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North American Triclad Turbellaria. 15 Three New Species

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The present report concerns one marine and two fresh-water triclads new to the North American fauna. The fresh-water species are associated with caves, the only type of habitat likely to continue to yield new species of fresh-water planarians in the United States.

ABBREVIATIONS FOR ALL FIGURES

1, Pharynx; 2, pharyngeal cavity; 3, mouth; 4, copulatory sac; 5, penis; 6, common gonopore; 7, ovaries; 8, penis bulb; 9, male antrum; 10, sperm duct; 11, penis papilla; 12, bursal canal; 13, bursa; 14, dorsal bursal pore; 15, common ovovitelline duct; 16, epidermis; 17, epidermal nucleus; 18, rhabdites; 19, elongated rhabdites; 20, cross sections of rhabdites; 21, bulbar lumen; 22, common antrum; 23, female antrum; 24, testes; 25, intestinal branches; 26, adhesive organ; 27, cilia; 28, epithelium; 29, circular muscle fibers; 30, longitudinal muscle fibers; 31, insunk nuclei; 32, inner gland layer; 33, eosinophilous mass; 34, eosinophilous glands; 35, duct of eosinophilous mass; 36, lining of male antrum; 37, mass of sperm; 38, muscles of penis bulb.

ORDER TRICLADIDA

SUBORDER MARICOLA

NESIONIDAE, NEW FAMILY

DEFINITION: Maricola with excessively muscular penis bulb and very long tubular male antrum and penis papilla; ovaries in usual anterior

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position; two gonopores; bursal canal long, recurved, and highly muscular; bursa opening by a middorsal pore.

NESION, NEW GENUS

DEFINITION: With the characters of the family.

TYPE SPECIES: *Nesion arcticum.*

Nesion arcticum, new species

Figures 2–4

Several preserved specimens were received from Dr. Robert Rausch, Arctic Health Research Center, Anchorage, Alaska. They had been collected September 6, 1954, in the intertidal zone of St. Andrew's Island in the Bering Sea. Examination of the sections showed that a new type of marine triclad was at hand, for which it has seemed necessary to create a new family.

The preserved worms have a maximum length of 8 mm. and a typical planarian shape (fig. 2), with somewhat triangular head, evident auricles, no doubt more prominent in life, and two eyes, each enclosed in a large clear space. In color the worms are dark gray or grayish brown, with a conspicuous white middorsal stripe. In the larger specimens there are also present elongated white areas to the sides of the median stripe.

Three sets of sagittal sections and one set of transverse sections were prepared, but the histological condition of the material does not justify consideration of general histological details. The histology of marine triclads is thoroughly described and illustrated in Wilhelmi's monograph (1909). The body wall of *Nesion arcticum* has the structure typical of the group, being composed of outer epithelium, thick basement membrane, and circular and longitudinal muscle layers. All of these layers are thicker ventrally than dorsally; the dorsal epithelium is loaded with rhabdites and its subepidermal musculature is abundantly interspersed with pigment granules. According to Wilhelmi, the histology of the pharynx is virtually identical throughout the Maricola, but *Nesion* differs in the much greater thickness of both the inner and outer circular muscle layers of the pharynx.

There is a pair of ovaries in the usual anterior position, shortly behind the eyes (fig. 2). Testes could not be found either in whole cleared specimens or in sections. The copulatory apparatus, situated as usual immediately behind the pharynx, is shown in sagittal view in figure 3. Its extreme muscularity is at once noticeable. Directly behind the pharynx is found the massive penis bulb, with a thick muscular wall of bundles

