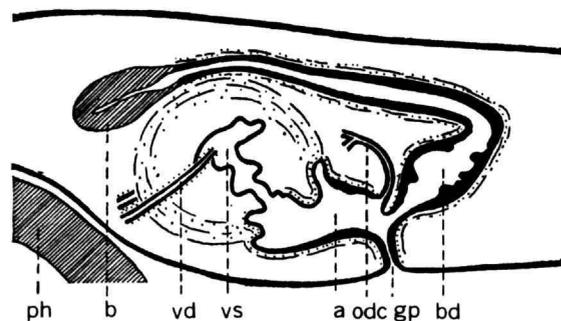


FIGURE 6.—Copulatory apparatus in sagittal section of *Dendrocoelopsis alaskensis* (after Kenk, 1953), $\times 57$. [See Figure 4 for abbreviations.]

coelopsis. The penis has a round, muscular bulb containing a cavity, the seminal vesicle (*vs*). The penis papilla in the original specimen is plump and short; in the second specimen, sent by Dr. Rausch, it is slightly more developed and is conical and pointed. The latter also shows the penial lumen better differentiated, into a bulbar seminal vesicle and a narrower ejaculatory duct which opens at the tip of the penis papilla. The two sperm ducts or vasa deferentia (*vd*) empty into the seminal vesicle separately. The genital atrium (*a*) is a single cavity, not divided into separate compartments. Its wall, as well as the outer wall of the penis papilla, has the usual circular and longitudinal muscle layers developed below the epithelium. The two oviducts unite above the atrium to form a common oviduct (*odc*) which opens into the posterior part of the atrium from the dorsal side. The copulatory bursa (*b*), situated dorsally anterior to the penis bulb, is rather small in both specimens and contains only a small cavity lined with a columnar epithelium. At full maturity the bursa will presumably be much larger and extend farther ventrally. Its bursal duct (*bd*) consists of a narrower anterior portion running in the dorsal midline above the penis and atrium, and a wider terminal portion, which bends ventrally and connects with the posterior part of the genital atrium. The musculature of the duct consists of intermingled circular and longitudinal fibers.

Dendrocoelopsis alaskensis, a stenothermic and rheophilic species, has been collected so far only in cold, fast streams in the White Mountains, a mountain range north of Fairbanks, Alaska. It generally occurs in the company of another white planarian, *Phagocata nivea* Kenk.

ALASKA. (1) and (2) Two streams on Steese Highway, at miles 82.5 and 84.0 (Kenk, 1953:180). (3) Stream crossing Elliot Highway at milepost 31.0, type-locality of the species (Kenk, 1953:180). (4) Stream on Elliot Highway at mile 25, several specimens collected by Dr. Robert L. Rausch, 27 August and 12 September 1971.

TAXONOMIC POSITION.—The majority of the species placed in the genus *Dendrocoelopsis* (in its wider sense, including *Amyadenium*) are devoid of body pigment, as is *D. alaskensis*. The five unpigmented species reported from France, i.e., *D. brementi* (de Beauchamp, 1919), *D. vandeli* (de Beauchamp, 1931), *D. chattoni* (de Beauchamp, 1949), *D. garmieri* (de Beauchamp, 1950), and *D.*

beauchampi (Gourbault, 1969), as well as the species living in Lake Tahoe, *D. hymanae* Kawakatsu (1968), are blind and are equipped with adhesive organs. Four white species with eyes, i.e., *D. spinosipenis* (Kenk, 1925), *D. americana* (Hyman, 1939a), *D. lactea* Ichikawa and Okugawa (1958), and *D. oculata* (Porfir'eva, 1958) (originally described as a subspecies of *D. brementi*), differ from *D. alaskensis* in the anatomy of their reproductive systems, and some differ in the number and arrangement of the eyes and the development of grasping or adhesive organs. The nearest relative of *D. alaskensis* appears to be *D. hymanae* from Lake Tahoe in California and Nevada.

