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Vorticeros praedatorium sp. nov. (Platyhelminthes: Prolecithophora: Plagiostomidae) from the Pacific coast of North America

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Abstract: *Vorticeros praedatorium* sp. nov. is described from Friday Harbor, Washington. This prolecithophoran feeds on ooecia of *Bugula californica* and *Dendrobeania lichenoides*, and deposits its egg capsules on colonies of these bryozoans. The only *Vorticeros* whose morphology has been described carefully is *V. pulchellum*, found at various localities in the Adriatic. It has been synonymized under *Vorticeros auriculatum,* known from the North Atlantic region, but until the morphology of *V. auriculatum* has been studied in detail, it is best to recognize *V. pulchellum* as a valid species. *Vorticeros praedatorium* differs from *V. pulchellum* in three major respects. It has only one penis sheath, instead of two; its seminal vesicle consists of two successive chambers; its two ovovitelline ducts do not unite to form a common duct, but enter the genital atrium separately.

Résumé : Vorticeros praedatorium *sp. nov. (Platyhelminthes: Prolecithophora : Plagiostomidae) de la côte Pacifique d'Amérique du Nord. Vorticeros praedatorium* sp. nov., abondant à Friday Harbor, Washington, est décrit. Ce prolécithophore se nourrit des ooécies de *Bugula californica* et *Dendrobeania lichenoides*, et les capsules d'œufs sont déposées sur les colonies de ces Bryozoaires. La seule espèce de *Vorticeros* décrite avec soin est *V. pulchellum*, des localités de l'Adriatique. Cette espèce a été mise en synonymie avec *V. auriculatum* de l'Atlantique Nord, mais tant que la morphologie de cette dernière espèce n'a pas été étudiée en détail, il paraît prudent de considérer *V. pulchellum* comme une espèce valide. *Vorticeros praedatorium* se distingue de *V. pulchellum* par trois caractères. Il possède une seule gaine péniale, au lieu de deux; sa vésicule séminale est composée de deux chambres successives ; ses deux canaux ovovitellins ne s'unissent pas, mais entrent séparément dans l'atrium génital.

Keywords: Platyhelminthes, Turbellaria, Prolecithophora, *Vorticeros*, North America

Introduction

The genus *Vorticeros* was established by Schmidt (1852) for a flatworm he named *V. pulchellum* Schmidt (1852). This was found at Lesina, Italy, located on the shore of Lago di Lesina, a saltwater lagoon joined by narrow channels to the Adriatic Sea. Originally placed in the now obsolete order Rhabdocoela, *Vorticeros* belongs to the order Prolecithophora Karling (1940), an assemblage usually characterized by poorly delimited gonads, vitellaria that are indistinctly separated from the ovaries, and absence of a statocyst. The genus is assigned to the family

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Plagiostomidae Graff (1907, in Graff, 1904-08), and is close to *Plagiostomum* Schmidt (1852), the type genus, from which it differs in having a pair of conspicuous cephalic tentacles. *Auriculifera rectata* Kulinich (1973) has two bristly, anteriorly directed lobes, but these do not closely resemble the tentacles of *Vorticeros*. This worm is also decidedly unlike *Vorticeros* with respect to several other morphological details. Its genital pore, for instance, is located at the posterior tip of the body, and its genital atrium is entered by a ductlike prolongation of the intestine.

Graff (1874) observed what he believed to be *Vorticeros pulchellum* at Messina (Sicily) and elaborated on some aspects of its morphology. Later, after Graff (1882) had decided that it was the same species as Müller (1784, 1788 [first illustration]) had found in Denmark and named *Planaria auriculata*, he proposed the combination *Vorticeros auriculatum*. Graff, however, presented no evidence that he had studied *Vorticeros* from waters of northern Europe. It therefore seems best to deal with *V. pulchellum* as a separate species, even though Böhmig (1890), in his detailed study of material from Trieste, followed Graff in using the name *V. auriculatum*.

In a paper concerned mostly with flatworms from North America, Graff (1911) reported finding what he believed to be *Vorticeros "auriculatum*" at Ancona, which is about halfway between Lesina and Trieste. In later publications (1904-1908, 1913), he dealt again with *V. "auriculatum*", but there is nothing in these works to indicate that he had made further observations on specimens from any locality.

Westblad (1956) published a short account of what he assumed to be *Vorticeros auriculatum*. He showed no concern for some discrepancies between his observations and those of Böhmig. Furthermore, some of his material came from northern Europe (west coast of Sweden, Isle of Man), and some came from the Adriatic (Dubrovnik), so there is a possibility that he was dealing with both *V. pulchellum* and *V. auriculatum*.

Other complications entered the systematics of the genus *Vorticeros* when Hallez (1879a, 1879b) proposed the name *V. pulchellum* var. *luteum* for bright yellow specimens he found at Wimereux, France. Graff (1882), after having encountered a yellow *Vorticeros* in the Adriatic and at Naples, raised *luteum* to the rank of species. According to Graff (1882, 1904-08, 1913), it differs from *V. "auriculatum*" not only in color (chrome-yellow, rather than red), but also in being larger (up to 8 mm long, instead of only 5 mm), more plump, and with proportionately shorter tentacles. It should be noted, however, that Hallez' specimens of *luteum* were no more than 3 mm long, and that he did not mention shape or tentacle length in his preliminary note (1879a), slightly more formal description (1879b), or catalogue of free-living flatworms of northern France (1894).

Records for the occurrence of worms tentatively referable to *V. luteum* are not so numerous or widespread as those for *V. "auriculatum*," but they include Plymouth (Gamble, 1893) as well as Wimereux and localities in the Mediterranean and Adriatic. Steinböck (1933) found what he assumed to be *V. auriculatum* and *V. luteum* in the vicinity of Rovinj (Rovigno), on the northeastern portion of the Adriatic, and cited a few localities based on records from other surveys. A recent paper on a worm thought to be *V. luteum* is that of Nigro and Gremigni (1987), who reported only on ultrastructural aspects of oogenesis; their material was collected subtidally at unspecified localities in the Mediterranean.

For a violet-red worm found at Wimereux, Hallez (1879a, 1879b) proposed the name *Vorticeros schmidtii*. He stated that it lacked tentacles and that its eyes and eggs were different from those of *V. pulchellum*. Graff (1882), however, believed it to be the same as *V. "auriculatum."* Although Böhmig (1890) questioned Graff's decision, Hallez, in his catalogue of flatworms (1894), accepted it. He stated that worms in water of poor quality may have been reluctant to extend their tentacles. He did not deal again with characteristics of the eggs, but he did state that specimens collected subtidally at some distance from the coast had eyes typical of *V. "auriculatum*" and that the pigment in the eyes of specimens collected at the shore was conspicuously constricted near the middle. Specimens from the shore, moreover, had a brown triangle between the eyes, the apex of the triangle reaching to the anterior end of the body. This patch of pigment was lacking in specimens collected subtidally. Until there is solid information about the morphology of the various specimens observed by Hallez, it is pointless to speculate about their identity and about the validity of Graff's contention that *V. schmidtii* is a junior synonym of *V. auriculatum*.

