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Source: *Transactions of the American Microscopical Society*, Vol. 50, No. 2 (Apr., 1931), pp. 124-135

Published by: Wiley on behalf of American Microscopical Society

Stable URL: <http://www.jstor.org/stable/3222281>

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STUDIES ON THE MORPHOLOGY, TAXONOMY, AND DISTRIBUTION OF NORTH AMERICAN TRICLAD TURBELLARIA

III. ON POLYCELIS CORONATA (GIRARD)

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Some years ago Professor J. H. Powers of Lincoln, Nebraska, informed me that a species of *Polycelis* was to be found in the streams of the Black Hills of South Dakota. Consequently, during a vacation in this region in the early fall of 1929, during which I searched all streams encountered for planarians, I was not surprised to discover the form in question. A number of specimens were obtained from a stream near Deadwood, South Dakota, and a few days later, the species was again seen in a brook near the State Game Lodge in the southern part of the Black Hills. Many of the specimens secured were in full sexual maturity and, consequently, I am able to furnish a complete description of the species. The arrangement of the eyes leaves little doubt that the form is *Polycelis coronata* (Girard, '91), previously recorded only from Fort Bridger, Wyoming.

The taxonomic history of this species is short and clear. According to Girard ('93, p. 173), the worm was discovered by Leidy on August 3, 1877, in a spring near Fort Bridger, Wyoming. Leidy apparently forbore to name the species but seems to have furnished Girard with some notes concerning it for Girard quotes him as saying that numerous individuals were present, crawling about on the aquatic plants, or feeding with protruded pharynx. I am unable to find that Leidy ever published any statements about the species. The first published description is that of Girard 1891 in which he gave the name *Phagocata coronata* to the animal. The description occupies a paragraph and was not accompanied by any figures. Freely translated, the original account reads as follows: Leidy saw this form in a stream in the neighborhood of Fort Bridger, Wyoming. Its anterior aspect resembles that of *Phagocata gracilis* except that the color is less dark. But whereas the latter possesses only one pair of eyes, *P. coronata* has a large number, disposed in an elongated trail on the periphery of the head and sides of the neck in the form of a diadem. They are less numerous in the young than in the old. Length, 4-8 mm., width $\frac{2}{3}$ to 1 mm. Uniformly brown on the whole body, darker along the median region than on the sides.

In 1893, Girard again described the species, with three figures. The account in much like the foregoing although some additional statements are made concerning the shape of the body and anterior end, to the effect that the body is elongated, lanceolate, with a truncate anterior margin, slightly bilobed or undulating, with moderately developed auricles, and a pointed

posterior end. Of the three figures (Girard, '93, figures 48 to 50, plate V), only one, figure 49, displays correctly the number and distribution of the eyes in fixed specimens. The other two figures, one of which, figure 48, has been copied into Ward and Whipple's *Fresh Water Biology*, p. 359, are apparently somewhat diagrammatic with respect to the disposition of the eyes, for figure 48 is stated to be drawn from the same worm as figure 49, but differs considerably from it in this regard. The number and arrangement of the eyes in Girard's figure 49, which is copied in this paper in figure 2, quite correspond to my fixed preparations and for this reason I consider his and my material identical. The shape of the anterior end in Girard's figures resembles preserved rather than living specimens.

I am unable to find anything in Girard's two accounts to indicate that he ever saw living specimens. One gains the impression, although this is nowhere stated, that his descriptions were based on preserved material obtained from Leidy. His figures give the impression of having been drawn from fixed specimens. The label "from life" attached to the figure copied from Girard into Ward and Whipple's *Fresh Water Biology*, p. 359, is therefore not justified by anything in Girard's text or legends of his figures and must be considered erroneous. The shape of the living animal, particularly of the head, differs somewhat from that presented in these drawings.