Dendrocoelopsis hymanae Kawakatsu, 1968

FIGURE 7

Dendrocoelopsis hymanae Kawakatsu, 1968:11.

HOLOTYPE.—From Lake Tahoe, Placer County, California, at depth of 1554-1623 feet, set of sagittal sections (USNM 42004).

This species is known only from Kawakatsu's description based on the study of two specimens, one sexually mature and the other immature. The specimens, collected by Ted C. Frantz and collaborators in the course of a joint California and Nevada fisheries study of Lake Tahoe, were dried up when they reached the describer. They were carefully softened but did not permit a thorough histological analysis of their anatomy. The following are the essential characteristics of the species.

The larger preserved specimen was 14 mm long and 2 mm wide, somewhat distorted and probably contracted. The species appears to be unpigmented and is blind. The shape of the head in the living animal is not known but is presumably truncate, as in other species of the genus. The anterior end has a subterminal adhesive organ consisting of a depression lined with a rhabdite-free epithelium perforated by numerous eosinophilic gland ducts and equipped with muscle fibers (apparently retractors) which attach to the epithelium. The ovaries are posterior to the second pair of intestinal branches, the numerous testes are ventral in position, forming on either side of the body a band extending from the level of the ovaries to the insertion of the pharynx. In the copulatory apparatus (Figure 7) the gonopore leads into an undivided

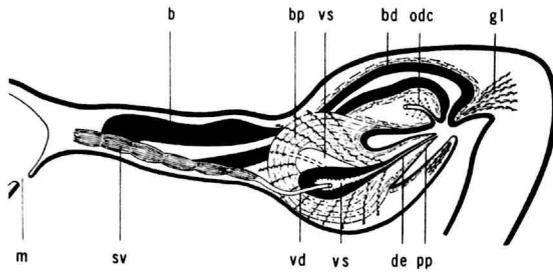


FIGURE 7.—Copulatory apparatus in sagittal section of *Dendrocoelopsis hymanae* (after Kawakatsu, 1968). [See Figure 4 for abbreviations.]

atrial cavity corresponding chiefly to the male atrium. The penis has a large, highly muscular bulb and a rather slender conical papilla (*pp*). The bulb contains a pair of elongated cavities (seminal vesicles, *vs*) which communicate at the base of the penis papilla and continue as a narrow canal, the ejaculatory duct (*de*), to the tip of the papilla. The lining of the seminal vesicles and the ejaculatory duct is a tall, glandular epithelium which decreases in thickness toward the tip of the penis papilla. The bulb is pierced by many eosinophilic gland ducts coming from the surrounding parenchyma. The common oviduct (*odc*) enters the posterior part of the genital atrium from the dorsal side. The copulatory bursa (*b*) is an elongated sac. Its duct (*bd*) runs posteriorly, gradually widening, and opens into the atrium behind the mouth of the common oviduct, close to the gonopore. The muscle coat of the bursal canal consists of intermingled circular and longitudinal fibers.

The species is known only from Lake Tahoe, California and Nevada, where it was collected by an Ekman grab from a depth of between 1554 and 1623 feet (474 and 495 m).

Dendrocoelopsis hymanae appears to be very closely related to *D. alaskensis*. It differs mainly in the development of a grasping organ, the absence of eyes, and the presence of a paired seminal vesicle. Both species are in need of more detailed study based on additional material.

Dendrocoelopsis americana (Hyman), 1939

FIGURES 1D, 2C, 3B, 8A, B, 9-12

Sorocelis americana Hyman, 1938:137 [nomen nudum]; 1939a: 422.

Dendrocoelopsis americana.—Kenk, 1972:62

HOLOTYPE.—From Bat Cave, Adair County, Oklahoma, whole mount (USNM 20403).