Another species that can definitely be assigned to *Vorticeros* is *V. ijimai* Tozawa (1918), found at the Misaki Marine Station, Kanagawa Prefecture, Japan. Kulinich (1979) studied some aspects of the morphology of what he thought to be *V. ijimai*. His material was collected at Antonovo, Sakhalin Island, and also in the Bay of Peter the Great. The prolecithophoran Tozawa (1918) described as *V. lobatum* lacks tentacles of the sort characteristic of the genus *Vorticeros* and therefore is more logically assigned to *Plagiostomum*. A similar worm found at Sakhalin and Kunashir islands and in the Bay of Peter the Great was described by Kulinich (1979) as *Plagiostomum lobatum* subsp. *kurilense*.

Two South American species, *Vorticeros cyrtum* (and its forma *amomum*) Marcus (1947) found in Brazil, and *V. dahli* Marcus (1954) collected in Chile, are probably distinct from all those already mentioned; *V. cyrtum* forma *amomum,* in fact, has such distinctive coloration that it may

also prove to be a separate species if its morphology is carefully studied. Unfortunately, even if the original descriptions and illustrations given by Marcus may enable zoologists in Brazil and Chile to recognize the worms he named, they are not detailed enough to permit close comparison with Böhmig's study of *V. pulchellum*.

The worm described by Riedl (1959) as *Vorticeros rudis* seems definitely to lack tentacles, and it is here excluded from *Vorticeros.* Perhaps this species, like *P. lobatum* of Tozawa, can be placed in *Plagiostomum*, but this decision must be left to a specialist who has a comprehensive knowledge of plagiostomid genera.

It should now be obvious that we need a careful comparative study of *Vorticeros pulchellum* from the Adriatic and of *V. auriculatum* from localities in Scandinavia. This will establish that *V. auriculatum* and *V. pulchellum* are identical or that they are separate species. Next in importance would be a redescription of *Vorticeros luteum* based on specimens collected at or near Wimereux, and a determination of the affinities of yellowish Mediterranean *Vorticeros* with genuine *V. luteum*, as well as with *V. pulchellum* and *V. auriculatum*.

A *Vorticeros* abundant at Friday Harbor, Washington, will be described here as a new species. It deviates decidedly from Böhmig's description *of V. pulchellum,* and also from Westblad's account of what could be *V. auriculatum* or *V. pulchellum*, or a mixture of both. In the absence of comparative material from Europe and the northwestern Pacific, giving the worm found at Friday Harbor an adequate description will at least enable zoologists who are certain they are working with this species to refer to it with a reliable name.

Material and methods

All material was collected on floating docks at Friday Harbor Laboratories on San Juan Island, Washington. The first specimens were obtained by vigorously swirling algae in buckets of sea water, pouring the water into dishes, then locating worms crawling on the bottom. After it was observed that this species is closely associated with the bryozoans *Bugula californica* Robertson, 1905 and *Dendrobeania lichenoides* (Robertson, 1905) (*Flustra lichenoides*), colonies of these were examined for the presence of *Vorticeros*. For the study of living specimens, these were quieted by addition of an isotonic solution of magnesium chloride. Specimens to be embedded in paraffin and sectioned were relaxed in the same way, then fixed in Bouin's fluid. Sections were cut at 6, 8, or 10 μm and stained with iron hematoxylin, sometimes counterstained with fast green. Sudan III and neutral red were used to a limited extent for staining fresh material.

Description

Vorticeros praedatorium sp. nov.
Figs 1-19

Type locality
Washington, San Juan Island, Friday Harbor, Friday Harbor Laboratories.
Type material
Holotype: USNM 187110. A set of serial frontal sections of a mature specimen.
Paratype: USNM 187111. A set of serial transverse sections of a mature specimen. Washington, San Juan Island, Friday Harbor, Friday Harbor Laboratories.

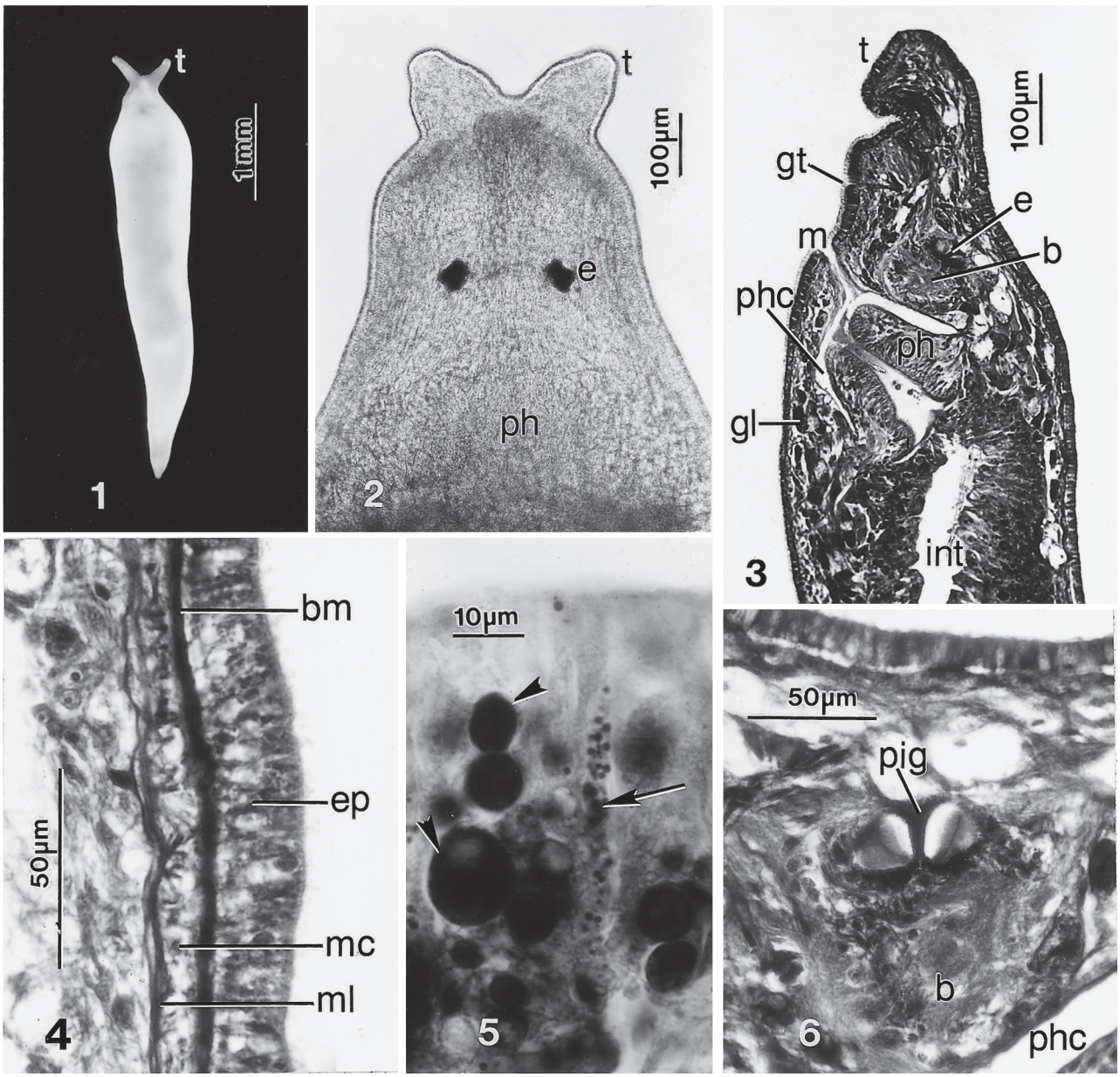
Other material deposited: USNM 187112, twenty-five entire specimens, fixed in Bouin's fluid, stored in 70% alcohol, for sectioning and study by future investigators concerned with systematics of species of *Vorticeros*.
Etymology. The species name is derived from Latin *praedatorius*, predatory.