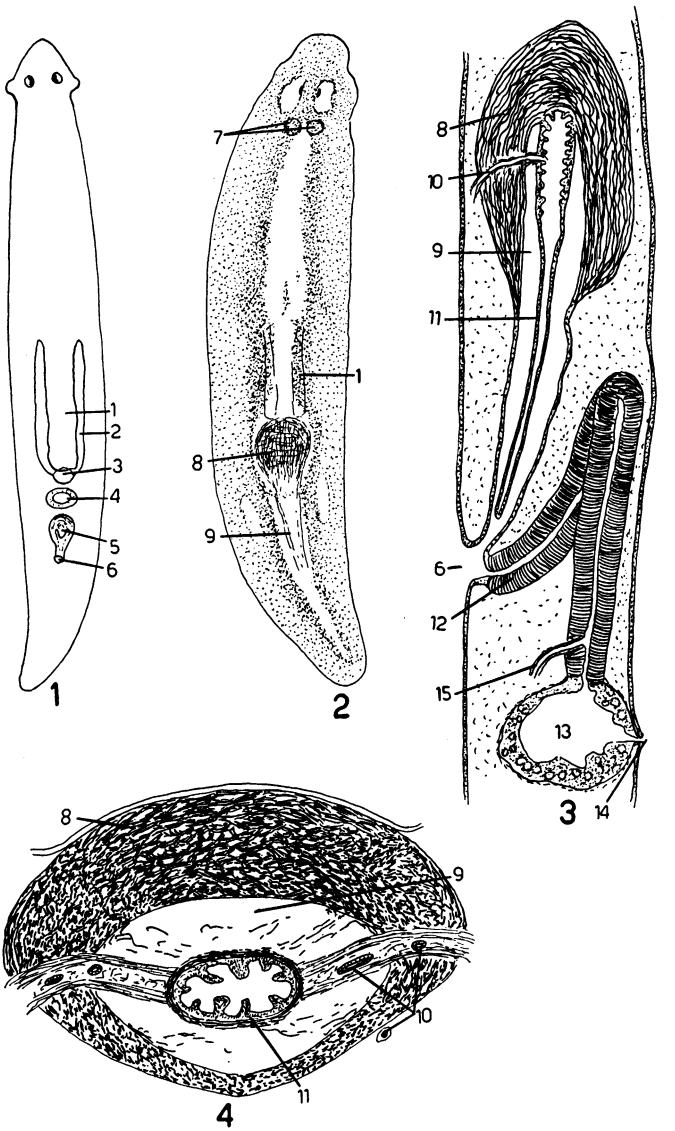


FIG. 1. *Dugesia diabolis*, from whole mount.

FIGS. 2–4. *Nesion arcticum*. 2. Entire animal from whole mount. 3. Sagittal view of copulatory apparatus. 4. Cross section through the penis bulb, at level of entry of the sperm ducts.

of fibers that parallel the surface contour of the bulb. Transverse sections show that the muscular wall of the bulb is thicker dorsally than ventrally (fig. 4) and that the muscle bundles are complexly intertwined. Posteriorly the wall of the penis bulb narrows abruptly and is continuous with the thin wall of the male antrum. The latter continues to the common gonopore as an elongated, thin-walled tube. In one of the sectioned specimens this tube is much longer than shown in figure 3. The penis papilla, also very long and tubular, occupies the male antrum. It is widest in the anterior part of the antrum which is enclosed by the penis bulb, being here lined by a scalloped epithelium underlain by a layer of circular muscle fibers; distally the wall of the papilla thins rapidly and was not histologically analyzable in the available sections. The proximal wide part of the penis papilla is slightly bound to the penis bulb by webs of fibrous tissue. The two sperm ducts enter the proximal part of the penis papilla separately, one from each side, crossing through the wall of the penis bulb and the anterior part of the male antrum in a strand of the same fibrous tissue. Figure 4 gives a transverse section of the penis at the level of the entry of the sperm ducts.

Whereas extensive muscularization of the penis bulb is not uncommon in marine triclads, the very long tubular male antrum and penis papilla seen in the present species appear unique in the group.

The female copulatory apparatus also presents unique features (fig. 3). The bursal canal extends from its entry into the posterior part of the common antrum far anteriorly, almost to the level of the penis bulb in some of the sectioned specimens, as a highly muscular tube with a small lumen and a thick wall of circular muscle fibers. It then curves backward, running shortly beneath the dorsal body wall, and, after receiving the common ovovitelline duct from below, enters the seminal bursa. This is a rounded sac with a wall of tall, glandular epithelial cells filled with vacuoles and inclusions and underlain by a slight musculature. The seminal bursa opens by a middorsal pore (fig. 3). This was evident in all four sets of sections and was especially obvious in the transverse series.