The species was first mentioned in the literature by Chase and Blair (1937:220) as “a new species of white turbellarian” occurring in a cave five miles south of Kansas, Oklahoma, i.e., Bat Cave in Adair County. Specimens were sent to Hyman (1938:137) who first reported on them in a meeting of the American Society of Zoologists. Hyman’s (1939a) original description was based on sexually immature specimens. Subsequently (1939b) she obtained additional material from A. P. Blair and from C. E. Mohr and K. Dearolf, including mature animals, and completed the description by adding an analysis of the reproductive system. Further data on the behavior of *D. americana* in the laboratory, including food, temperature tolerance, and regenera-

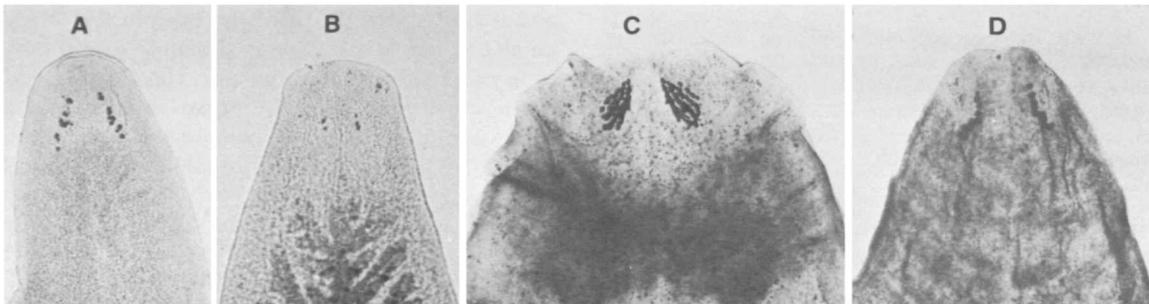


FIGURE 8.—Photographs of anterior ends of whole mounts, $\times 44$: A, *Dendrocoelopsis americana* from Bat Cave, Oklahoma; B, *D. americana*, young specimen from Brown Springs, Arkansas; C, *Sorocelis nigrofasciata* (Grube) from Lake Baikal, Siberia; D, *S. (Baikalobia) guttata* (Gerstfeldt) from Lake Baikal, Siberia.

tive ability, were given by Levensgood (1940). Mohr (1950:7) published a photograph of the species taken in Bat Cave, showing the great abundance of the animals in the shallow stream of the cave in the vicinity of a deposit of bat guano. He also listed additional locality records in northwestern Arkansas. Dearolf (1953:226) reported the species from three caves and one spring in Oklahoma and Arkansas. *Dendrocoelopsis americana* was again mentioned in an article by Nicholas (1955:100), using Mohr's photograph of the specimens. Carpenter (1970:117-127), who collected his materials in Bat Cave, discussed the external features of the immature animal and the structure and function of its adhesive organ and furnished a beautiful photograph of a gliding specimen. I received a dozen preserved specimens from Mr. Leslie Hubricht who had collected them in Brown Springs, Mount Magazine, Arkansas. In 1970 I visited this locality and obtained about 20 animals, which were taken to the laboratory for further study.

Dendrocoelopsis americana (Figures 1b, 2c) may be up to 23 mm long and 3 mm wide, but usually is smaller, even at sexual maturity. The head is truncated, with a slightly bulging frontal margin and rounded auricular borders projecting slightly laterally. The subterminal adhesive pit is visible below the center of the frontal bulge. Behind the auricular projections the head narrows to a neck, then the body widens again. The animal is unpigmented, white. The pharynx, measuring about

one-sixth the body length, is inserted at the middle of the body or slightly more posterior. The copulatory complex occupies approximately one-half the length of the postpharyngeal region. The eyes are multiple, arranged in two almost parallel longitudinal rows at a distance from each other of one-fourth to one-third the width of the head. The most anterior pair of eyes is farther removed from the frontal margin than from the lateral edges of the body. The eyes are of different sizes, are somewhat irregularly spaced, and are variable in number, usually between three and ten in each row. Carpenter (1970:118) observed a maximum of over 20 eyes on either side. There seem to be differences in the average number of eyes in populations of different provenances, the worms from Brown Springs having fewer eyes than those of Bat Cave. Smaller (younger) specimens (Figure 3B) also have a smaller number of eyes than larger ones. Besides the fully developed eyes, frequently there are irregular clumps of eye pigment scattered in the parenchyma of the ocular region.

