

## Two new species of umagillid flatworms from the 20-rayed antarctic crinoid *Promachocrinus kerguelensis*<sup>1</sup>

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Two new endosymbiotic turbellarians from the 20-rayed crinoid *Promachocrinus kerguelensis* are described from specimens collected off the western coast of the Antarctic Peninsula. *Desmote antarcticus* sp.n. differs from previously described members of the genus in the shape of the penis stylet, orientation of the terminal branches of the ovaries, and connections of the genital ducts to the exterior. *Parafallacohospes bransfieldensis* gen. et sp.n. is distinctive among known umagillids in having a pair of broad lobes projecting from each side of the body. The anatomy of the reproductive system is similar to that of *Fallacohospes inchoatus* Kozloff except that *P. bransfieldensis* lacks a secondary uterus. In addition, *P. bransfieldensis* has a functional digestive tract with small intestinal ceca, whereas *F. inchoatus*, the only species in the genus *Fallacohospes*, lacks a digestive tract. In this respect, *Parafallacohospes* appears to be intermediate between *Desmote*, which has large intestinal ceca, and *Fallacohospes*. Both new species belong to the subfamily Bicladiinae, which includes all other crinoid-inhabiting umagillid flatworms.

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On trouvera ici la description de deux nouveaux turbellariés endosymbiotes du crinoïde à 20 rayons *Promachocrinus kerguelensis* au large de la côte ouest de la péninsule antarctique. *Desmote antarcticus* n.sp. diffère des autres espèces du genre par la forme du stylet pénien, l'orientation des ramifications terminales des ovaires et les connections entre les conduits génitaux et l'extérieur. *Parafallacohospes bransfieldensis* n.gen. et n.sp. se distingue des autres umagillidés en ce qu'il possède une paire de grands lobes qui font saillie de chaque côté de son corps. L'anatomie de son système reproducteur ressemble à celle du système reproducteur de *Fallacohospes inchoatus* Kozloff, mais *P. bransfieldensis* n'a pas d'utérus secondaire. De plus, le nouveau taxon possède un tube digestif fonctionnel muni de petits caecums intestinaux, alors que *F. inchoatus*, la seule espèce du genre *Fallacohospes*, ne possède pas de tube digestif. *Parafallacohospes* semble donc être intermédiaire entre *Desmote*, qui possède des caecums intestinaux importants, et *Fallacohospes*. Les deux nouvelles espèces appartiennent à la sous-famille des Bicladiinae qui contient tous les autres umagillidés parasites de crinoïdes.

[Traduit par la revue]

### Introduction

Crinoids, echinoids, holothuroids, and sipunculans are commonly parasitized by turbellarian flatworms belonging to the neorhabdoceol family Umagillidae. Over 60 species of these flatworms have been described (reviewed by Cannon 1982). Umagillids have been reported from the oceans around all continents, but there are many parts of the world for which knowledge of the umagillid fauna is very incomplete. A single species of umagillid has been reported from Antarctica, but the specimens were so badly preserved that no formal taxonomic description was provided (Westblad 1952). Echinoderms and sipunculans are abundant around Antarctica (Dearborn and Rommel 1969; Dell 1972; Edmonds 1969; Pawson 1969a, 1969b), and many undescribed species can be expected to occur there.

During January 1982 the author made a small collection of echinoderms from Bransfield Strait, which is located just west of the Antarctic Peninsula. The 20-rayed crinoid *Promachocrinus kerguelensis* was found to contain two new species of umagillid flatworms which are described in this paper. One species is a member of the genus *Desmote* and is given the name *Desmote antarcticus*. The other species is assigned to a new genus, *Parafallacohospes*, and is named *Parafallacohospes bransfieldensis*.