Whereas bursal pores separate from the regular gonopore are known in other marine triclads, they open ventrally in all species hitherto studied. There is one such pore, located midventrally between pharynx and penis bulb, in the family Uteriporidae, and two lateroventral pores at the level of the mouth in the family Bdellouridae. A single middorsal pore is therefore novel among marine triclads and justifies the erection of a new family for the present species.

The holotype as a set of sagittal sections (two slides) is deposited in

the invertebrate section of the American Museum of Natural History, together with a whole mount of the worm.

SUBORDER PALUDICOLA

FAMILY PLANARIIDAE

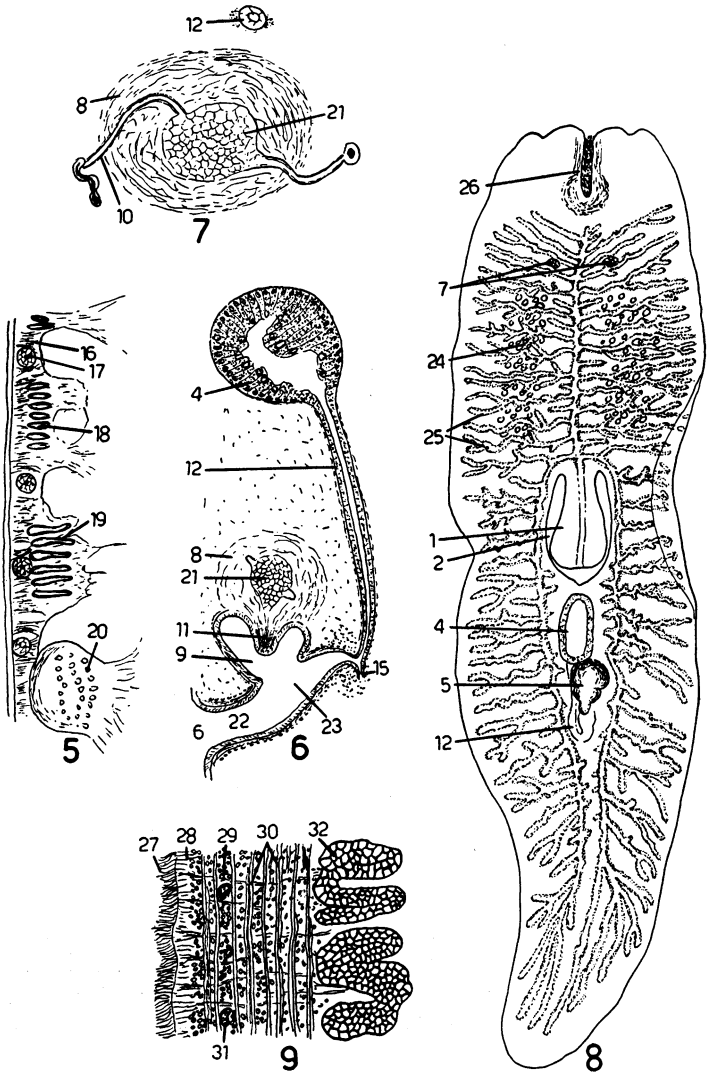
Dugesia diabolis, new species

Figures 1, 5–7

Several specimens without any locality record were sent alive by E. E. Simmons of Pasadena, California, on December 2, 1954. It was learned later from Dr. Carl Hubbs that the worms came from a pool in the Devil's Hole, Nevada. This is a large pit or chasm situated about 70 miles west of Las Vegas in the midst of the Nevada desert. The walls of the chasm drop about 50 feet to give access to a very deep pool of warm water (93° F.) in which is found the famous tiny desert spring fish, *Cyprinodon diabolis* Hubbs, as well as the planarians. An interesting account of the explorations of the pool and adjacent area is given by Halliday (1955).