The adhesive organ is rather weak, consisting mainly of a small pit lined with a nucleate epithelium lacking rhabdites and pierced by many ducts filled with eosinophilic secretion originating from parenchymal gland cells. The organ appears to be an extension of the marginal adhesive zone from which it is separated by two areas, right and left, covered with normal surface epithelium.

The two ovaries are situated behind the second

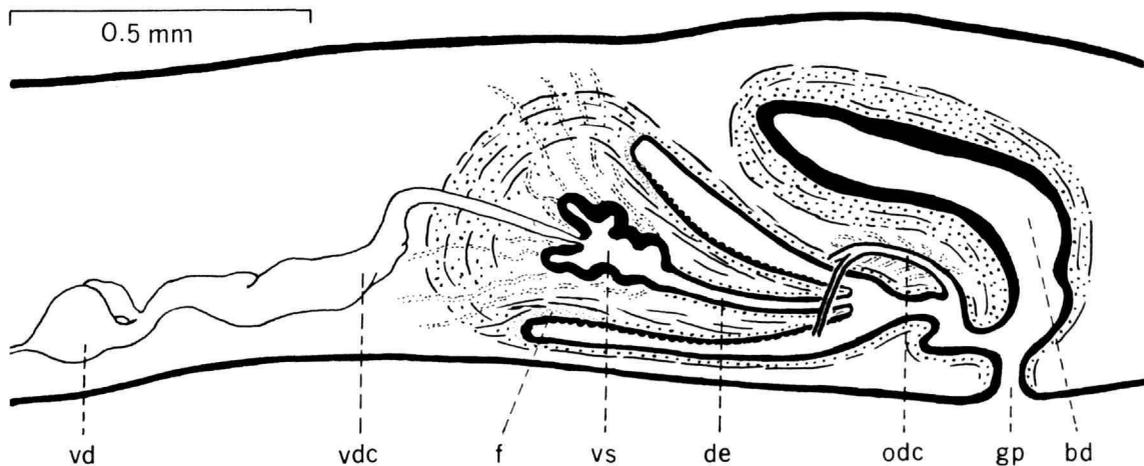


FIGURE 9.—*Dendrocoelopsis americana*, semidiagrammatic view of copulatory complex in sagittal section (after Kenk, 1972). [See Figure 4 for abbreviations.]

or third lateral branches of the anterior intestinal trunk. The testes, of moderate number, are arranged in a pair of bands beginning a short distance behind the ovaries and extending posteriorly to a level about half-way between the copulatory complex and the tail end of the body. They are rather large and predominantly dorsal, although individual testes may be located close to the ventral side.

The copulatory apparatus (Figure 9) has several distinguishing characteristics. The gonopore (*gp*) leads into a small common genital atrium, not always well defined, into which the bursal duct (*bd*) opens from the dorsal side. Anteriorly the common atrium connects with the male atrium from which it is separated by a stricture. The penis consists of a muscular bulb and a well-developed conical papilla. The bulb contains a cavity of lobate outline, the seminal vesicle (*vs*), which is lined with a tall glandular epithelium. This cavity continues into the penis papilla as a narrower canal, the ejaculatory duct (*de*), lined with a nonglandular cuboidal epithelium. The outer covering of the papilla consists of an epithelium which forms wart-like protuberances packed with short, pointed spines (Figures 10–12). Each wart represents one large epithelial cell with a basal nucleus. The distal part of the cell contains the bases of perhaps two dozen spindle-shaped spines, pointed at both ends, each with a small swelling in the middle, about 10 microns long and 2 microns thick in the widest part. These spines give the impression of mineral bodies, not accepting any stain when treated with hematoxylin, eosin, and phloxine-B. They have a higher refractive index than the surrounding protoplasm and are optically isotropic. They are insoluble in diluted acetic, hydrochloric, and sulfuric acids applied for 30 minutes, and are not affected by potassium hydroxide nor by chitinase. Dr. Kenneth M. Towe kindly subjected a specimen of a freeze-dried penis to the Debye-Scherrer powder X-ray diffraction test and found the spines to be amorphous. Analysis of a section through the penis by X-ray concentration mapping in the electron microprobe, carried out by Mr. Charles R. Obermeyer, revealed that the spines contained no appreciable amounts of magnesium, calcium, aluminum, silicon, phosphorus, or sulfur. Their composition is, therefore, still open to further investigation.