Description
The body (Figs 1, 7) is elongated, attenuated at the posterior end, usually widest near the end of the first fifth and about as high as wide. Two tentacles originate dorsolaterally at the anterior end, and behind them are two prominent eyespots (Fig. 2). The largest specimens observed were 5.5 mm long, 1 mm wide when extended and crawling on a glass surface. The tentacles of such individuals were about 0.8 mm long when fully extended.

The color is usually pinkish orange or brownish orange, but some specimens, especially those less than 2 mm long, are whitish or nearly clear yellow; almost all of the color is concentrated in the intestine, but flattened specimens, when examined with transmitted light, often show a faint tinge of pink in tissue peripheral to the intestine.

The epidermis is ciliated over the entire body, and rich in rhabdites. The largest of these are about 6.5 μm long, 1 μm wide. Beneath the epidermis (Fig. 4), there is a prominent basement membrane, then a layer of circular muscle and a layer of longitudinal muscle. In the parenchyma there are scattered muscles whose orientation is more or less longitudinal, transverse, dorsoventral, or oblique. Muscles of the pharynx and reproductive organs will be dealt with in connection with these structures.

Gland cells whose ducts extend to the surface (Figs 3, 17) are abundant close to the epidermis of nearly all areas of the body. Other glands not closely associated with the pharynx or reproductive organs are those in the head region, which open ventrally near the anterior tip of the body, and those at the posterior end, whose secretion enables a worm to cling tightly to a firm substratum. On the ventral side of the head, anterior to the mouth, there is a conspicuous transverse ciliated groove (Figs 3, 7) entered by ducts from a substantial complex of glands.

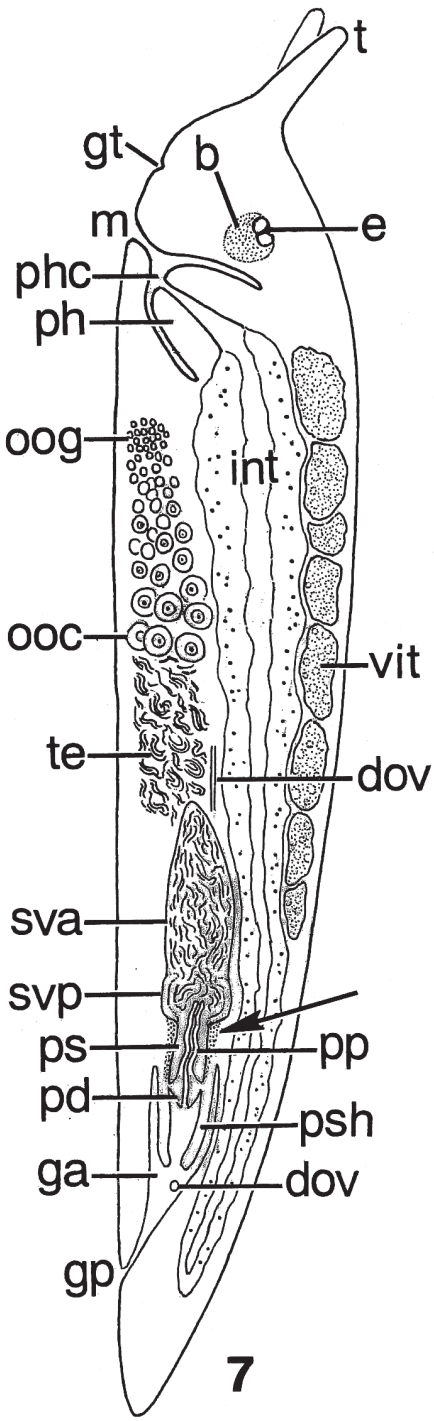


Figures 1-6. *Vorticeros praedatorium* sp. nov.; photomicrographs.

1. Living specimen about 4 mm long, in reflected light, dorsal view. **2**. Anterior portion of specimen about 2.5 mm long, slightly flattened, dorsal view. **3**. Anterior portion of nearly mature specimen, sagittal section. **4**. Dorsal epidermis and underlying tissues, sagittal section. **5.** Epithelium of intestine, transverse section, showing large inclusions (*arrowheads*) and concentration of small granules (*arrow*). **6.** Brain and eyespots. (*b*) brain; (*bm*) basement membrane; (*e*) eyespot; (*ep*) epidermis; (*gl*) subepidermal glands; (*gt*) transverse groove; (*int*) intestine; (*m*) mouth; (*mc*) circular muscle; (*ml*) longitudinal muscle; (*ph*) pharynx; (*phc*) pharyngeal cavity; (*pig*) pigment enclosing lenses of eyespots; (*t*) tentacle.

Figures 1-6. *Vorticeros praedatorium* sp. nov.; photomicrographies.

1. Spécimen vivant, vue dorsale. **2**. Partie antérieure d'un petit spécimen, légèrement comprimé. **3**. Partie antérieure d'un spécimen presque mûr, coupe sagittale. **4**. Epiderme dorsal et tissus sous-jacents, coupe sagittale. **5.** Epithelium intestinal, coupe transversale, montrant les grandes inclusions (*têtes de flèches*) et une concentration des petits granules (*flèche*). **6**. Cerveau et taches oculaires. (*b*) cerveau, (*bm*) membrane basale ; (*e*) tache oculaire; (*ep*) épiderme ; (*gl*) glandes sous-épidermiques. (*gt*) sillon transversal ; (*int*) intestin ; (*m*) bouche ; (*mc*) muscles circulaires ; (*ml*) muscles longitudinaux ; (*ph*) pharynx ; (*phc*) cavité pharyngienne ; (*pig)* pigment enveloppant les lentilles des taches oculaires ; (*t*) tentacule.