### Materials and methods

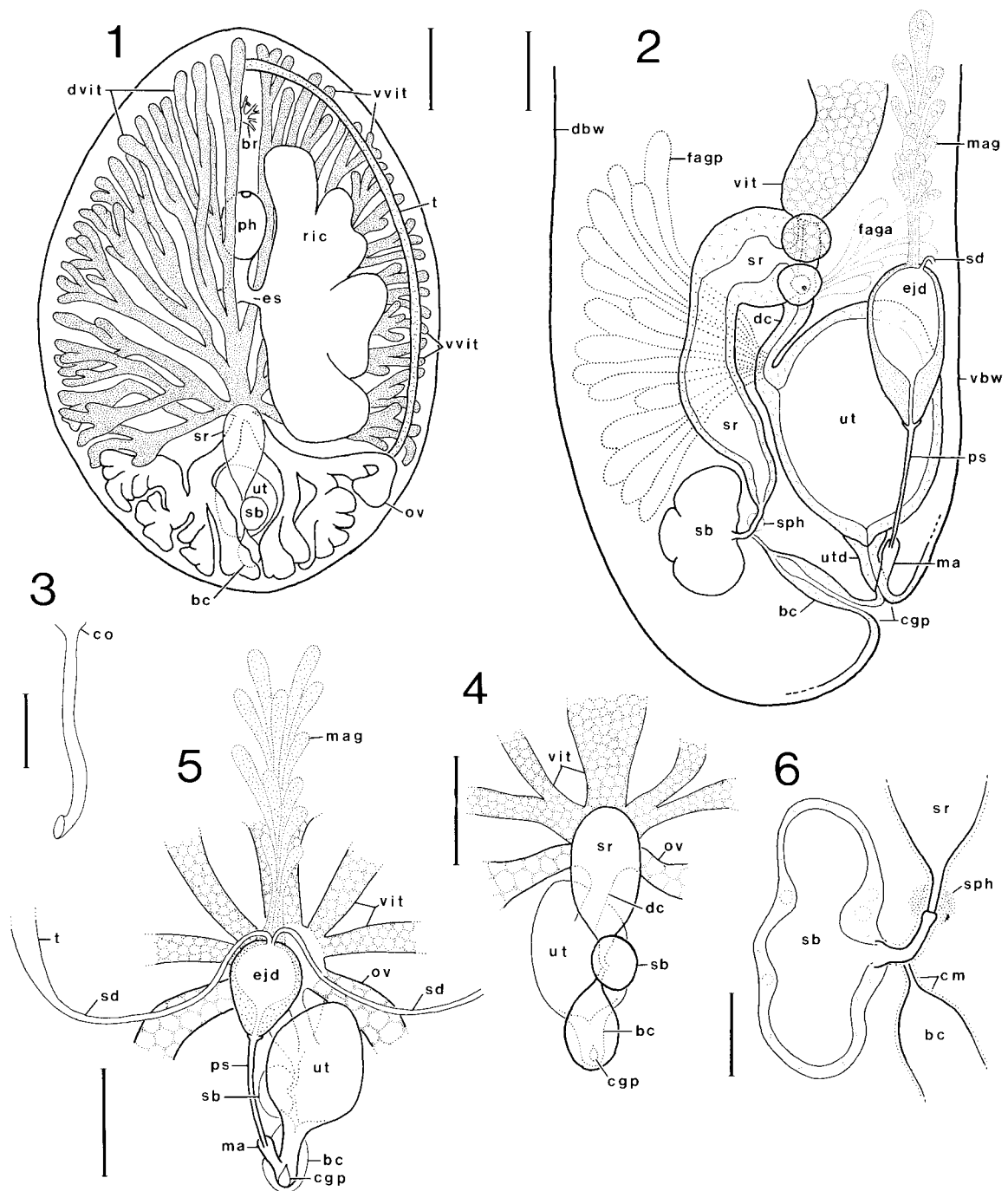
Specimens of the host crinoid *Promachocrinus kerguelensis* were dredged, using an otter trawl from the U.S. *R/V Hero* (see type locality

in descriptions). Some of the crinoids were dissected aboard the *Hero*; the rest were kept alive in a shipboard running seawater aquarium and transported to Palmer Station, Antarctica. The latter crinoids were dissected within a week of the collection date. Because the digestive tract of *P. kerguelensis* is bound to the body wall by connective tissue, it was not possible to dissect out the intestine intact. Fine-tipped scissors were used to cut around the edge of the tympanum. Forceps were used to tease the viscera into a bowl of seawater. The calyx was then flushed with seawater. The viscera and washings of the calyx were examined with a dissecting microscope for worms. Worms were preserved, without compression, in warm (60–70°C) fixative (Zenker's, Bouin's, or 10% formalin). Whole mounts were stained with acetocarmine. Some specimens were embedded in paraffin, sectioned at 7 µm and stained with Weigert's hematoxylin and erythrosin B (cf. Galigher and Kozloff 1971). Except where specified, the descriptions are based on the larger worms that were recovered and measurements were taken after the specimens had been preserved, mounted on slides, and stained.

### *Desmote antarcticus* sp.n. (Figs. 1–6)

TYPE SPECIMENS: The holotype (a whole mount) and paratype (a set of sagittal sections) have been deposited in the U.S. National Museum Helminthological Collection (Nos. 79563 and 79564, respectively). Specimens of *Desmote antarcticus* were found in 13 of 41 (32%) specimens of the crinoid *Promachocrinus kerguelensis*. The latter were collected from Bransfield Strait, off Nelson Island, Antarctica (62°21.73' S; 58°50.48' W; 150–200 m depth). Up to three *D. antarcticus* were found in a single host. Most of the worms were found clinging to the luminal side of pieces of the host's gut wall. Thus, the worms probably inhabit the intestine of the host. This description is

<sup>1</sup>Contribution No. 539 of the Harbor Branch Oceanographic Institution.



ABBREVIATIONS (Figs. 1-11): *bc*, bursal canal; *br*, brain; *cgp*, common gonopore; *cm*, circular muscle; *co*, collar; *dbw*, dorsal body wall; *dc*, ductus communis; *dvit*, dorsal vitellaria; *ejd*, ejaculatory duct; *es*, esophagus; *faga*, anterior female accessory glands; *fagp*, posterior female accessory glands; *fmb*, fold of margin of body; *ic*, intestinal cecum; *ma*, male antrum; *mag*, male accessory glands; *ov*, ovary; *ph*, pharynx; *ps*, penis stylet; *ric*, right intestinal cecum; *sb*, seminal bursa; *sd*, sperm duct; *sph*, sphincter; *sr*, seminal receptacle; *t*, testis; *ut*, uterus; *utd*, uterine duct; *vbw*, ventral body wall; *vit*, vitellaria; *vvit*, ventral vitellaria.

FIGS. 1-6. *Desmote antarcticus* sp.n. Fig. 1. Camera-lucida drawing of whole specimen; dorsal view. Dorsal vitellaria omitted from right side. Scale bar = 250  $\mu$ m. Fig. 2. Reproductive system viewed from right side; reconstructed from serial sections. Scale bar = 100  $\mu$ m. Fig. 3. Penis stylet; freehand drawing from live specimen. Scale bar = 50  $\mu$ m. Fig. 4. Camera-lucida drawing of female reproductive organs; dorsal view; accessory glands omitted. Scale bar = 200  $\mu$ m. Fig. 5. Camera-lucida drawing of female reproductive organs and male copulatory apparatus; ventral view; uterus and penis stylet displaced slightly to opposite sides. Scale bar = 200  $\mu$ m. Fig. 6. Arrangement of ducts connecting the vagina, seminal bursa, and seminal receptacle; sagittal view; reconstructed from serial sections. Scale bar = 50  $\mu$ m.

based upon six specimens: two that were examined alive, two that were preserved and mounted whole, and two that were serially sectioned.