The musculature of the penis bulb consists of the usual concentrically arranged layers of inter-

laced fibers. The penis papilla has a layer of circular fibers below the external epithelium, followed by longitudinal fibers which, in part, also enter the bulb. At the base of the papilla the external circular layer is modified, consisting of fine fibers (*f*), much thinner than muscle fibers and not

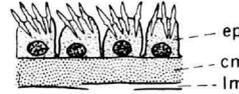


FIGURE 10. — *Dendrocoelopsis americana*, penial armature in sagittal section of penis. [*cm* = circular muscle layer, *ep* = epithelial cell, *lm* = longitudinal muscle layer.]

staining like muscles. This is apparently a fibrous layer of an elastic rather than contractile nature, such as is frequently seen also in other species (e.g., *D. vaginata*). The ejaculatory duct has a coat of circular muscles. Many gland ducts with a granular eosinophilic secretion enter the penis bulb from the surrounding parenchyma and open into the seminal vesicle.

The sperm ducts or vasa deferentia (*vd*), which lateral to the pharynx are expanded to form the tortuous false seminal vesicles, unite outside the penis to a common vas deferens (*vd*) that retains its sinuous expansion until it enters the penis bulb



FIGURE 11.—*Dendrocoelopsis americana*, view of squashed freshly extirpated penis in the light microscope, $\times 1090$.

to open into the seminal vesicle (*vs*). The two oviducts unite above the male atrium, and the common oviduct (*odc*) empties into the atrium from the dorsal side, near the transition between the male and common atria.

There is no copulatory bursa developed. A thick-walled bursal duct (*bd*), opening into the common atrium dorsally, then curving anteriorly and ending blindly above the male atrium, obviously corresponds to the expanded terminal portion (vagina)

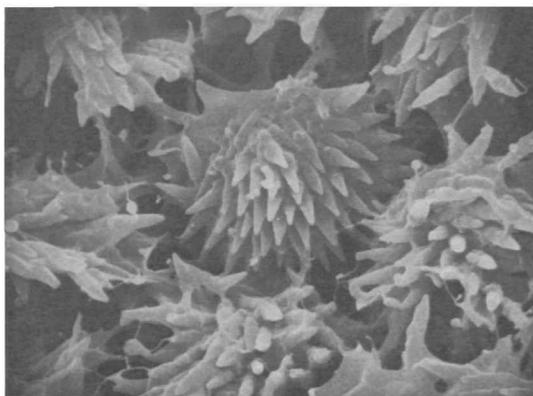


FIGURE 12.—*Dendrocoelopsis americana*, scanning electron micrograph of surface of freeze-dried penis papilla, $\times 1725$.

of the bursa stalk of other species of the genus. This duct is lined with a columnar, secretory epithelium. Its thick muscle coat consists mainly of circular fibers with less numerous interspersed longitudinal muscles.