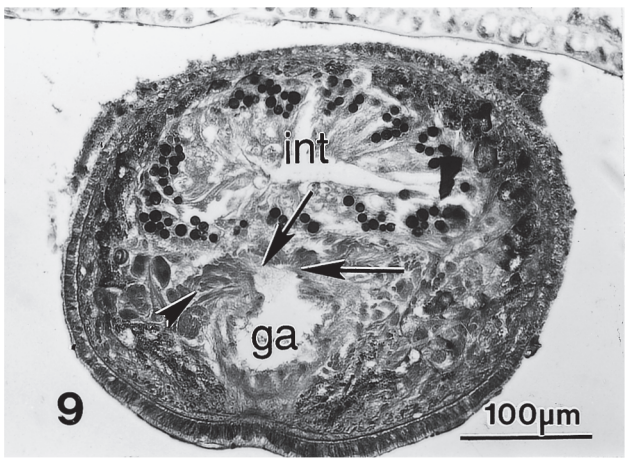


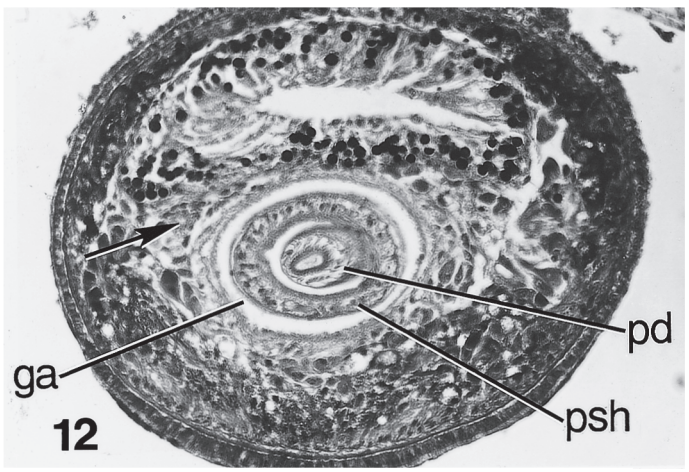
Figures 7-8. *Vorticeros praedatorium* sp. nov. **7**. Semidiagrammatic representation, based on sections, of reproductive system and some other structures, viewed from left side. The brain, pharynx, intestine, vitellarium, posterior portion of the testis, and copulatory organs are shown as they appear in sagittal sections on the midline. The left ovovitelline duct is lateral to the copulatory organs, so only an anterior portion and the entry of the duct into the genital atrium are shown. **8.** Sperm. (*b*) brain; (*dov*) left ovovitelline duct; (*e*) eyespot; (*ga*) genital atrium; (*gp*) genital pore; (*gt*) transverse groove; (*int*) intestine; (*m*) mouth; (*ooc*) oocytes; (*oog*) oogonia; (*pd*) distal portion of penis; (*ph*) pharynx; (*phc*) pharyngeal cavity; (*pp*) proximal portion of penis; (*ps*) penis sac; (*psh*) penis sheath; (*sva*) anterior chamber of seminal vesicle; (*svp*) posterior chamber of seminal vesicle; (*t*) tentacle; (*te*) testis; (*vit*) vitellarium.

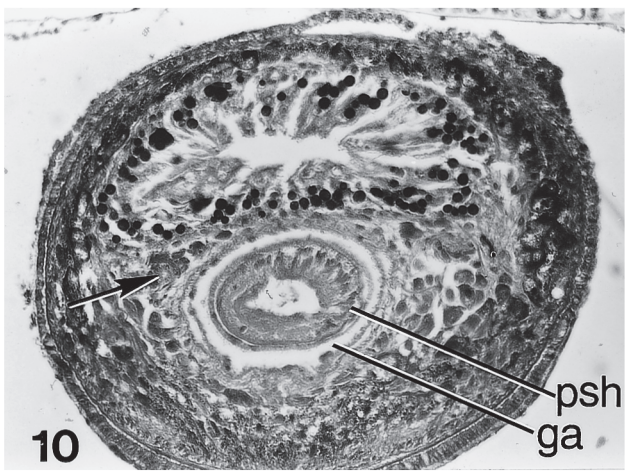
Figures 7-8. *Vorticeros praedatorium* sp. nov. **7**. Schéma, d'après des coupes, montrant le système reproducteur et quelques autres structures, vue du côté gauche. Cerveau, pharynx, intestin, et appareil copulateur sont mis en évidence tels qu'ils sont sur des coupes sagittales. Le canal ovovitellin gauche est latéral à l'appareil copulateur, donc seulement une portion antérieure et l'entrée du canal dans l'atrium génital sont montrées. **8**. Spermatozoïde. (*b*) cerveau ; (*dov*) canal ovovitellin gauche ; (*e*) tache oculaire ; (*ga*) atrium génital ; (*gp*) pore génital ; (*gt*) sillon transversal ; (*int*) intestin ; (*m*) bouche ; (*ooc*) ovocytes ; (*oog*) oogonies ; (*pd*) portion distale du pénis ; (*ph*) pharynx ; (*phc*) cavité pharyngienne; (*pp*) portion proximale du pénis ; (*ps*) sac du pénis ; (*psh*) gaine du pénis ; (*sva*) chambre antérieure de la vésicule séminale ; (*svp*) chambre postérieure de la vésicule séminale ; (*t*) tentacule ; (*te*) testicule; (*vit*) glande vitellogène.

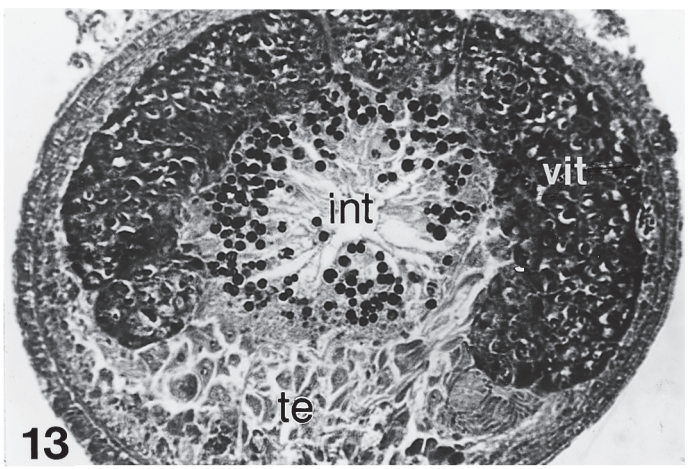
The thin epithelium (probably insunk, but this not definitely determined) of the pharyngeal cavity is not ciliated. The rather well developed musculature beneath its basement membrane consists mostly of longitudinal fibers; distinctly circular fibers are relatively few. The prominence of longitudinal muscle suggests that protrusion of the pharynx for feeding is aided by shortening of the pharyngeal cavity by action of the predominately longitudinal muscles. The pharynx, when retracted (Figs 3, 7) is about as wide as long. The thin, apparently insunk epithelium lining its lumen, and a portion of its external epithelium near the tip, are ciliated. The muscles closest to the pharyngeal epithelia are longitudinal; circular muscles are slightly deeper. The pharynx also has abundant transverse muscles; these are presumed to function as dilators. Gland cells whose ducts empty into the lumen are located at varying distances from the lumen.

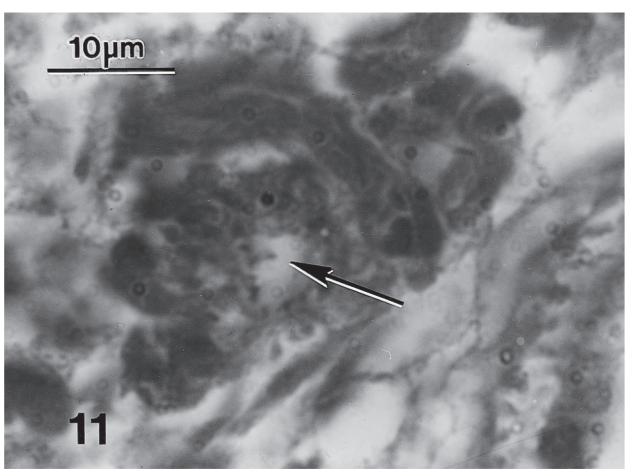
The pharynx leads directly to the intestine (Figs 3, 7, 9, 10, 12-16), which occupies a considerable portion of the body and reaches nearly to the posterior end. In a small or medium-sized live specimen that has been flattened, it usually shows some obvious lateral diverticula. The cells that form its epithelium are tall and slender. Spherical intracellular bodies, mostly about 4 µm to 15 µm in diameter are conspicuous in the intestinal epithelium (Fig. 5). In fresh preparations, these bodies stain faintly with Sudan III, indicating a slight lipid content; in paraffin sections, they stain darkly with hematoxylin, and most of them are vacuolated. The significance of these bodies is not known. Some cells of the epithelium have concentrations of