#### *External morphology*

The body is ovoid in outline and dorsoventrally flattened when relaxed. The ventrolateral rim of the body can be contracted so that the entire worm assumes the form of a sucker. This enables the worms to adhere tenaciously to the tissues of the host. Some specimens were also attached to the intestinal epithelium by the mouth. In reflected light the body is opaque white, except for the intestinal ceca which are olive-brown in color. The largest specimen was 2.6 mm long  $\times$  1.9 mm wide.

#### *Body wall, parenchyma, and nervous system*

The epidermis is a simple cuboidal epithelium varying from 9 to 15  $\mu$ m in height. Live specimens were observed to be completely ciliated, but because of sloughing of cilia after the worms were removed from the host, large patches of the epidermis appeared unciliated in sectioned specimens. The nucleus of the epidermal cells is located basally. The cells lack secretory inclusions such as rhabdites, but some epidermal cells of most specimens contained sporozoan parasites. The body wall musculature consists of outer transverse and inner longitudinal fibers. Diagonal body wall muscles are lacking.

Spherical, basophilic cells are scattered in a fairly discrete layer immediately subjacent to the dorsal body wall muscles and, less commonly, subjacent to the ventral body wall muscles. The cells average 10  $\mu$ m in diameter. Because they lack secretory inclusions, they are believed to be epidermal replacement cells rather than the cytons of gland cells. Compact nests of smaller (5  $\mu$ m diam.) basophilic cells are present subjacent to the putative epidermal replacement cells and may be the source of the latter cells. The margins of the body and the areas dorsal and ventral to the vitellaria contain large, acidophilic, parenchymal cells. Dorsoventral muscles are abundant throughout the body, but are particularly conspicuous in these areas.

No protonephridial system was seen in sections or in two specimens that were compressed and examined while still alive.

The brain lies subjacent to the ventral body wall, halfway between the anterior end of the body and the mouth (see below). The brain consists of a bilobed neuropile surrounded by numerous cell bodies. Four large nerves arise from each lobe. These extend in the following directions: anteriorly, anterolaterally, laterally, and posterolaterally. The anterolateral nerves fork soon after they leave the neuropile, and each of the anterior nerves has a branch that extends posterolaterally. There are no eyespots or statocysts.

#### *Digestive system*

The mouth is located on the ventral midline about 3/10 of the body length from the anterior end. A small buccal cavity precedes the large, elongate, doliiform pharynx. The latter measures 150–225  $\mu$ m in length and 90–140  $\mu$ m in outside diameter in fully grown specimens. The pharynx lies almost horizontally. An esophagus leads posteriorly from the pharynx to about the midlevel of the body. As in most other members of the Bicladiinae, the posterior end of the esophagus divides into two laterally directed arms, each of which connects with a laterally positioned intestinal cecum. Most of the esophageal cells are cuboidal, but the apices of the cells bordering the pharynx extend down the inside of the pharynx toward the

mouth. Some of these extensions contain a nucleus, unlike similar projections of esophageal cells in many other species of umagillids (cf. *Syndisyrinx franciscanus* Lehman, 1946; *Anoploidium hymanae* Shinn, 1983). The esophageal cells lack secretion granules and food vacuoles; these cells apparently do not function in digestion. The epithelium of the esophagus is surrounded by longitudinal and circular muscles.

Each intestinal cecum has a large central lumen and shallow anteriorly and laterally directed lobes. The ends of the ceca lie about 1/6 the body length from the anterior end and about 1/5 the body length from the posterior end of the body. The ceca are separated from the lateral margins of the body by the testes and numerous lobes of the vitellaria (see below). Food vacuoles in cecal cells and the lumen of the ceca of all specimens contained cellular debris. In life, the debris was identical in color with the host intestinal epithelium and is, therefore, presumed to be host intestinal tissue.

#### *General aspects of the reproductive system*

The arrangement of the reproductive organs resembles that of other species of *Desmote*. The common gonopore is an elongate opening on the ventral midline near the posterior end of the body. The common genital atrium is very shallow, consisting of little more than a depression within the gonopore. The cells lining the common atrium are cuboidal to columnar in shape; their cytoplasm stains much less intensely than that of the adjacent epidermal cells. The bursal canal arises from the posterodorsal wall of the atrium; the uterine duct and male antrum enter the anterior wall of the atrium.

#### *Male reproductive system*

Two testes are located ventrolaterally in the body. Each consists of a narrow chord of spermatogenic cells that extends from 1/20 the body length from the anterior end to about 1/4 the body length from the posterior end. The anterior ends of the testes curve mesially and in some specimens, connect at the midline, anterior to the brain. A narrow sperm duct arises from the posterior end of each testis. Immediately after their origin, the sperm ducts turn mesially; they pass beneath the most anterior branches of the ovaries (see below) to near the midline, and then turn anteriorly. The sperm ducts extend along the sides of the ejaculatory duct and, separately but very close together, enter the anterior end of the ejaculatory duct. The anteriorly directed limbs of the sperm ducts are reinforced by a thickened, refractile basement membrane. This part of each sperm duct measures 5  $\mu$ m in diameter.

The pear-shaped ejaculatory duct is located just within the ventral body wall. Its anterior end lies along the midline but the posterior end is displaced to the right by the uterus. The ejaculatory duct is 150–225  $\mu$ m long and has a maximum diameter of 85–130  $\mu$ m. The anterior 5/8 of the ejaculatory duct is thin walled and has a wide lumen which was filled with sperm in my specimens. The epithelial lining of the posterior part of the ejaculatory duct is greatly thickened and the lumen there is very narrow. Acidophilic male accessory gland cells are scattered among the parenchyma cells in the region just anterior to the ejaculatory duct. Capillary necks of the gland cells extend to and into the wall of the ejaculatory duct. The swollen posterior ends of the gland necks contribute to the thick-walled nature of the posterior part of the ejaculatory duct.