Dendrocoelopsis americana inhabits subterranean streams and epigeal springs in the Ozark region of eastern Oklahoma and northwestern Arkansas:

ARKANSAS. LOGAN COUNTY: Brown Springs, on Mt. Magazine, Ozark National Forest. 26 May 1966 and 21 May 1968: several specimens collected by Mr. Leslie Hubricht, some of them mature. 12 June 1970: trickle of water forming a shallow pool at the spring, 14.5° C, about 20 specimens, 3 of them sexually mature, under fallen leaves. WASHINGTON COUNTY: (1) Watson Cave, near Prairie Grove (Hyman, 1939b:283; Mohr, 1950:7; Dearolf, 1953:226). (2) Spring near Watson Cave (Hyman, 1939b:283; Mohr, 1950:7).

OKLAHOMA. ADAIR COUNTY: (1) Bat Cave, in northwest corner of the county, type-locality of the species (Chase and Blair, 1937:220; Hyman, 1939a:423, 1939b:283; Mohr, 1950:6; Dearolf, 1953:226; Carpenter, 1970:119). (2) Spring near Bat Cave (Hyman, 1939b:283). (3) Ozark Cave spring (Dearolf, 1953:226). (4) First Cave (Dearolf, 1953:226).

The species must be considered a troglophile rather than an obligate troglobite. Levengood (1940), who studied its behavior in the laboratory, reports that it is more photophobic than the epigeal species *Dugesia dorotocephala*. It accepted

as food pieces of beef liver, of cave isopods, snails, and earthworms. Levengood stated that in the cave the specimens appeared to be feeding on bat feces. Chase and Blair (1937:220) pointed out that in Bat Cave the planarian habitat is shared by numerous isopods (*Caecidotea macropropoda*), which may be the natural food of *Dendrocoelopsis*. Levengood demonstrated the great tolerance of the species to variations in the osmotic pressure by keeping them in mammalian Ringer solution and in distilled water for six days without observing any signs of disintegration. When exposed to a temperature gradient from 14° to 23.5° C, the species showed no preference for any specific temperature, but disintegrated at temperatures above 28° C. It may live indefinitely at 24° C and for at least four weeks at 6°–10° C.

I have kept specimens of *D. americana* in cultures at 14° C for 27 months, feeding them beef liver. The animals, which were immature when collected, developed sexual structures and, in the course of several months, deposited seven cocoons. The cocoons are spherical or subellipsoidal, with a diameter of 1.7–2.3 mm. Three of the cocoons hatched about six weeks after deposition and released one, two, and three young. The freshly hatched young (Figures 3B, 8B) were up to 6 mm long and 1 mm wide, similar in shape to the adult, bearing 2–4 eyes on either side. They matured, or at least developed indications of a copulatory complex, in 4–5 months. No asexual reproduction was observed.

The species has considerable regenerative ability. In the course of this study, the postpharyngeal regions of several specimens were removed for the investigation of the armature of the penis. All animals operated on survived and regenerated the severed parts. Levengood (1940:34) had already shown that specimens cut transversely into fifths are capable of regeneration, though the process of reconstitution is slower than in *Dugesia dorotocephala*.

TAXONOMIC POSITION:—Hyman (1939a:423) had placed the species in the genus *Sorocelis*, based principally on the combination of a dendrocoelid type of pharynx with multiplicity of the eyes, which are arranged in two rows or clusters in *Sorocelis*. It must be kept in mind, however, that *Sorocelis* in the classical sense (Kenk, 1930:298), the geographic range of which is confined to the area of Lake