Alive the worms were of a dark brown color, somewhat mottled under magnification, and about 10 mm. long, with a markedly triangular head provided with slender, pointed auricles. Unfortunately no drawing was made of the living worm, as it was not supposed to be a new species. Figure 1, drawn from a whole mount, does not give a correct idea of the auricles in life; they resemble those of *Dugesia dorotocephala* (drawing from life in Kenk, 1944, pl. 1, fig. 4) and in fact the worms were at first supposed to be juveniles of this species. Examination of fixed, cleared specimens showed, however, the presence of the reproductive system; hence the worms despite their small size were fully mature. As the pool in which they live is well exposed to the light, they do not have any of the characteristics of true cave planarians, but are dark colored, with the usual two eyes, and are members of one of the most common epigean genera of fresh-water triclads.

Good fixation was obtained with the standard fixative I am accustomed to employ (0.7% sodium chloride saturated with mercuric chloride). One set of sagittal and one set of transverse sections were prepared. The only interesting point in the general histology is the seeming discharge of the rhabdites in both series of sections. As usual the rhabdites are more abundant in the dorsal than in the ventral epidermis, but in the median anterior region of both surfaces they are so thickly present as to form a



FIGS. 5–7. *Dugesia diabolis*. 5. Epidermis, showing rhabdite discharge. 6. Sagittal view of the copulatory apparatus. 7. Transverse section through the penis bulb, showing asymmetrical entry of the sperm ducts.

FIGS. 8–9. *Macrocotyla glandularis*. 8. Entire animal from whole mount. 9. Cross section through inner part of pharynx wall.

darkly staining band; elsewhere they occur in groups. Everywhere they are continuous with delicate webs and strands extending out from the surface and concomitantly the epidermis is thickened (fig. 5). In some

of these thickened areas the rhabdites appear much elongated, as at 19 in figure 5; and where the webs are cut parallel to the surface a number of holes appear, as at 20 in figure 5; these seem to be cross sections of these elongated rhabdites. These appearances do not seem explicable except as material emanating from the rhabdites that also apparently elongate on discharge. The function of rhabdites has never been demonstrated, but it is usually believed that they discharge adhesive material, and the appearances in these sections support this belief. No other deviations from the usual histology were noticed. The epidermis has the usual striated, vacuolated structure, with large round nuclei at intervals. Ventrally it is underlain by a basement membrane, followed by a circular muscle layer, a thin strand of longitudinal muscle, a diagonal layer, and finally inner longitudinal fibers which, however, are well developed only in the anterior part of the body. The dorsal epidermis and basement membrane are thicker than the ventral ones, but the muscular arrangement dorsally could not be made out satisfactorily because of the dark pigment granules thickly permeating the muscle layers. The layers of the pharynx wall also appear typical. From the outer surface inward are found: the anucleate epithelium with short stiff cilia, a basement membrane, a thin layer of longitudinal fibers, a thick layer of circular fibers, and the zone of nuclei belonging to the epithelium. The layers from the lumen outward are: a rather indefinite anucleate epithelium apparently devoid of cilia, a thick layer of circular fibers, a thinner layer of longitudinal fibers, and the nuclei belonging to the epithelium. A basement membrane of the lining epithelium of the pharynx was not detectable.

The reproductive system is typical of the genus. There is a pair of ovaries in the usual anterior position, between the third and fourth diverticula of the intestine. The numerous testes are ventrally located in the usual longitudinal lateral tracts and extend as characteristic of the genus from the level of the ovaries to the posterior end of the body. The copulatory apparatus, located immediately behind the pharynx (fig. 1), differs in some details from that usual for the genus. It is shown in sagittal view in figure 6. The large, rounded, copulatory sac, located immediately behind the pharynx, is lined by the usual tall, bulging epithelium of glandular appearance and here lacking muscular investment. The bursal canal leads posteriorly from it, above and to the right of the male complex. It is lined by a nucleated epithelium having a slight muscular provision. The bursal canal, having attained the level of the penis papilla, curves ventrally, receiving into its posterior wall the short, common, ovovitelline duct accompanied by eosinophilous glands, and then