Girard placed the worm in the genus *Phagocata* apparently from a resemblance of the contours of the head (in preserved animals) to those of *Phagocata gracilis*. It obviously belongs in the genus *Polycelis*, but I have been unable to determine who first made the transfer. Stringer in *Fresh Water Biology*, p. 359, remarks that it is quite possible, as noted by Hallez, that *P. coronata* is identical with the European *Polycelis nigra*. I have spent some time searching through Hallez' papers but I have been unable to locate any reference to *P. coronata*. In any event, the supposition is incorrect, for an examination of the sexual apparatus of *P. coronata* proves it to be distinct from all other described species of the genus *Polycelis*. The correct name is therefore *Polycelis coronata* (Girard).

At the present time three species of *Polycelis* (sensu strictu) are recognized in Europe for it has recently been shown by Komarek ('27) and Sekera ('27) that *Polycelis tenuis* Iijima is distinct from *P. nigra* (O. F. Müller) with which it had been confused for years. The third species is *P. cornuta* (Johnson). The distinguishing characters of these species may be briefly compared with those of *P. coronata*. In *P. tenuis* the bursa copulatrix (seminal receptacle, uterus) is H-shaped, the penis is long, armed externally with simple hooks, there are two adenodactyls ("muscular gland-organs"), auricles are scarcely evident, and the eyes are arranged in a single row near the margin of the anterior third of the body. In *P. nigra* the auricles and eyes are similar, but the bursa is a simple sac, the penis is shorter and armed with beak-shaped,

forked hooks, and adenodactyls are wanting. *P. cornuta* possesses elongated pointed auricles, an eye arrangement similar to the other species, a sac-like bursa, well-developed penis, and two adenodactyls opening into a pore posterior to the genital pore. In all three European species the penis bulb is small and inconspicuous. The shape of the head and auricles of *P. coronata* is somewhat like that of *P. cornuta*, but the eyes form a band several rows wide which extends only a short distance behind the auricles. The bursa is saccular, there are no adenodactyls, the penis is small and unarmed but the penis bulb is huge and conspicuous, forming the most noticeable part of the genital apparatus.

Attention may again be called to the fact that up to the present time no American triclad has been found to be identical with any European species. It is also a curious phenomenon that none of the American triclads possess those enigmatic structures formerly known as muscular gland-organs and now called adenodactyls.

Kenk ('30 b) has recently proposed to enlarge the genus *Polycelis* by including in its some other genera, particularly *Sorocelis* in part, and to divide the species into two groups, one without adenodactyls (subgenus *Polycelis*) and one with these organs (subgenus *Iijima*). Since *P. coronata* lacks adenodactyls it would be named by this system *Polycelis (Polycelis) coronata* (Girard). Kenk's definition of the genus *Polycelis* is as follows: Planariidae whose oviducts without embracing the stalk of the bursa copulatrix unite to an unpaired duct which opens into the genital atrium; testes extending to the region of the pharynx; masculine portion of the atrium without radial muscle plates; eyes numerous. Our species complies with this definition.

The following description is based on whole mounts and serial sections of material which I collected in the Black Hills and on living specimens sent me by A. C. McIntosh of the South Dakota State School of Mines, to whom I wish here to express my thanks for his courtesy and trouble.

Polycelis coronata (Girard), 1891

Phagocata coronata Girard, 1891, Le Naturaliste 13, p. 80.

Phagocata coronata Girard, 1893, Ann. Sci. Nat. Zool. ser. 7, vol. 15, p. 173.

Polycelis coronata (Girard), Stringer, Fresh Water Biology, p. 359, 1917.

1. **External characters.** The form of the living worm is shown in figure 1. The anterior margin is gently convex. From the sides of the head project broad, rounded auricles, which in life are kept in constant activity and vary greatly in shape. Behind the auricles the body narrows, then widens again, and finally terminates in a rather pointed posterior end. Numerous eyes are present near the anterior margin of the head. In front of the auricles they are irregularly arranged on the anterior margin in a broad curved band several rows wide; the band narrows as it crosses the base of the auricles and extends

for a short distance on each side behind the auricles finally tapering to a single row. The whole arrangement is somewhat irregular and differs from that of the common European species of *Polycelis*, where the eyes are disposed in a single row which extends back almost one third of the body length. The eyes are absent from the auricles. Figure 2 is a copy of Girard's drawing of the head and eyes of *P. coronata*, presumably from a fixed specimen, in which the auricles are somewhat contracted. The eyes are small, black, usually more or less reniform, spots which are not accompanied by a white area. The unusually long pharynx is noticeable in whole mounts or living specimens.