The ejaculatory duct connects posteriorly with a "sclerotized" penis stylet (125–175  $\mu$ m long). The anterior end of the stylet is expanded into a flange (25  $\mu$ m diam.) which is

embedded between the epithelium and musculature of the posterior tip of the ejaculatory duct. The rest of the stylet is uniform in diameter (about 6  $\mu\text{m}$ ). The stylet angles posteriorly toward the midline, and is more or less curved depending on the degree of expansion of the uterus. The posterior tip of the stylet bears a smooth 90° curve, and terminates in an oval opening. Because the posterior curve lies in the dorsoventral plane, it is difficult to see in whole mounts that have not been compressed. The posterior end of the ejaculatory duct and the anterior end of the stylet are ensheathed by several large cells. The cells become attenuated posteriorly until, around the posterior third of the stylet, they are extremely thin. The posterior tip of the stylet projects freely into the male antrum. The latter is an evagination of the right side of the anterior wall of the common genital atrium and is lined by a cuboidal epithelium.

#### *Female reproductive system*

The vitellaria are long, thin, and moderately branched. They are bilaterally arranged in dorsal and ventral fields, and are typically restricted to the anterior 3/4 of the body. In one specimen, however, the vitellaria reached the posterior margin of the body. The blind ends of the vitellaria contain the germinative cells. The vitelline ductules arising from the germinative regions converge medially into a smaller number of vitelline ducts which in turn converge upon the anterior end of the seminal receptacle. The latter is located on the midline about 1/3 to 1/4 the body length from the posterior end.

Two bilaterally arranged ovaries fill most of the posterior 1/3 to 1/4 of the body. They lie midway between the dorsal and ventral surfaces. Each ovary has approximately 20 ultimate branches, each of which terminates in a germinative region. The ultimate branches of the ovaries converge anteromedially into three to five major branches, which in turn fuse into a single stem on each side. The latter connect with the seminal receptacle immediately posterior to the entrance of the vitellaria.

The ductus communis arises from the ventral side of the anterior end of the seminal receptacle (see below), and extends posteriorly to the mid-dorsal side of the uterus. Its low cuboidal epithelium is ensheathed by a thin layer of longitudinal muscles. The ductus communis receives two sets of accessory glands. The cell bodies of one set are located dorsal and lateral to the ejaculatory duct, and enter the ventral side of the anterior end of the ductus communis. These glands have moderately basophilic cytoplasm. The second set of accessory glands have intensely basophilic cytoplasm. They lie in a broad field beneath the dorsal body wall, extend ventrally and mesially around either side of the seminal receptacle, and enter the dorsal side of the posterior end of the ductus communis.

The uterus lies across the midline but bulges more into the left than the right side of the body. It is situated immediately subjacent to the ventral body wall, except along its right side where it is displaced dorsal to the ejaculatory duct. When the uterus is distended with an egg capsule (as it was in all specimens examined) it is approximately spherical in outside shape. The epithelium of the uterus consists of cuboidal to columnar cells (12–25  $\mu\text{m}$  tall) and is underlain by circular and longitudinal muscles. The uterus opens posteriorly into a short uterine duct. The latter lies just to the left of the midline and connects with the anterior wall of the common genital atrium, to the left of the male antrum. The expanded anterior end of the uterine duct is occluded by the bulging apical ends of the adjacent cells of the uterus. The lumen of the remainder of the uterine duct is collapsed unless an egg capsule is passing down it.

The egg capsules of *Desmote antarcticus* are roughly tetrahedral in shape but have bluntly rounded corners. The sides of the capsule are about 200  $\mu\text{m}$  long. The numbers of zygotes and yolk cells per capsule were not determined. There are no filaments or stalks extending from the capsules.

The bursal canal (= vagina) arises from the posterodorsal side of the common genital atrium. For most of its length, it is lined by columnar cells and is surrounded by inner longitudinal and outer circular muscles. The anterior end of the bursal canal narrows over a short distance into a fine "sclerotized" duct. The latter curves to the right of the midline, toward the seminal bursa. The anterior end of the wide part of the bursal canal typically has an expanded lumen and contains a small mass of sperm.

The seminal bursa is approximately kidney shaped. It lies to the right of the midline, dorsal to the uterus. The epithelial cells lining the seminal bursa are irregular in shape and contain scattered small phagocytic vesicles; the lumen of the bursa is spacious. At the site where the cuticularized end of the bursal canal approaches the seminal bursa, a wider cuticularized duct exits from the bursa and extends anteriorly to a connection with the seminal receptacle. It is not clear from my specimens whether the bursal canal enters the bursa independently or whether it is confluent with the extreme posterior end of the wider duct that exits the bursa. The latter duct is only 5–10  $\mu\text{m}$  long. It is joined to the narrow, duct-like, posterior end of the seminal receptacle within a small, but distinct, spherical sphincter. The seminal receptacle expands into a thick-walled, sperm-filled organ soon after its exit from the sphincter. It extends dorsal to the uterus along the midline. The cells forming the most anterior end of the seminal receptacle are pyramidal in shape and have more homogeneous cytoplasm than more posteriorly positioned cells. The seminal receptacle receives a large median vitelline duct on its anterior side, and smaller vitelline ducts and the ovaries on its anterolateral sides. The ductus communis leaves the seminal receptacle ventrally.