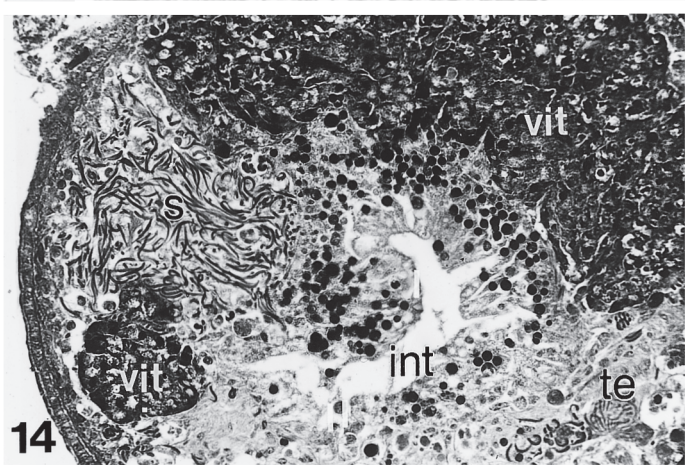












small granules (Fig. 5) that perhaps represent a secretory product, as Böhmig proposed in connection with his description of similar cells in the intestinal epithelium of *V. pulchellum*.

The brain, just anterior to the pharyngeal cavity, is not conspicuous in living specimens, but is prominent in sections (Figs 3, 6, 7). Its structure has not been studied in detail, but appears to conform closely to that of the brain of *V. pulchellum* as described by Böhmig. Each eyespot, in the dorsal ganglion cells of the brain, consists of two lenses embedded in a mass of blackish pigment (Fig. 6).

The testis (Figs 7, 13-16) is a substantial mass beneath the intestine. It begins a short distance behind the pharynx to just beyond the middle of the body length. Clusters of

Figures 9-14. *Vorticeros praedatorium* sp. nov., paratype; photomicrographs of transverse sections (8 µm). All figures, except Fig. 11, are to the scale shown on Fig. 9, and are arranged from posterior to anterior. **9**. Section through genital atrium, showing entrance of left ovovitelline duct, location of entrance of right duct in adjacent section (*arrows*), and glands concerned with formation of egg capsules (*arrowhead*). **10**. Section through genital atrium and posterior portion of penis sheath; (*arrow*) indicates left ovovitelline duct (right ovovitelline duct, sectioned obliquely, not distinct). **11**. Left ovovitelline duct of section shown in Fig. 10. **12**. Section through genital atrium, distal portion of penis, and penis sheath; (*arrow*) indicates left ovovitelline duct. **13**. Section through posterior portion of testis. **14.** Section slightly anterior to ovaries, showing mass of sperm between follicles of vitellarium. (*ga*) genital atrium; (*int*) intestine; (*pd*) distal portion of penis; (*psh*) penis sheath); (*te*) testis; (*vit*) vitellarium.

Figures 9-14. *Vorticeros praedatorium* sp. nov., paratype ; photomicrographies des coupes transversales (8 µm). Toutes les figures, sauf Fig. 11, sont à la même échelle que Fig**.** 9. **9.** Coupe à travers l'atrium génital, l'entrée du canal ovovitellin gauche, l'emplacement de l'entrée du canal ovovitellin droit dans la coupe sous-jacente (*flèches*), et les glandes coquillières (*tête de flèche*). **10**. Coupe à travers l'atrium génital et la gaine du pénis. **11**. Canal ovovitellin gauche de la coupe montrée en Fig. 10. **12**. Coupe à travers l'atrium génital, la portion distale du pénis, et la gaine du pénis. **13**. Coupe à travers la portion postérieure du testicule. **14**. Coupe juste en arrière des ovaires, montrant une masse de spermatozoïdes entre les follicules de la glande vitellogène. (*ga*) atrium génital ; (*int*) intestin ; (*p*) pénis ; (*pd*) portion distale du pénis ; (*psh*) gaine du pénis ; (*s*) spermatozoïdes ; (*te*) testicule ; (*vit*) glande vitellogène.

mature sperm are most conspicuous in lateral areas of the posterior portion (Figs 13, 14). Although the testis may develop as two separate testes that later become united, there is no evidence for this in mature specimens.

The ovaries begin as small clusters of oogonia lateral to the anterior part of the testis (Figs 7, 16). As the oogonia are displaced posteriorly, they grow into large oocytes concentrated slightly anterior to the middle of the body length (Figs 7, 15, 16). Thus although the ovaries become more prominent posteriorly, they do not reach as far posteriorly as the testis does.

The vitellarium (Figs 7, 13-16) consists of a loosely organized mass of follicles. From the portion that is above the intestine, lateral lobes of the vitellarium reach down nearly to the gonads.

The common genital pore (Fig. 7), on the ventral surface close to the posterior end of the body, opens into the genital atrium (Figs 7, 9-11, 17). The sequence of basement membrane, circular muscle, and longitudinal muscle beneath the epithelium of the atrium is the same as that beneath the epidermis; this arrangement is also characteristic of the penis and penis sheath, a tubular structure that envelops the penis.

The distal portion of the penis, directed posteriorly, forms a short cone that is bound to the wall of the penis sheath (Figs 7, 17). The proximal portion of the penis is relatively long and slightly coiled, and extends anteriorly through the penis sac (Figs 7, 17, 18) into the posterior chamber of the seminal vesicle. This cavity, usually containing at least some sperm, has a broad opening into the anterior chamber of the seminal vesicle (Figs 7, 17), which typically is completely filled with sperm.

In the wall of the penis sac, especially its anterior half, there is a thick layer of circular muscle just beneath the epithelium (Fig. 7); longitudinal muscle is here external to circular muscle. In the proximal portion of the penis, longitudinal muscle is well developed, but circular muscle is inconspicuous.

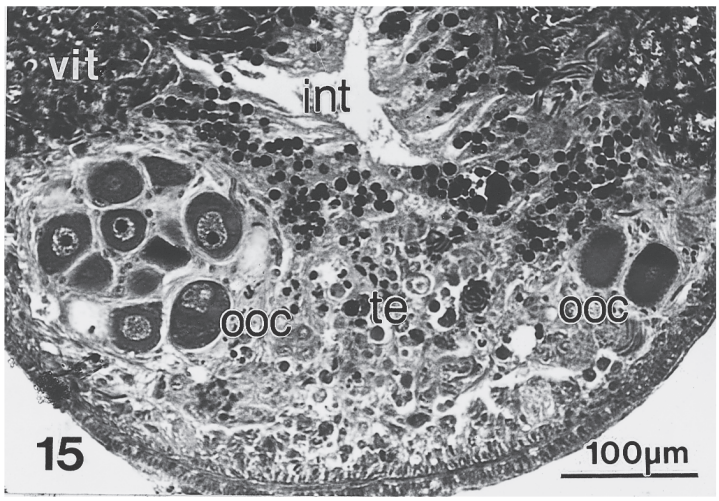
The posterior chamber of the seminal vesicle is perhaps homologous to what is called the prostatic vesicle in other plagiostomids. In sections, its epithelium consists of poorly preserved tall cells (Fig. 18). As a whole, this epithelium has a frayed look and sometimes resembles a coagular coating more than a layer of cells. Nevertheless, structures that are probably lightly stained, homogeneous nuclei can be seen in some of the cells.