The color is uniform black or very dark brown. Girard records a maximum length of 8 mm. I saw many specimens 15 to 20 mm. long. As these were sexually mature, this may be considered the maximum length.

2. General structure. The specimens were fixed in the field in a saturated solution of corrosive sublimate but the fixation was poor and there was much swelling in the alcohols so that my histological preparations are rather unsatisfactory. I am consequently unable to furnish an exact account of the histological details but these appear to present nothing peculiar or unusual.

The body surface is clothed in a typical epithelium varying from cuboidal to columnar. The dorsal epithelium is taller than the ventral, contains a moderate number of rhabdites, and is everywhere unciliated. The ventral epithelium is more cuboidal than the dorsal, bears fewer rhabdites, and is ciliated at least in part. My preparations are not sufficiently good to enable me to determine the ciliation exactly but they indicate that only the posterior half of the ventral surface is completely ciliated. Anteriorly cilia appear to be lacking ventrally except near the margins, just medial to the zone of adhesive cells. In short, the central anterior part of the ventral surface is probably unciliated. It very much resembles in its histological appearance the dorsal epithelium. There is a well-developed marginal zone of adhesive cells which widens at the head. The auricles are clothed in a beautifully ciliated epithelium which presumably is of the nature of an auricular sense organ.

Under the surface epithelium are the usual layers of circular, diagonal, and longitudinal muscle fibers. The longitudinal layer is particularly wide in the anterior ventral region. Internal to the longitudinal muscle layer occurs a layer of rhabdite-forming cells which are very abundant dorsally. Large numbers of gland cells, which from their taking the aniline blue of Mallory's triple stain, are considered of a mucous nature, occur in the anterior fourth of the body, above, below and around the intestinal diverticula. Posteriorly they decline decidedly in numbers but still occur sparsely throughout the length of the worm near the ventral surface. Intermingled with them are typical heavily granular fuchsinophilic gland cells. In the anterior fourth there also occurs a short longitudinal strip of the large fuchsinophilic cells containing small rod-like bodies which are called *Eiweisszellen* by some Ger-

man workers and which I described and figured in my account of *Procotyla fluviatilis* (Hyman, '28), a species abundantly provided with them.

There is nothing distinctive about the digestive epithelium or the pharynx. The anterior end of the pharynx is situated at about the middle of the body so that the pharynx lies in the posterior half. The pharynx is unusually long. The branches of the intestine do not form longitudinal anastomoses. The two posterior rami embrace first the pharynx and then the large genital complex so that they are practically devoid of branches to their medial sides. Behind the atrium they extend but a short distance and do not unite with each other. The layers of the pharynx wall display the usual arrangement, from the external surface to the lumen; outer epithelium, thin zone of longitudinal muscles, thick layer of circular muscles, zone of nuclei, broad band of gland cells, containing (presumably) a nerve net, wide layer of circular muscles, narrow band of longitudinal muscles, lining epithelium. Kenk ('30 a, b) has attempted what seems to me the most rational classification of the fresh-water triclads yet proposed. He divides them into two families on the basis of the arrangement of the muscle fibers of the inner muscular zone of the pharynx. In the family Planariidae he places those forms in which the circular and longitudinal bands of this zone are distinct, as here described for *Polycelis*. Those forms where the longitudinal and circular muscles of the inner muscular zone of the pharynx are intermingled as in *Procotyla fluviatilis* (Hyman, '28) are placed in the Dendrocoelidae. Kenk states that the systematic importance of the disposition of these muscle fibers was first recognized by Böhmig in 1893.

The excretory system has not been seen.

The nervous system is similar to that of other members of the genus. The brain consists of two elongated ganglia situated at a level a little posterior to the auricles and united with each other by a cross connective. From each cerebral ganglion a strong nerve passes to the auricle of the corresponding side and from the anterior ends of the ganglia nerves proceed to the front margin of the head.