#### *Comparison with other species*

The species described above possesses all distinguishing characteristics of the genus *Desmote*: the body is oval in outline, the uterus is simple (i.e., the uterine duct is not elaborated into an egg capsule retaining secondary uterus) and there are two elongate, lateral testes located anterior to the paired ovaries (Stunkard and Corliss 1951; Kozloff 1965; Cannon 1982).

Two other species of *Desmote* have been described: *Desmote vorax* Beklemishev, 1916 and *Desmote inops* Kozloff, 1965. *Desmote antarcticus* differs from them in the following combination of characteristics: the gonopore is single and subterminal, the terminal branches of ovaries are directed posterolaterally from the posterolaterally directed main stem of the ovaries, and the posterior end of the penis stylet is broadly curved and has a terminal pore.

Like *Desmote antarcticus*, *D. inops* has a single, subterminal gonopore, but the terminal branches of the ovaries of the latter species extend anterolaterally from their main stems. In *D. inops* the posterior end of the penis stylet is much more sharply hooked than in *D. antarcticus*.

In *Desmote vorax* the uterus opens to the surface via a separate uterine pore rather than into the common genital atrium as it does in *D. antarcticus*. The dorsal wall of the common atrium of some *D. antarcticus* protrudes ventrally to a considerable extent, and thus partially separates the part of the common atrium that receives the uterus and male antrum from the part

that connects with the bursal canal. If these specimens were interpreted as having two gonopores, the penis and uterus would share the same pore in contrast to the situation in *D. vorax*. The ovaries of *D. vorax* and *D. antarcticus* are similar in form although, according to Beklemishev's (1916) illustrations, some of the terminal branches of the ovaries extend anteriorly. The penis stylet of *D. vorax* is irregularly curved along its length, and is conspicuously expanded at the posterior tip. The site of the opening of the stylet was not reported (Beklemishev 1916). *Desmote vorax* also differs from *D. antarcticus* in lacking a seminal bursa (but see comments of Kozloff 1965) and in living in the parenchyma of the host (Beklemishev 1916). *Desmote vorax* reportedly lacks external ciliation when mature (Beklemishev 1916). The observation that *D. antarcticus* sloughs large patches of cilia when removed from the host suggests that lack of cilia in *D. vorax* may be an artifact.

*Bicladus metacrini* was considered by Steinbock (1925) and Kozloff (1965) to be a species of *Desmote*, but Cannon (1982) reemphasized the distinct characteristics of that genus. These include possession of a secondary uterus in which numerous egg capsules are held, compact form and posterior location of testes, lack of seminal bursa, and lack of a direct connection between the bursal canal and the seminal receptacle (Kaburaki 1925). *Desmote antarcticus* differs from *Bicladus metacrini* in all of those characteristics. Kozloff (1965) mentions, however, that Kaburaki (1925) may have missed seeing a seminal bursa and a connection between the bursal canal and seminal receptacle in *Bicladus metacrini*. Even if these features were present, I agree with Cannon (1982) that the other differences are significant enough to warrant placement of that species into a separate genus.

***Parafallacohospes bransfieldensis* gen. et sp. n.**  
(Figs. 7–11)

**TYPE SPECIMENS:** The holotype (a whole mount of a fully grown specimen) and a paratype (transverse sections of a medium sized specimen) have been deposited in the U.S. National Museum Helminthological Collection (Nos. 79561 and 79562, respectively). *Parafallacohospes bransfieldensis* was found in 4 of the 41 specimens of *Promachocrinus kerguelensis* that were examined. The latter were collected from Bransfield Strait, off Nelson Island, Antarctica (62°21.73' S; 58°50.48' W; 150–200 m depth). The infested crinoids contained up to four worms of this species, as well as one or two specimens of *Desmote antarcticus*. For the reasons given in the description of *D. antarcticus*, it is concluded that this species also inhabits the digestive tract. The following description is based on six specimens: two were examined alive, two were mounted whole, and two were sectioned.

**External morphology**

Live specimens of *Parafallacohospes bransfieldensis* are translucent white except for the intestinal ceca, which are olive-brown in color. The body is dorsoventrally flattened. The anterior end is narrow and smoothly rounded; the posterior end is more broadly rounded. Two blunt lobes project from each side of the body. The ends of the lobes are either flexed dorsally or projected laterally. The margin of the rest of the body is turned ventrally. Folding of the margins of the body becomes greatly exaggerated if the worms are kept in seawater for more than 2–3 min. The largest specimen recovered was 2.0 mm in length and 1.25 mm in greatest width. The worms were immobile in seawater.

**Body wall, parenchyma, and nervous system**

The epidermis consists of low cuboidal, ciliated cells. The cells are 5–12  $\mu\text{m}$  tall; cilia average 4  $\mu\text{m}$  long. There are no obvious secretory inclusions in the epidermal cells nor are epidermal gland cells evident. The body wall musculature consists of outer transverse fibers, middle diagonal fibers that cross in opposite directions, and inner longitudinal fibers. Of these, the ventral transverse muscles are especially well developed. Dorsoventral muscles are abundant throughout the body.

Spherical cells with homogeneous basophilic cytoplasm are scattered individually beneath the body wall musculature. Their function is unknown but they may be epidermal replacement cells. Irregularly shaped, acidophilic parenchyma cells are present in the narrow spaces between various organs and around the dorsoventral muscles. The parenchyma is relatively more spacious in large worms than in small worms.

No protonephridial system was found in sections or in either of two live specimens that were compressed on a slide and examined with the compound microscope.

The brain is located ventrally, about 1/5 the body length from the anterior end. It consists of numerous cell bodies around a central neuropile. Three nerves extend from each side of the neuropile; these lead anteriorly, laterally, and posteriorly. A short distance from their origin, the lateral nerves branch into anterolateral and posterolateral nerves. There are no eyes or statocysts.