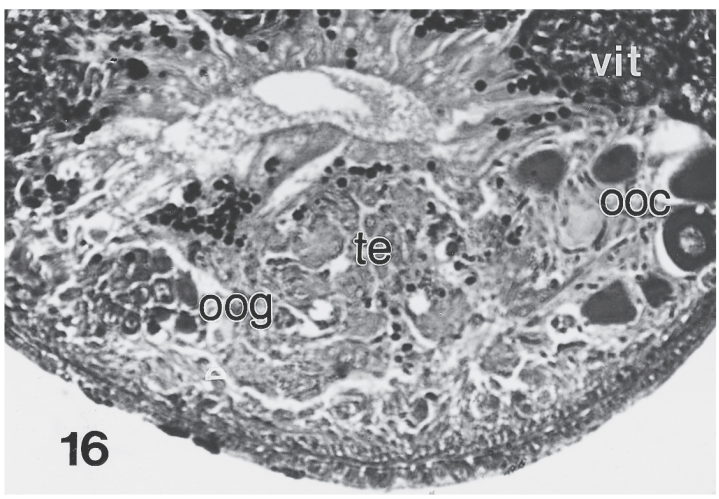
In most parts of the wall of the anterior chamber of the seminal vesicle, muscles whose orientation is primarily longitudinal are closer than circular muscle to the lumen. The epithelium is apparently of the insunk type, for nuclei are not evident in the thin layer external to the basement membrane. In the case of the posterior chamber, longitudinal muscle is also, in general, closer than circular muscle to the lumen. Due to curvatures in the walls of both chambers, however, there are places where the orientation of the two layers may seem to be reversed. Nevertheless, it is likely that the seminal vesicle, as a whole, and perhaps also the proximal portion of the penis, do not develop from the epidermal invagination that presumably differentiates into the genital atrium, penis sheath, and short distal portion of the penis.

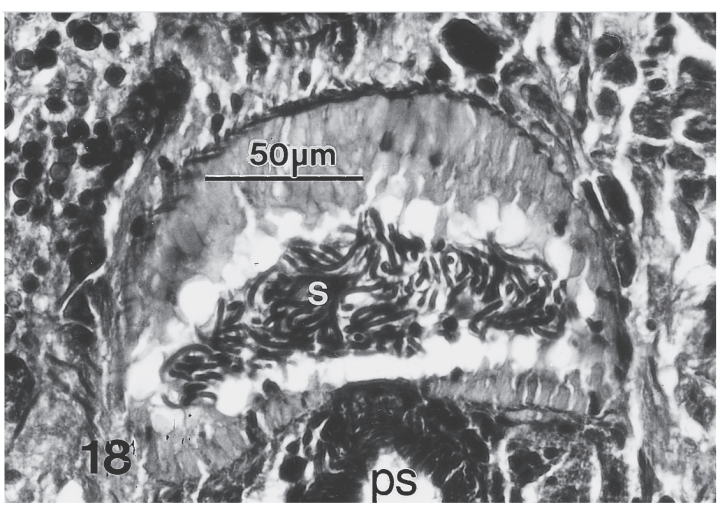
Mature sperm (Fig. 8) are about 55 µm long. They are bordered on both sides by what resembles an undulating membrane, but there is no evidence that flagella are present. While in the anterior chamber of the seminal vesicle, sperm are not motile. Perhaps they become motile while they are in the posterior chamber or in the penis.

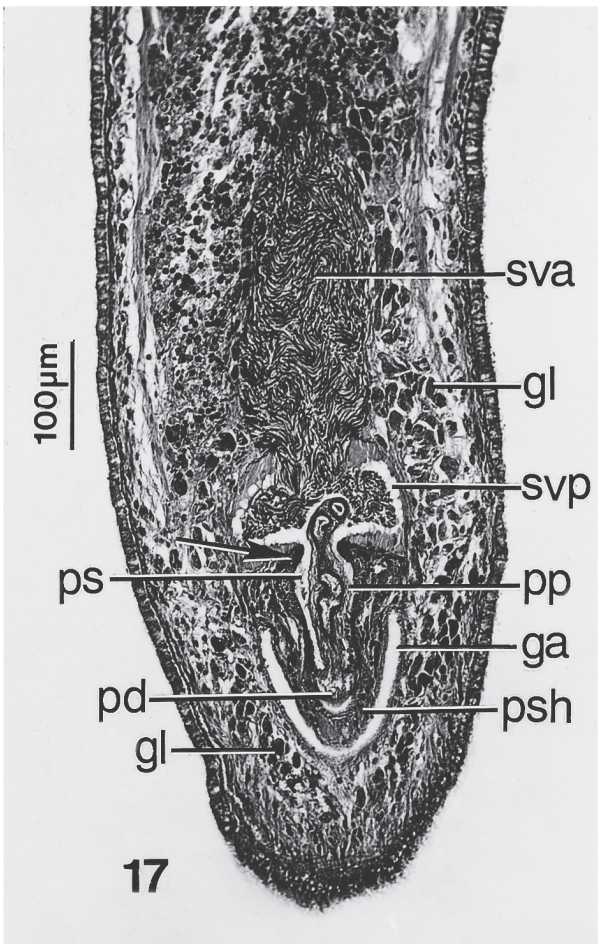
We have not identified a duct or ducts from the testis to the seminal vesicle. Böhmig stated that there is a single vas deferens extending from the testis to what he called the seminal vesicle of *Vorticeros pulchellum*, but the course of this duct was not illustrated. Hallez (1879b) briefly mentioned and illustrated two vasa deferentia in "*V. schmidtii*".

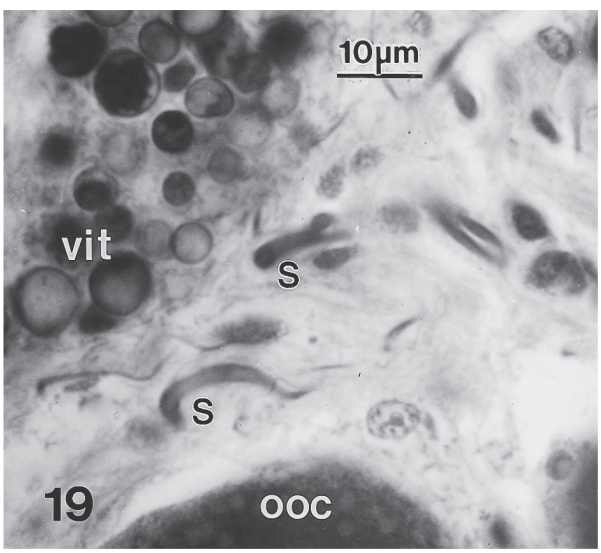
Joining the dorsal side of the genital atrium, at about the middle of its length, are two slender ducts (Figs 7, 9-12). In











paraffin sections, the lumen of these is only about 4 to 6 µm in diameter. The posterior portions of these ducts have what appear to be long cilia, but over much of their length cilia seem to be absent. The epithelium is underlain by sparse muscles, both circular and longitudinal. Because these ducts are believed to function in the transport of vitelline material

Figures 15-19. *Vorticeros praedatorium* sp. nov.; photomicrographs. Figs 15-16 (paratype) continue the series of Figs 9-14. **15.** Section through posterior portions of ovaries. **16**. Slightly oblique section through anterior portion of left ovary and slightly more posterior portion of right ovary. **17.** Holotype; frontal section, showing male copulatory organs and some other structures. **18**. Holotype; frontal section, slightly dorsal to that of Fig. 17, showing posterior chamber of seminal vesicle and portion of penis sac. **19.** Transverse section, showing sperm in tissue between ovary and vitellarium. (*ga*) genital atrium; (*gl*) subepidermal glands; (*int*) intestine; (*ooc*) oocyte; (*oog*) oogonia; (*pd*) distal portion of penis; (*pp*) proximal portion of penis; (*ps*) penis sac; (*psh*) penis sheath; (*s*) sperm; (*sva*) anterior chamber of seminal vesicle; (*svp*) posterior chamber of seminal vesicle; (*te*) testis; (*vit*) vitellarium.