3. Reproductive system. This follows the general plan common to the genus *Polycelis*, that is, the male and female atria are almost separate, there is a common oviduct opening into the male or the common atrium, and the testes do not extend beyond the pharynx. Certain details of the male system are, however, unique to the species.

The general arrangement of the male reproductive system is shown in figure 12, from a whole mount. Figure 13 is a diagrammatic sagittal view of the atrial complex and figures 3 to 11 represent roughly successive transverse sections through this complex.

The testes are ventral and prepharyngeal (figure 12). They occur in two bands, one immediately to each side of the anterior ramus of the intestine.

They begin anteriorly at about the level of the third pair of intestinal diverticula and extend back to the root of the pharynx. They cease at this level. The vasa efferentia and anterior parts of the vasa deferentia were not seen. The vasa deferentia are first noticeable as expanded sinuous tubes (false seminal vesicles), packed with sperm, lying to each side of the pharynx (figure 12). They run posteriorly to the penis bulb in a ventral position shortly above the ventral nerve cords (figure 3).

The penis bulb is the most peculiar feature of this species. It is large and massive and highly muscular, composed chiefly of a thick layer of interlacing muscle fibers which course mostly in a transverse direction. Its cavity, or true seminal vesicle, is large and lined by a tall secretory epithelium. Figures 3 to 6 show successive transverse sections through the penis bulb and figure 13 gives a diagrammatic sagittal view. It is seen that the cavity is small and ventrally situated in the anterior part of the penis bulb, but grows larger and extends dorsally in the posterior part. Its middle part is narrowed laterally so that a cross section presents an hour-glass shape (figure 5). The entrance of the vasa deferentia into the penis bulb is peculiar. The left vas enters the anterior part of the bulb (figure 4), while the right vas enters at about the middle (figure 5) somewhat behind the left one. They enter the bulb at the middle of its lateral surfaces (figure 13). At the posterior end of the penis bulb is the short, broad penis (figures 7 and 13), unarmed externally. It lies in the male atrium (figures 7 and 8, *ma*), which narrows into a tube (figures 9 and 10) leading into the small common atrium (figure 10, *ca*). The male atrium is lined with a secretory epithelium.

The small unarmed penis, the massive penis bulb, and the asymmetrical entrance of the vasa deferentia into the seminal vesicle or lumen of the penis bulb are features peculiar to *P. coronata* and serve to distinguish it from other species of the genus.

The female reproductive system is typical. The paired ovaries occur in the usual anterior position. Each may consist of two or three apparently separate masses, a situation similar to that noted by Iijima ('84) for *Polycelis tenuis*. In some specimens masses of sperm occur in the ampullae of the oviducts which are separated from the ovary by the usual closing plate. The oviducts proceed posteriorly ventral and slightly lateral to the vasa deferentia (figure 3). The left one is below the bursa stalk (figures 6 and 7). At about the level of the penis, the oviducts bend more medially and begin to be accompanied by long-stalked shell glands (figures 7, 9, 10). They lie one to each side of the male atrium (figures 8 and 9) and where the latter enters the common atrium (figure 10) they approach and fuse (figure 11) into a common oviduct which descends ventrally and opens into the dorsal wall of the common atrium (figure 11) to the medial side and a little posterior to the entrance of the male atrium

into the common atrium. The terminal parts of the oviducts and the common oviduct receive numerous shell glands, which presumably secrete the cocoon or egg capsule.

The bursa copulatrix or seminal receptacle (old name, uterus) is an irregularly rounded sac lying between the rear end of the pharynx and the anterior end of the penis bulb (figures 12 and 13, *bc*). It is lined with the usual tall epithelium composed of pyriform cells whose bulbous inner ends, filled with spheres of secretion, project into the lumen. In one whole mount a mass of sperm occurs in the lumen of the bursa, showing that this organ, as in other triclads, receives the sperm at copulation. From the bursa a wide stalk proceeds posteriorly to the left of the penis bulb (figures 3 to 9). It is lined with a secretory epithelium, similar to that of the bursa, taller ventrally than dorsally. Both bursa and stalk are coated externally with muscle fibers. At about the level of the penis (figures 6 and 7), the bursa stalk turns ventrally and becomes larger and somewhat sacculated (figure 13). Beyond these sacculations, the bursa stalk enters the female atrium or vagina (figures 9 and 10), characterized by a narrow lumen and thick muscular walls. This proceeds ventrally and unites with the terminal part of the male atrium (figure 10), to form a small chamber, the common atrium (figures 10 and 11), which receives dorsally, between the vagina and male atrium, the common oviduct, and opens ventrally by the genital port. No glands were observed around the common atrium or genital pore. Throughout its course the bursa stalk lies to the left of the penis bulb and the vagina to the left of the male atrium. This could not be shown in the diagrammatic figure 13 but appears clearly in the series of transverse sections, figures 3 to 11.