**Digestive tract**

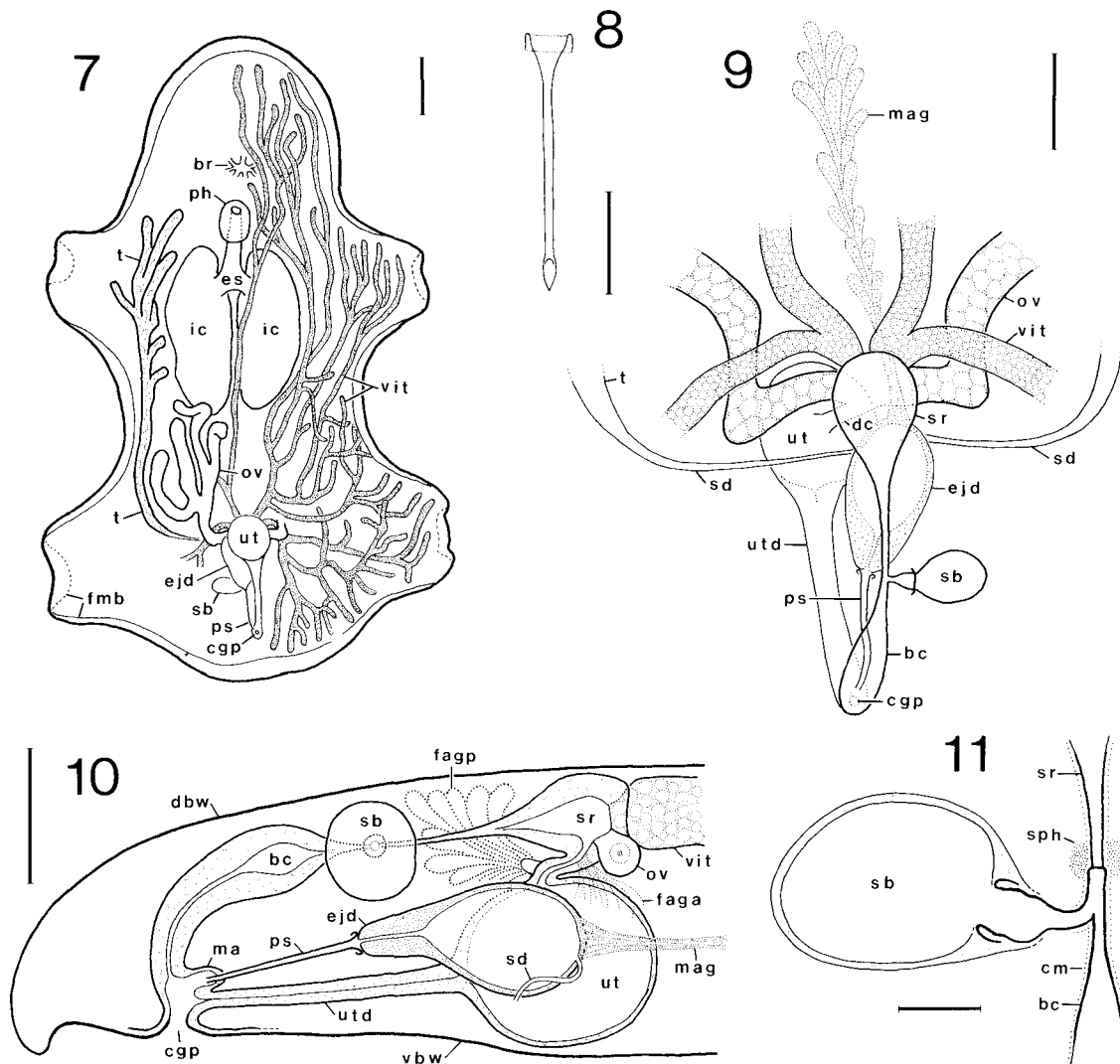
The mouth is located on the ventral midline about 1/3 the body length from the anterior end. A small buccal cavity precedes the doliiform pharynx. In large worms the pharynx measures about 95  $\mu\text{m}$  tall and 105  $\mu\text{m}$  in outside diameter. It extends posterodorsally to the esophagus. Cells lining the pharynx are elongate in the axis of the pharynx and contain flattened nuclei. The large esophagus extends posteriorly along the midline for 150–200  $\mu\text{m}$ , and then divides into two short posterolaterally directed arms. Each of the latter connects with a laterally positioned intestinal cecum. The esophagus is circular in cross section. It is lined by a columnar epithelium (food vacuoles and secretory granules lacking) and is surrounded by inner longitudinal and outer circular muscle fibers.

The intestinal ceca are small. They extend from the level of the pharynx to about the middle of the body or, in small specimens, to the end of the second third of the body. Although the walls of the intestinal ceca of some specimens are slightly infolded, the ceca are not conspicuously lobed. The ceca extend from the midline to one third of the way to the edges of the body. They are circular in cross section, filling the entire space between the dorsal and ventral body walls. The intestinal epithelium consists of large cuboidal cells of a single type. The intestine of all specimens examined was filled with cellular debris which, in life, was identical in color with the intestinal epithelium of the host.

**Male reproductive system**

Two elongate, sparsely branched testes are located ventrolaterally in the body. The most anterior branches of the testes are level with the mouth. The branches converge into a single stem that extends posteriorly to about 1/4 the body length from the posterior end of the worm. The branches of the testes are uniformly thin; in transverse sections, they vary in shape from laterally compressed to dorsoventrally compressed.