Figures 15-19. *Vorticeros praedatorium* sp. nov.; photomicrographies. Figs 15-16 (paratype) suite de la série des Figs 9-14. **15.** Coupe à travers l'ovaire gauche, montrant les grands ovocytes. **16**. Coupe, un peu oblique, à travers la portion antérieure de l'ovaire gauche et une portion légèrement postérieure de l'ovaire droit. **17.** Holotype, coupe frontale, montrant l'appareil copulateur et quelques autres structures. **18**. Holotype, coupe frontale, légèrement dorsale à celle de la Fig. 17, montrant la chambre postérieure de la vésicule séminale et une portion du sac du penis. **19.** Coupe transversale, montrant les spermatozoïdes dans le tissu entre l'ovaire et la glande vitellogène ; (*ga*) atrium génital ; (*gl*) glandes sous-épidermiques; (*int*) intestin ; (*ooc*) ovocytes ; (*oog*) oogonies ; (*pd*) portion distale du pénis ; (*pp*) portion proximale du pénis ; (*ps*) sac du pénis ; (*psh*) gaine du penis ; (*s*) spermatozoïde ; (*sva*) chambre antérieure de la vésicule séminale ; (*svp*) chambre postérieure de la vésicule séminale ; (*te*) testicule ; (*vit*) glande vitellogène.

as well as oocytes, they are here designated ovovitelline ducts. Böhmig, who called them oviducts, stated that anteriorly each of them divides, one branch entering an ovary, the other entering the vitellarium; in addition, he said that further branching, without diminution of diameter, took place within the ovaries and vitellarium. These ducts are difficult to trace, and although we have been able to follow them until they reach a point between the vitellarium and the ovaries, we have not observed them to branch or to enter either of these components of the reproductive system.

Nothing comparable to a seminal bursa has been described for any species of *Vorticeros.* It is not known how or where sperm reach the oocytes. Because formation of egg capsules takes place in the atrium, oocytes presumably are inseminated either before they are delivered to the atrium or just after they have entered it. Our discovery of sperm close to or within one or both ovaries of sectioned specimens may shed some light on this problem. Usually, only a few scattered sperm are found at the edges of an ovary or between the oocytes (Fig. 19); in one specimen, however, there was a single large mass of sperm between follicles of the vitellarium (Fig. 14). Because sperm are not motile while in the testis and even after they have reached the anterior chamber of the seminal vesicle, they probably do not simply wander into the areas where we have observed them. It seems more likely that sperm deposited by the penis of one worm into the atrium of its partner enter the ovovitelline ducts and thereby are delivered to a place adjacent to the oocytes, or at least close to them. There could even be a poorly developed seminal bursa associated with each ovary, but we have not discerned such a structure.

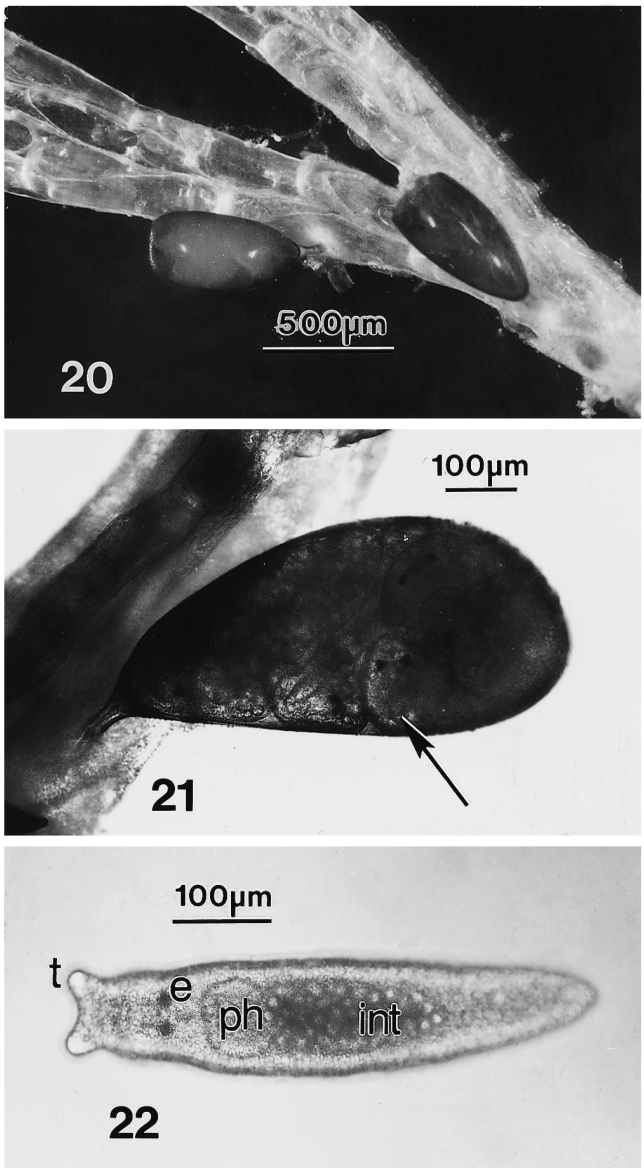
The prominent glands (Fig. 9) associated with the dorsal part of the genital atrium, at the level where the ovovitelline ducts enter the atrium, are believed to be concerned with production of egg capsules, almost certainly by modifying vitelline material. Böhmig found a yellowish brown capsule in the atrium of a specimen of *V. pulchellum*, but we have not seen stages of capsule formation in *V. praedatorium*. Fully formed egg capsules are usually present, however, on bryozoan colonies frequented by this species, and will be described in the next section.

Vorticeros praedatorium has been observed to suck out the contents of the ooecia of *Bugula californica* and *Dendrobeania lichenoides*. It apparently does not attack feeding zooids or avicularia of these bryozoans.

Egg capsules of *Vorticeros praedatorium* Figs 20-22

At Friday Harbor, nearly all extensive colonies of the two bryozoans inhabited by *V. praedatorium* have at least a few egg capsules of this worm. In the case of *Dendrobeania lichenoides*, the capsules are usually deposited on the underside of the leaflike lobes of the colony or on the rootlike zooids that anchor the lobes to the substratum or to one another. In the case of *Bugula californica,* they are most often attached to the basal portion of a colony, where feeding zooids and avicularia no longer exist. The capsules (Figs 20, 21), of a dark, translucent brown color, are ovoid, about twice as long as wide, and attached by a stalk. At most points, the wall of a capsule is about 1.5 µm thick. In ten specimens, the ovoid portion measured 415 by 182 µm to 644 by 308 µm. The stalk was from one-quarter to one-third the length of the ovoid portion; its thickness ranged from 11 µm to 28 µm. Shorter stalks are usually proportionately thicker than longer ones.