4. Natural history. The worms were found in flowing streams in the hills in the Black Hills of South Dakota. They were seen crawling actively about on the bottom among and on the stones and resting on the under surface of the stones. One of these streams was traced for some distance and was found to disappear into the ground, from which one may suppose it to be spring-fed. The species seems to be an unusually active one for planarians are ordinarily, during the daytime at least, concealed on vegetation or under stones, but these were crawling around in plain sight on the bottom of the stream. The streams in which the worms were found contained no vegetation.

Many of the worms taken in the stream near Deadwood were sexually mature. The date of collection was August 30, 1929, but of course it cannot be stated that sexual reproduction is limited to that time of the year. Some living specimens received immediately after collection in January from A. C. McIntosh of Rapid City, South Dakota, were devoid of sex organs. At the time when the sexually mature worms were collected search was made for cocoons on the stones in the stream but none were found. Probably, as in other species

of *Polycelis*, the cocoons are unstaked and hence fall to the bottom. There were no indications of the occurrence of fission.

Copulation was not observed but from the fact that sperm are present in the bursa copulatrix of one specimen, it may safely be inferred that as in other triclads the bursa receives the ejaculate at copulation. In some of the sectioned series, sperm are absent from the bursa but are present in a mass at the head of each oviduct (ampulla of the oviduct). This concurs with the present well-established view that the sperm do not remain in the bursa but travel along the oviducts to their anterior ends where fertilization occurs as the eggs leave the ovaries.

The distribution is uncertain as the only records are the old one from Fort Bridger, Wyoming, and the present record from the Black Hills, South Dakota. One may expect that the species will be found in streams throughout the lower parts of the Rocky Mountains. Elevation of South Dakota localities, about 3,000 feet.

5. **Summary** a. The North American representative of the many-eyed triclad genus *Polycelis* is distinct from European or other members of the genus. Its correct name is *Polycelis coronata* (Girard), 1891.

b. Its distinctive characters are: eyes in a broad short band, several rows wide, extending only a short distance behind the auricles; bursa copulatrix saccular; penis bulb massive and muscular; penis small, unarmed; vasa deferentia entering the cavity of the penis bulb separately and asymmetrically, the left one anterior to the right one; common oviduct opening into the dorsal wall of the small common atrium; terminal part of the bursa stalk highly muscular.

c. Distribution: mountain streams, in some cases spring-fed, Wyoming, South Dakota.

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PLATE XII

- FIG. 1. *Polycelis coronata*, from life.
- FIG. 2. Head of *Polycelis coronata*, showing eyes. Copied from Girard, 1893, plate V, fig. 49.
- FIGS. 3 to 11. Successive transverse sections through the genital region to show the parts and their relations.
- FIG. 3. Cross section through the anterior end of the penis bulb. The penis bulb, *pb*, occupies the center of the section. It is highly muscular. Its cavity, the seminal vesicle, *sv*, lies in its ventral part. To either side of the penis bulb are seen the vasa deferentia, *vd*, the oviducts, *o*, and the ventral nerve cords, *nc*. Above and to the left (apparent right in the sections) is seen the stalk of the bursa copulatrix (*bs*).
- FIG. 4. Section showing the entrance of the left vas deferens, *vd*, into the penis bulb.
- FIG. 5. Section through the middle of the penis bulb, *pb*, showing the entrance of the right vas deferens, *vd*. Note hourglass shape of the seminal vesicle, *sv*. Bursa stalk, *bs*, above and to the left of the penis bulb.
- FIG. 6. Section through the posterior end of the penis bulb. Bursa stalk, *bs*, curving ventrally, *o*, oviducts.
- FIG. 7. Section through the penis, *p*, showing also the posterior end of the penis bulb, *pb*. The penis projects into the cavity of the male atrium, *ma*, to either side of which is an oviduct, *o*, the left one accompanied by shell glands. Ventral curve of the bursa stalk, *bs*, to the left of the penis.
- FIG. 8. Extreme posterior end of penis bulb, showing also penis, *p*, *o*, oviducts, *ma*, male atrium, *fa*, beginning of the vagina or female atrium.