becomes continuous with the female part of the antrum. This merges into the common antrum which slants posteriorly to open by the common gonopore. The antrum has a fair muscular investment of inner longitudinal and outer circular fibers. The male copulatory apparatus is notable for its slight muscularity. The rounded penis bulb shows a slight content of muscle fibers outlining its contours and contains a rounded lumen filled with a web-like tissue; from this a narrow canal leads along the center of the penis papilla. The sperm ducts enter the penis bulb separately, one from each side, and, strangely enough, their entry is asymmetrical, as shown in figures 6 and 7. Figure 7 is drawn from a cross section and illustrates the weakly muscular penis bulb, the interior cavity (bulbar lumen) filled with a web of tissue, and the asymmetrical courses of the two sperm ducts. These characteristics appear on both sets of sections and hence are typical of the species. The penis papilla is small and weak, with hardly any musculature and a very narrow lumen.

Dugesia (formerly *Planaria* in part, *Euplanaria*) is the most common genus of fresh-water planarians, found in lakes, ponds, and streams of all continents. It is distinguished by the triangular head with definite auricles, dark coloration, numerous testes extending the body length, separate entry of the sperm ducts into the penis bulb, and entry of the ovovitelline ducts into the curve of the bursal canal. Nearly 60 species have been named, but of course the validity of all of these has not been established. The present species differs from the others in the combination of weakly developed penis bulb and papilla, single cavity in the penis bulb, and asymmetrical entry of the sperm ducts into the latter.

HOLOTYPE: One set of sagittal sections (two slides) deposited in the invertebrate section of the American Museum of Natural History; also one whole mount of the worm.

FAMILY DENDROCOELIDAE

MACROCOTYLA, NEW GENUS

DEFINITION: Dendrocoelidae with highly developed adhesive organ, of the *Speophila* type; testes prepharyngeal; common ovovitelline duct entering the roof of the male antrum; penis excessively glandular, partly embraced by an eosinophilous mass discharging by a pair of ducts into the sperm ducts; no adenodactyls.

TYPE SPECIES: *Macrocotyla glandulosa.*

Macrocotyla glandulosa, new species

Figures 8–17

A number of specimens of this planarian were received from P. W. Frank, of the Department of Zoology of the University of Missouri, who had collected them April 30, 1955, from a stream below the outlet of a cave at Rock Bridge, 5 miles south of Columbia, Missouri.

This is a large species, up to 28 mm. long (preserved), with all the typical characteristics of a cave planarian, although found outside the cave: white color, want of eyes, conspicuous adhesive organ in the center of the anterior margin (fig. 8). The worm is broad and thin, about 6 mm. wide through the widest area, with a truncate anterior end. Behind the middle the body tapers to a rounded posterior end. The pharynx appears relatively short but is probably contracted as a result of preservation. The digestive branches are slender and numerous as usual in the family Dendrocoelidae.

One set of sagittal sections of the entire worm and three sets of transverse sections of the pharyngeal-copulatory region were prepared; the histological preservation was found fairly good. The general histology presents some features of interest. The rhabdites in many places show the same explosions into webs and filaments described for the preceding species. The subepidermal musculature appears rather thin, composed of outer circular and inner longitudinal fibers, but the circular layer is greatly thickened dorsally over the adhesive organ. The latter is a deep tubular invagination with lateral outfolding; its lumen is filled with eosinophilous secretion and lined by a layer containing eosinophilous granules. The inner end is provided with protractor and retractor muscles. The entire organ is practically identical with that of the genus *Speophila,* and as this was figured in detail in Hyman (1954) an illustration appears unnecessary here. Because of the structure of the adhesive organ, of a type hitherto unknown in the family Dendrocoelidae, the worm was long supposed to belong to the genus *Speophila,* of the family Kenkiidae. However, careful study of the inner musculature of the pharynx showed this musculature to be of the dendrocoelid type. The arrangement of the inner muscle layers of the pharynx is accepted as an absolute distinction between the family Dendrocoelidae on the one hand and the Planariidae and Kenkiidae on the other. Unless one supposes the present worm to form an exception to the rule, one is obliged to place it in the Dendrocoelidae, whereupon a new genus is necessitated.