A narrow sperm duct arises from the posterior end of each



FIGS. 7–11. *Parafallacohospes bransfieldensis* gen. et sp. n. Fig. 7. Camera-lucida drawing of whole specimen; ventral view; vitellaria omitted from right side; testis and ovary omitted from left side. Scale bar = 250  $\mu$ m. Fig. 8. Penis stylet, freehand drawing from live specimen. Scale bar = 50  $\mu$ m. Fig. 9. Camera-lucida drawing of female reproductive organs and male copulatory apparatus; dorsal view. Scale bar = 100  $\mu$ m. Fig. 10. Reproductive organs viewed from right side; reconstructed from serial sections. Scale bar = 100  $\mu$ m. Fig. 11. Arrangement of ducts connecting to the seminal bursa; dorsal view; reconstructed from serial sections. Scale bar = 25  $\mu$ m.

testis. The sperm ducts extend either directly or along a posteriorly oriented course toward the midline. Upon reaching the sides of the ejaculatory duct, they bend anteriorly. The sperm ducts enter the anterior end of the ejaculatory duct several micrometres apart. The pear-shaped ejaculatory duct is located ventrally. The anterior 7/10 of the ejaculatory duct has a thin epithelium and a spacious lumen that is typically filled with sperm. Behind this region, the epithelium becomes abruptly thicker and the lumen much narrower.

Male accessory gland cells are located on the midline, immediately anterior to the ejaculatory duct. Necks of these acidophilic glands extend directly to the ejaculatory duct and become incorporated into the epithelium of the latter. The gland cell bodies are interspersed with retractor muscles that extend anteriorly from the muscles that ensheath the ejaculatory duct.

A "sclerotized" penis stylet is attached to the posterior end of the ejaculatory duct. The anterior end of the stylet is expanded into a collar that is folded back on the outside of itself. From the collar, the stylet narrows rapidly and is of fairly uniform diameter (about 5  $\mu$ m) for the rest of its length (95–140  $\mu$ m).

The posterior end of the stylet is extended on one side into a point. The stylet of some specimens is slightly constricted just anterior to the aperture.

The ejaculatory duct and stylet of large and small specimens are similar in size and morphology. Thus, their positions relative to the digestive and female reproductive organs vary with the size of the worm. In small specimens (about 1 mm long), the anterior end of the ejaculatory duct lies just behind the intestinal ceca. The ejaculatory duct is entirely anterior to the uterus, and the stylet curves around the right dorsal side of the uterus. In large specimens (about 2 mm long), the ejaculatory duct is located halfway between the posterior ends of the ceca and the posterior end of the body; it is level with the posterior end of the uterus. When the uterus of large specimens is empty, the ejaculatory duct lies along the midline. When the uterus contains an egg capsule, the ejaculatory duct is displaced to the right. Because the stylet of large worms lies entirely posterior to the uterus, the stylet is straight when the worms are alive. In fixed specimens, however, the stylet is often strongly curved due to contraction of the body during fixation.

The penis stylet is ensheathed by a thin cytoplasmic layer which is continuous at its posterior end with the male antrum. The latter is very short but has a conspicuous lumen and distinct cuboidal epithelium. It connects with the anterodorsal wall of the small common genital atrium. The common genital pore lies on the ventral midline, 100–150  $\mu\text{m}$  from the posterior tip of the body.

#### *Female reproductive system*

The vitellaria consist of thin, ramified, yolk cell filled ductules and ducts that extend to and terminate at all margins of the body. Germinative cells are located at the marginal ends of the vitelline ductules and in small bulges along their sides. The ductules converge into two or four main ducts which meet at the midline at the anterior end of the seminal receptacle (see below). This convergence is located about 1/4 the body length from the posterior end of the worm.

The two ovaries are located posterior to the intestinal ceca, in the region medial to the testes. Each ovary has four or five main branches which are variously subdivided. Oocytes are produced at the blind ends of the sub-branches. The sub-branches and branches extend posteriorly and medially, and converge into a single stem on each side. The two main stems extend posteriorly to the level of the capsule forming part of the uterus, where they make a 90° turn toward the midline. They pass dorsal to the male copulatory organs and uterus and enter the sides of the anterior end of the seminal receptacle, immediately behind the vitelline ducts.

The ductus communis is short and composed of cuboidal cells. It exits the anteroventral side of the seminal receptacle (see below), and passes posteriorly along the midline to the dorsal wall of the uterus. Two groups of accessory glands connect with the ductus communis. One group enters the ventral side of its anterior end; the other group enters the dorsolateral walls of its posterior end. At the latter site, the ductus is elaborated into two short lobes. The cell bodies of the anterior accessory glands lie ventral to the ductus, at the sides of the ejaculatory duct and uterus. The majority of the cytoplasm of these glands is strongly basophilic, although the part of the cells from which the necks emerge and the capillary necks of the glands are acidophilic. Most of the cell bodies of the posterior accessory glands are located subjacent to the dorsal body wall, anterolateral and posterolateral to their connection with the ductus communis. Some of the cell bodies are, however, located lateral to the first set of female accessory glands. The posterior glands are the more extensive of the two groups of glands, and have an opalescent, lightly basophilic cytoplasm.

The spherical uterus is located medially, just within the ventral body wall. When distended with an egg capsule, the anterior end of the uterus lies even with the confluence of the vitellaria at the seminal receptacle. Cells forming the simple uterine epithelium vary in shape from low cuboidal to columnar depending on whether or not the uterus contains an egg capsule. Egg capsules are spherical and 100–120  $\mu\text{m}$  in diameter. A relatively long uterine duct extends along the midline, from the posterior end of the uterus to the anteroventral wall of the common genital atrium. The uterine duct consists of a simple cuboidal epithelium that is ensheathed by a thin layer of circular and longitudinal muscle.