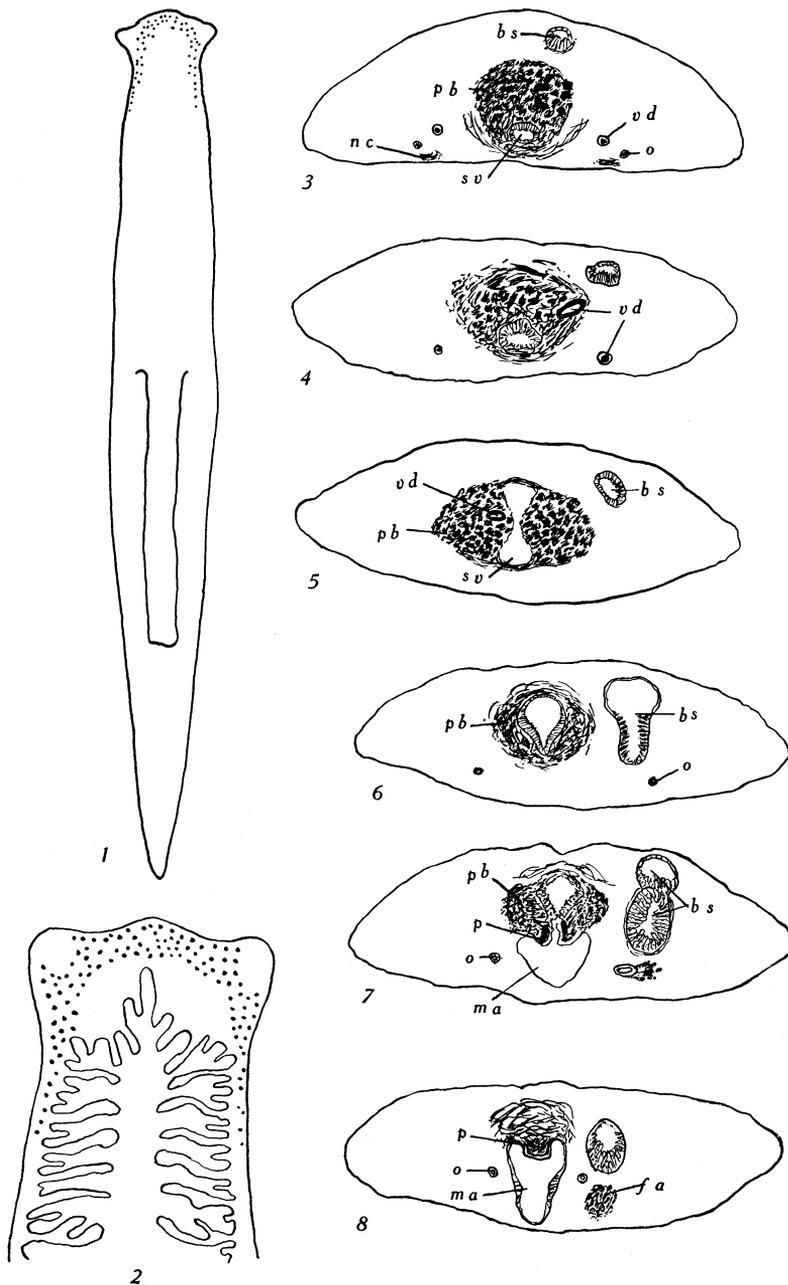


PLATE XII

PLATE XIII

- FIG. 9. Entrance of the bursa stalk, *bs*, into the female atrium, *fa*. Male atrium, *ma*, curving ventrally. Oviducts, *o*, to either side of the male atrium, accompanied by shell glands.
- FIG. 10. Junction of male atrium, *ma*, and female atrium, *fa*, to form the common atrium, *ca*, which opens ventrally by the genital pore. Note highly muscular walls of the female atrium. *o*, oviducts, accompanied by shell glands, *gl*.
- FIG. 11. Union of the oviducts, *uo*, to form the common oviduct, *co*, which enters the roof of the common atrium, *ca*. *gl*, shell glands, *gp*, genital pore.