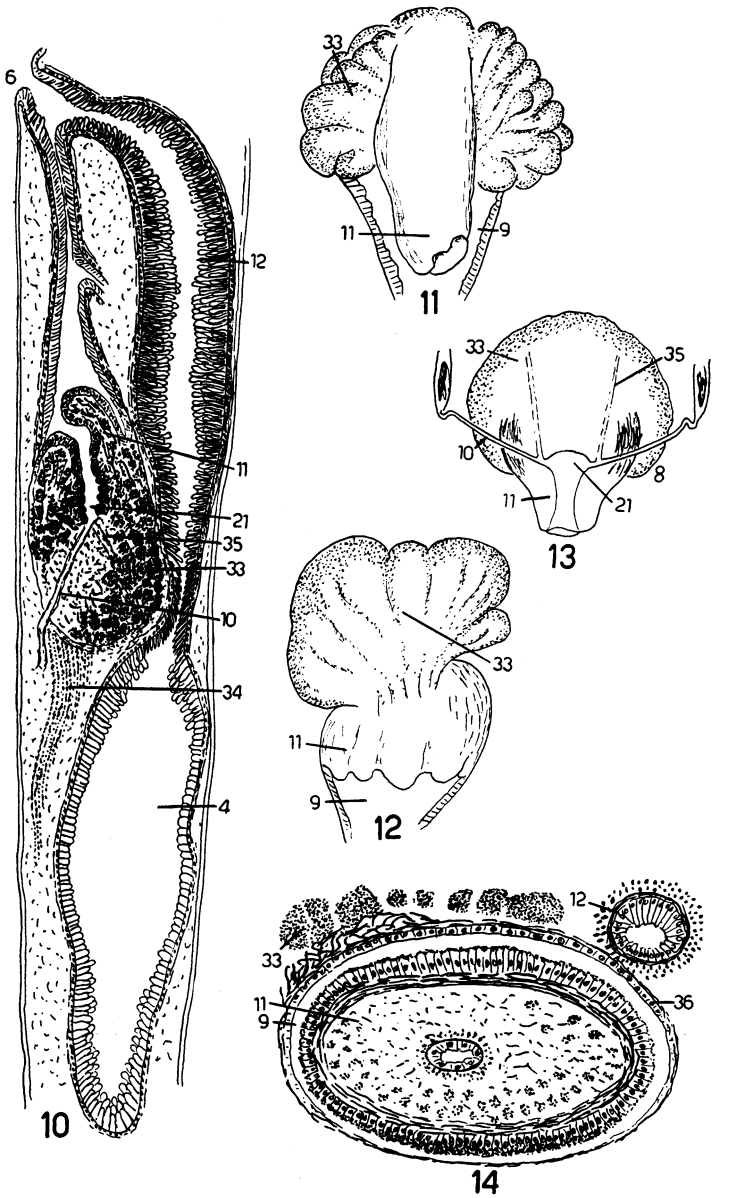
The histology of the inner part of the pharynx wall is illustrated in

figure 9. The pharynx is lined by what appear to be long cilia borne on the usual syncytial anucleate lining epithelium, not separated from the underlying musculature by a basement membrane. The muscular layer consists of the intermingling of circular and longitudinal fibers characteristic of the Dendrocoelidae, whereas in the other two paludicolous families this musculature is separated into distinct circular and longitudinal layers. Especially in tangential sections of the pharyngeal wall the lattice effect produced by the interlacing of the circular and longitudinal fibers is very evident. The muscular zone is followed by the usual glandular layer; this is not cyanophilous as typical of the paludicolous pharynx, but instead stains heavily with hematoxylin and appears as reticulate masses (fig. 9). No other histological peculiarities of the pharynx were noticed.