Baikal in Siberia, is a very extensive and diversified genus, still incompletely known, which is only now being intensively studied by N. A. Livanov and N. A. Porfir'eva of the University of Kazan. The crucial point in the placement of *D. americana* is the interpretation of the great number of eyes. In *Sorocelis* (and *Polycelis*) the multiple eyes are of about equal size (Figures 8c, 8d) and are more or less evenly spaced, with hardly any rudimentary eye spots or pigment clumps between them. *Dendrocoelopsis americana* shows all intergrades between fully differentiated eyes and apparently nonfunctional accumulations of ocular pigment granules, characteristic of some supernumerary or accessory eye spots (cf. Ghisalberti, 1919; Balázs, 1962). One frequently sees a certain variability in the number of eyes in various species of triclads: *Procotyla fluviatilis* Leidy regularly has several pairs of eyes in the northern parts of its distributional range and generally a single pair in southern areas; Anderson (1951:83) and Stewart (1972:542) observed two eye spots in freshly hatched young and usually about six in adults of this species. Other instances of multiple eyes in usually two-eyed genera are *Phagocata uenoi* Okugawa (1939:157), *Dendrocoelum album* (Steinmann, 1910), and *Dendrocoelum romanodanubiale* (Codreanu, 1949). I cannot agree with Codreanu (1951:618–619, 636–637) who considers the multiplicity of the eyes to be of generic value and uses it in the characterization of his genus *Palaedendrocoelum*. A case quite analogous to the condition of *D. americana* is the development of two longitudinal rows of eyes in *Phagocata morgani polycelis* Kenk (1935:103), while the nominate subspecies normally has a single pair. Within the genus *Dendrocoelopsis* the occurrence of occasional accessory eyes is known in the species *D. alaskensis* and *D. piriformis* and regular pluriocularity occurs in *D. lactea* Ichikawa and Okugawa (1958:10), *D. chattoni* (de Beauchamp, 1949:60), and *D. oculata* (Porfir'eva, 1958:46, described as *Amyadenium brementi oculatum*) where the eyes are arranged in a pair of longitudinal rows. *Dendrocoelopsis americana* fits well into this series.

Another peculiarity of *D. americana* is the development of a spiny armature on the penis surface. Similar structures have been described in various freshwater triclads: the European *Polycelis nigra* (O. F. Müller), *P. tenuis* Ijima, and *Dendrocoelopsis*

spinosipenis (Kenk) and the Baikal planarians *Armillaria armata* (Zabusov), *A. pardalina* (Grube), *Protocotylus flavus* Korotnev, *P. fungiformis*, (Zabusov), and *Planaria* (?) *adhaerens* Korotnev (see discussions by Kenk, 1925:143–144; Livanov, 1961:280; Porfir'eva, 1970:106–108, 1971:89). The penial spines must have developed in several genera and even some species independently as they differ widely in their shape, composition, and relation to the tissues in which they originate. At first glance, the spines of *Dendrocoelopsis americana* resemble those of *D. spinosipenis* to some extent, but upon closer examination this resemblance proves to be only superficial. In *D. spinosipenis* the rather large, club-shaped spines consist of calcium carbonate in the form of crystalline aragonite (Schmidt, 1942) while in *D. americana* they are amorphous and of unknown composition, not containing any calcium. Functionally the penial armatures of the various species probably coincide, serving either for the fastening of the penis in the vagina of the partner during copulation, or for sexual stimulation, or possibly performing both functions at the same time.

The third outstanding characteristic of *D. americana* is the absence of a bursal sac, which it shares with two other quite unrelated freshwater triclads, *Cura foremanii* (Girard) (see Kenk, 1935:81) and *Rimacephalus arecepta* Porfir'eva (1969:1305). In *Cura foremanii* the bursal stalk is well developed and opens into the posterior intestinal ramus of one side. *Rimacephalus arecepta* apparently has only the terminal portion of the bursal duct differentiated as a blindly closed, highly muscular posterior extension of the genital atrium, very similar in structure to the duct of *D. americana* (Porfir'eva considers this outgrowth to be part of the atrium although in its position it corresponds to the enlarged distal section or vagina of the bursal duct of the closely related *R. pulvinar* [Grube]). In all instances the close relatives of the three species are provided with a normal sac-shaped copulatory bursa. The absence of the bursa can, therefore, not be given any taxonomic significance beyond being a good species characteristic.

The combination of pluriocularity, presence of penial spines, and absence of a copulatory bursa distinguishes *D. americana* from all other species of the genus *Dendrocoelopsis*.

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