- FIG. 12. Digestive and reproductive systems of *Polycelis coronata*, from a whole mount, ventral view. *bc*, bursa copulatrix, containing a mass of sperm; *bs*, bursa stalk; *e*, eyes; *gp*, genital pore; *pb*, penis bulb; *t*, tests; *vd*, vas deferens.
- FIG. 13. Diagrammatic sagittal view of the genital complex. Simple cross-hatching indicates glandular epithelium; diagonal cross-hatching in two directions indicates muscle layers. *bc*, bursa copulatrix; *bs*, stalk of the bursa copulatrix; *ca*, common atrium; *co*, common oviduct; *fa*, female atrium or vagina; *ma*, male atrium; *o*, oviducts; *p*, penis; *pb*, penis bulb; *sv*, seminal vesicle; *vd*, vasa deferentia.

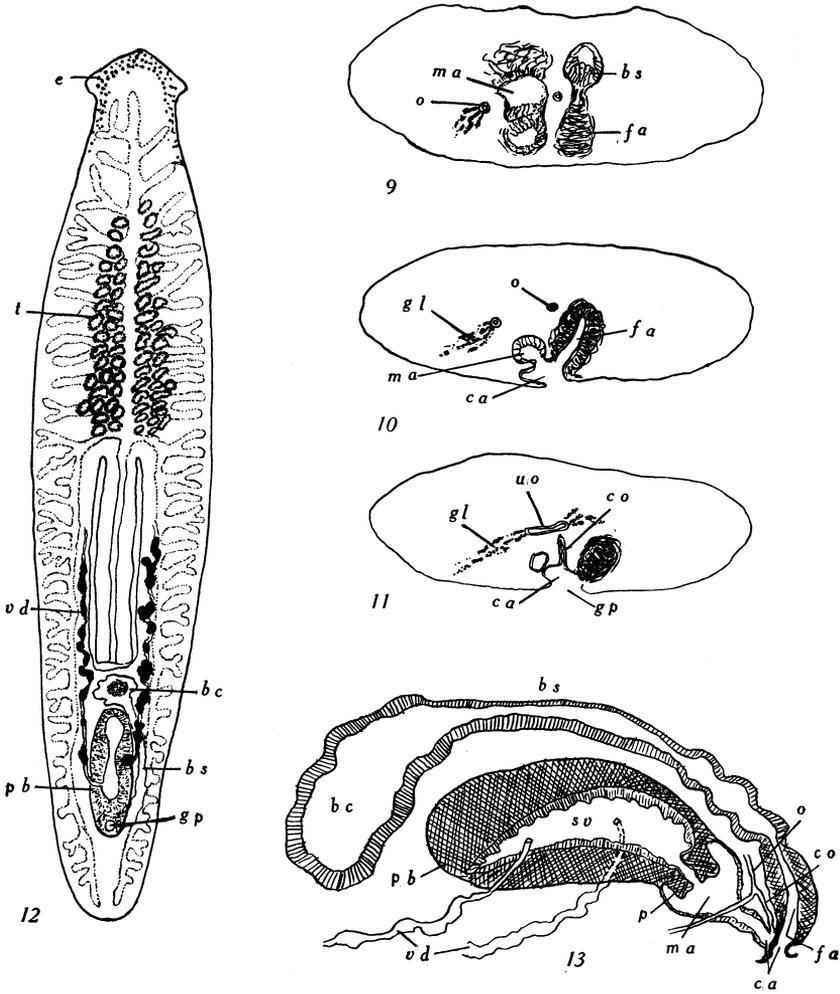


PLATE XIII