All specimens are sexually mature. The pair of ovaries is located at a distance from the anterior margin about twice the length of the adhesive organ. The testes are ventrally situated and are limited to the prepharyngeal region (fig. 8). They occur in a pair of lateral bands beginning some distance behind the ovaries and ceasing shortly before the root of the pharynx.

The copulatory apparatus, shown in sagittal view in figure 10, presents striking features. The copulatory sac or bursa is very large and elongated and continues with a slight constriction into an unusually broad bursal canal. Both sac and canal are lined throughout with the same type of bulging epithelial cells, especially prominent in the bursal canal. In transverse sections of the sac this epithelium usually appears shorter dorsally and ventrally and very elongated laterally. The whole female system is unusually muscular, provided with circular fibers next the epithelium, followed by longitudinal fibers. The sac was filled in all sections with a great mass of eosinophilous material, probably part of the male ejaculate. At its distal end the bursal canal curves ventrally, narrows somewhat, and then expands into the terminal chamber that opens below by the common gonopore and receives the male antrum into its anterior wall. The male antrum, lined by a tall epithelium, underlain by circular and longitudinal muscle fibers, proceeds anteriorly, receiving the common ovovitelline duct into its dorsal wall and expands around the penis papilla.

The penis is of very strange construction, unique in my experience, and even after long and intensive study of the four sets of sections I am not certain that I have understood it correctly. The penis bulb is embraced dorsally and laterally by a great mass of eosinophilous material which appears in whole mounts as shown in figures 11 and 12. This mass

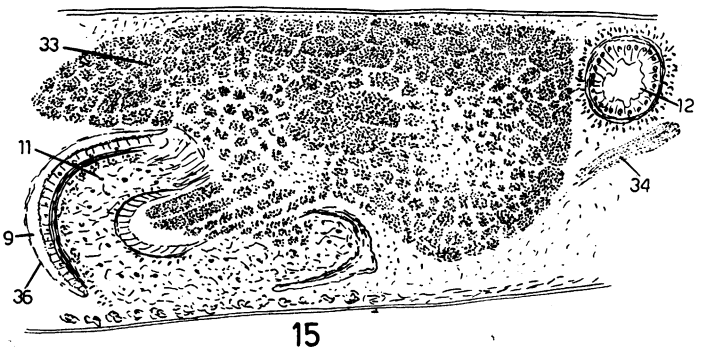


FIGS. 10–14. *Macrocotyla glandularis*. 10. Sagittal view of copulatory apparatus. 11. Penis from whole mount. 12. Penis from another whole mount. 13. Scheme of penis and ducts. 14. Transverse section through the penis papilla.

does not seem to be definitely attached to anything and hence is subject to distortion and displacement as a result of preservation, something that adds to the difficulties of interpretation. The eosinophilous mass appears to have no histological construction but consists simply of granules staining deeply with eosin; it is broken up by fissures into numerous smaller masses of various shapes and sizes. Some sort of arrangement is seen in one small area behind the bulbar lumen (figs. 16 and 17) where the small eosinophilous masses take on a columnar form. The strangest feature about this great eosinophilous mass is that it is provided with a pair of ducts (figs. 16 and 17); each duct begins vaguely in the mass, shortly becomes more definite, and enters the sperm duct of its side just before the latter opens into the bulbar lumen. Figure 13 gives a schematic view of the duct arrangement.

The penis bulb is composed chiefly of a tangle of muscle fibers (figs. 16 and 17) that is traversed by the two sperm ducts. These enter it separately, one from each side near the ventral body wall, and pursue a diagonal course through the bulb (fig. 16) to the small, rounded, bulbar lumen. Just before entering this lumen each sperm duct, as already noted, receives a duct from the eosinophilous mass. However, in only one case was the actual entry of the sperm duct into the bulbar lumen traceable. In the other cases there was direct continuity of the sperm duct with the duct of the eosinophilous mass of that side. This continuity explains the presence of aggregations of sperm along the borders of the eosinophilous mass in all series of sections (figs. 16 and 17). The occurrence of sperm in these locations, not connected with anything, was very puzzling at first, until the ducts leading from the sperm ducts into the eosinophilous mass were discovered. These ducts differ in histological appearance from the sperm ducts, taking a paler stain, and lacking the very definite muscular wall of the latter.