The number of eggs, embryos, or young worms within an egg capsule is commonly six or five, sometimes four**.** While still in a capsule, worms ready or nearly ready to escape are approximately ovoid and have an opaque white gut region. Their tentacles and eyespots (Fig. 21) are already conspicuous. When the capsule opens, about a quarter of it breaks off in one or more pieces. The rim of the now goblet-



Figures 20-22. *Vorticeros praedatorium* sp. nov**. 20.** Photomicrograph of egg capsules on colony of *Bugula californica*. **21**. Egg capsule *on B. californica;* (*arrow*) indicates a young worm whose eyespots are visible. **22**. Juvenile just after emerging from egg capsule. (*e*) eyespot; (*in*) intestine; (*ph*) pharynx. (*t*): *tentacle.*

Figures 20-22. *Vorticeros praedatorium* sp. nov. **20**. Photomicrographies de capsules d'oeufs sur une colonie de *Bugula californica*. **21**. Capsule d'oeufs sur *B. californica*; (*la flèche*) indique un jeune ver montrant les taches oculaires. **22**. Jeune ver peu après l'éclosion. (*e*) tache oculaire ; (*in*) intestin ; (*ph*) pharynx ; (*t*) tentacules.

shaped capsule is usually jagged, which suggests that there is not a sharp line of dehiscence, and it may also mean that dehiscence depends mostly on activity of the young worms rather than on secretions. On leaving the capsule, they quickly elongate and in a few minutes resemble larger worms in general shape (Fig. 22), although their tentacles are proportionately broader and less elongated. They crawl actively and exhibit the same behavior as larger worms in adhering tightly to glass by a glandular secretion produced at the posterior tip of the body.

Discussion

Three major points of disagreement between our account of the morphology of *Vorticeros praedatorium* and the observations of authors who have studied other species concern the penis sheaths, seminal vesicle and ovovitelline ducts. It is therefore necessary to deal with each of these structures in order to establish the distinctive features of *V. praedatorium*.

According to Böhmig (1890), the penis of *Vorticeros pulchellum* is enclosed by two sheaths. In his Plate XVIII, Figure 3, which shows a sagittal section of the penis in its relaxed condition, the inner sheath reaches nearly to the tip of the penis, whereas the outer sheath extends decidedly beyond the penis. In Figure 4 on the same plate, the penis is shown deeply withdrawn, and in Figure 5 it is shown in a partly extended position. In the text dealing with these illustrations, Böhmig accounted for both sheaths even though their positions with respect to the penis is deceptively different. Böhmig's analysis is not easy to understand, partly because the lithographic reproductions of his drawings are not sharp and also because the labeling is difficult to follow. Nevertheless, we must tentatively accept his view that there are two penis sheaths in the *Vorticeros* he found at Trieste, which makes this species decidedly different from *V. praedatorium*.

Graff (1874), in a description of the worm he found at Messina and first identified as *V. pulchellum*, showed a single sheath enveloping the penis. His observations, however, were based on living specimens, not on serial sections. In summaries of turbellarian systematics (1904-08, 1913), Graff relied to a large extent on descriptions of *Vorticeros* "*auriculatum*" given by Böhmig, and accepted the idea that there were two penis sheaths. Although a few figures of *V. pulchellum* taken directly from Böhmig's study were used in Graff's 1904-08 monograph, they did not include any showing the general layout of reproductive organs. Graff substituted a diagram of the copulatory apparatus, based on Böhmig's work, and it shows two penis sheaths. Hallez (1879), in describing *V. pulchellum* variety *luteum*, did not discuss or illustrate penis sheaths, but he did show a single sheath in connection with his description of *V.* "*schmidtii*".

Westblad (1956), in somewhat diagrammatic drawings based on sagittal and transverse sections of *V. "auriculatum*", showed only one penis sheath. Furthermore, the drawing of a sagittal section of *V. "auriculatum*" shows the penis sheath reaching nearly to the genital pore. This is confirmed by a statement in the text, but the arrangement is very different from that of *V. praedatorium* and from that shown by Böhmig for *V. pulchellum*.

Tozawa's (1918) description, for *V. ijimai*, of "a double-layered" penis sheath "whose inner portion seems to be shorter than the penis" is simply neither clear enough nor detailed enough to be reliable. Kulinich (1979), after studying worms he thought belonged to Tozawa's species, described and illustrated a single sheath.

The division of the seminal vesicle of *V. praedatorium* into two rather distinct portions would also seem to set this species apart from *V. pulchellum*. Nevertheless, the structure Böhmig identified as the entire seminal vesicle of *V. pulchellum* appears to be so similar to the posterior chamber of the seminal vesicle of *V. praedatorium* that perhaps we should consider the possibility that Böhmig somehow overlooked a sperm-filled anterior chamber. Westblad also did not mention or illustrate such a structure, but Kulinich's figure of the male copulatory apparatus of the worm he believed to be *V. ijimai* shows, rather sketchily, what appear to be a large anterior chamber and small posterior chamber. Why sperm in the anterior chamber are depicted as ovoid bodies was not explained.

In describing the ovovitelline ducts (oviducts) of *V. pulchellum*, Böhmig stated they unite posteriorly to form a single duct that empties into the atrium. If this is correct, the arrangement is very different from that in *V. praedatorium*, whose two ducts enter the atrium separately. Westblad's account, like Böhmig's, has the two ovovitelline ducts uniting. Westblad applied the term vagina to the common duct, although there was no evidence at the time to suggest that it does anything more than transport oocytes and vitelline material to the genital atrium. If the ovovitelline ducts convey sperm to the regions between the ovaries and the vitellarium, then the term vagina for a common duct would be appropriate. An odd feature of Westblad's Figure 17, B5 is the placement of the two ovovitelline ducts dorsal to the intestine. This is unlikely, if they lead to the region between the ovaries and the vitellarium.

Another small problem with Westblad's account is the statement that there are two longitudinal grooves anterior to the mouth. These are not shown in a sketch of the preoral region. The figure of a median sagittal section shows a transverse groove, which is typical also of *Vorticeros pulchellum*, *V. ijimai*, and *V. praedatorium.*

General coloration may, in some cases, be helpful in defining species of *Vorticeros*. Coloration depends, however, to a considerable extent on what a worm has eaten. Nevertheless, it may be useful to compare the coloration of named species that definitely belong to *Vorticeros*. *Vorticeros auriculatum*, from northern Europe, is dark red, and *V. pulchellum* from the Adriatic and western Mediterranean is said to be crimson or cherry-red. *Vorticeros luteum* is chrome-yellow; *V. cyrtum* is also yellow, but has reddish eyespots; *V. cyrtum* forma *amomum* is mostly reddish brown, except for whitish tentacles and epidermis and a streak of yellow that extends from between the eyespots to the anterior tip of the body. The color of *V. dahli* was not reported in the description. *Vorticeros praedatorium* is usually pinkish orange or brownish orange, although some specimens, especially small ones, may be yellow. *Vorticeros ijimai* was said to have a meshlike purplish middorsal band and a yellow or orange intestine. Kulinich remarked that the pigmentation and form of the body of the worm he took to be *V. ijimai* did not conform to Tozawa's description, but unfortunately he did not describe the coloration except to say that it was yellowish. In terms of their color patterns, *V. ijimai* (*sensu* Tozawa) and *V. cyrtum* forma *amomum,* among all described species, seem to be the most distinctive.

Acknowledgements

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