The eosinophilous mass extends posteriorly above the penis papilla (figs. 14 and 15). The latter is relatively short, with a lobulate tip (figs. 11 and 12); hence the lumen may not be terminal, depending on variations of the lobes with fixation (fig. 10). A cross section of the penis papilla enclosed in the male antrum is shown in figure 14. The papilla is covered with a tall epithelium also containing eosinophilous material, and this is underlain by a definite layer of circular muscles. The interior of the papilla also contains a good deal of eosinophilous accumulation, as does also the lower part of the penis bulb (fig. 16). In three of the four series of sections the eosinophilous mass was seen converging into the folds of the penis papilla but not entering the lumen of the latter (fig. 15). It thus appears that this great mass of eosinophilous material dis-



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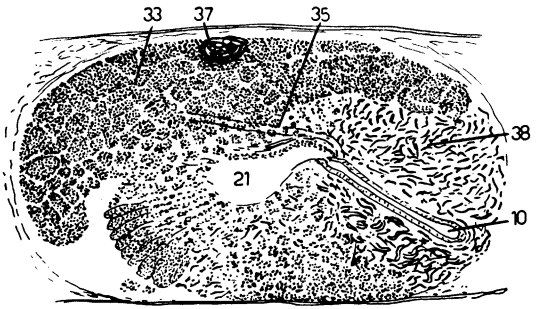

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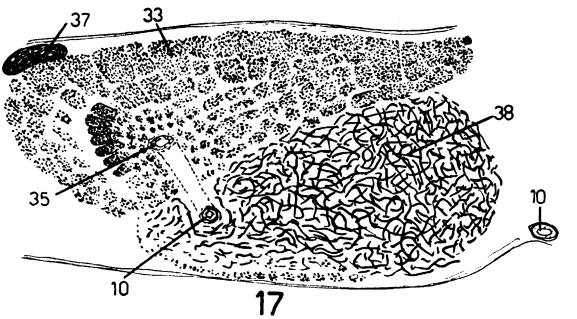

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FIGS. 15–17. *Macrocotyla glandularis.* 15. Transverse section through the level of the penis papilla. 16. Transverse section through the bulbar lumen. 17. Transverse section through the main part of the penis bulb.

charges directly into the male antrum. It can also discharge into the bulbar lumen and so into the lumen of the penis papilla, but no evidence of such discharge was seen.

It is certainly puzzling what can be the purpose of this immense amount of eosinophilous material or whence it comes. There are, to be

sure, the usual streamers of long-necked eosinophilous glands extending away from the male apparatus (a few of these glands are shown in figs. 10 and 15), but they seem inadequate to produce this great mass of granules. That the material is ejaculated at copulation appears evident, because all the copulatory sacs are filled with what certainly seems to be a mass of this material.

Figures 14, 16, and 17 are successive sections from the same series of transverse sections to show the strange structure of the penis. Figure 14 passes through the penis papilla with the posterior part of the eosinophilous mass above it and the bursal canal above and to one side. The bursal canal is omitted from figures 16 and 17. Figure 16 passes through the main part of the eosinophilous mass, and figure 17, more anterior, through the main part of the penis bulb. Figure 15, from another transverse series, shows the eosinophilous mass streaming into the male antrum.

I do not know of anything in the literature with which to compare the copulatory equipment of this species. We have here an outstanding example of the immense variety of morphological expression possible to the few parts that make up the copulatory apparatus of the Turbellaria.

The holotype as a whole mount together with the set of sagittal sections is deposited in the invertebrate section of the American Museum of Natural History.

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