The bursal canal (= vagina) arises from the posterodorsal wall of the common genital atrium. It passes dorsally and anteriorly to the posterior end of the seminal receptacle. The long posterior part of the bursal canal is composed of cuboidal

cells and measures about 25  $\mu\text{m}$  in outside diameter. At its anterior end, the bursal canal narrows to about 5  $\mu\text{m}$  in diameter. The epithelium in this region is squamous and the surrounding basement membrane is "sclerotized." The "sclerotized" part of the bursal canal is about 20  $\mu\text{m}$  long. A curved, laterally directed duct arises from its right side, about 10  $\mu\text{m}$  from its anterior end. The lateral duct, which is also "sclerotized" and which is regarded as the proximal portion of the insemination canal by Kozloff (1965), connects with the medial side of the seminal bursa. The part that inserts into the seminal bursa is conspicuously expanded. The seminal bursa lies entirely to the right of the midline. It is oval in shape (about 75  $\times$  50  $\mu\text{m}$ ) with the long axis more or less perpendicular to the sagittal plane. The wall of the seminal receptacle is very thin; its epithelium lacks the phagocytic vesicles that are so conspicuous in the seminal bursa of many other umagillids.

The connection of the bursal canal to the posterior end of the seminal receptacle is surrounded by a short but conspicuous sphincter. The seminal receptacle passes dorsal and to the right of the ductus communis. Just anterior to the lobes of the ductus communis that receive the posterior female accessory glands, the seminal receptacle becomes greatly expanded. This part of the seminal receptacle lies along the midline, dorsal to the uterus and ejaculatory duct. It is composed of cuboidal cells. It receives the median vitelline duct on its anterior side and the lateral vitellaria and ovaries on the sides of its anterior end.

#### *Systematic position*

*Parafallacohospes bransfieldensis* has all of the diagnostic characteristics of the subfamily Bicladae (emended by Kozloff 1965). The most distinctive feature is the form of the digestive tract. This consists of a doliiform pharynx, a forked esophagus, and two bilaterally positioned intestinal ceca. The only species in the bicladin genus *Fallacohospes* lacks a digestive tract, however. Members of the other subfamilies of the Umagillidae (i.e., the Umagillinae and Collastominae), as well as most free-living dalyellioid turbellarians, have a single, saccate intestine and a short, unbranched esophagus.

Cannon (1982) suggested that the shape of the penis stylet is a diagnostic feature for the Bicladae: "the male stylet has a spatulate end like a "bent spoon" (Kozloff 1965)." Although *Parafallacohospes bransfieldensis* unquestionably belongs in the Bicladae, the posterior end of the stylet is not routinely bent or expanded. Thus, the spatulate form of the stylet is not universal to the subfamily but still characterizes species that have it as belonging to the subfamily.

Previously unrecognized defining features of the Bicladae are the forms of the uterus and egg capsules. The uterus of members of the Bicladae is roughly spherical, and has the opening from the ductus communis separate from that leading to the uterine duct. The uterus of the Bicladae could be viewed as an enlargement of the ductus communis – uterine duct axis. In the Umagillinae and Collastominae, the uterus is a blind evagination of the ductus communis – uterine duct axis; the uterus has only one opening. Members of the Bicladae lack filament glands, and the spherical or tetrahedral egg capsules lack filaments or stalks. Most members of the other two subfamilies have filament glands, and their egg capsules have one or more filaments projecting from one end. In the species that lack filament glands (e.g., members of the umagillin genus *Anoplodium*), one end of the egg capsule is drawn out into a stalk.

All members of the Bicladae inhabit crinoids. The Bicladae

TABLE 1. Characteristics of the genera of the Bicladiniac

	<i>Desmote</i>	<i>Bicladus</i>	<i>Fallacohospes</i>	<i>Parafallacohospes</i>
Body outline	Oval	Oval	Numerous fine ruffles	Two pairs of large lobes
Gut	Pharynx, ceca large	Pharynx, ceca large	Absent	Pharynx, ceca small
Secondary uterus	Absent	Present	Present	Absent
Genital pores	1 or 2	1	1	1
Testes	Midlateral, elongate, unbranched	Posterolateral compact, lobed	Midmedial, elongate, branched	Midlateral, elongate, branched
Penis stylet	Present	?Absent	Present	Present
Sperm ducts	Entirely separate	Joined	Entirely separate	Entirely separate
Seminal bursa	Present or ?absent; receives bursal canal and seminal receptacle separately	?Absent	Present; receives a single duct which communicates with both bursal canal and seminal receptacle	Present; receives a single duct which communicates with both bursal canal and seminal receptacle

inae contains three previously described genera: *Desmote* Beklemishev, 1916, *Bicladus* Kaburaki, 1925, and *Fallacohospes* Kozloff, 1965 (see Cannon 1982). Characteristics of these genera and of the new genus *Parafallacohospes* are summarized in Table 1.

In body form and in most features of the reproductive tract, *Parafallacohospes* is most similar to *Fallacohospes* among the other genera of the Bicladiniac. These two genera are clearly differentiated by the presence in the former and the absence in the latter of a digestive tract. Although there has been no doubt about the validity of Kozloff's assignment of *F. inchoatus* to the Umagillidae and, more specifically, to the Bicladiniac, *P. bransfieldensis*, with its reduced but functional bicladous digestive tract, constitutes an obvious intermediate form between *Fallacohospes* and the genera (*Desmote* and *Bicladus*) that have an elaborate bicladous digestive tract. Further studies of crinoid-inhabiting umagillids are needed to determine whether the degree of lobing of the lateral margins of the body wall represents a consistent difference between these two genera.

The presence or absence of a secondary uterus has been used to distinguish genera throughout the Umagillidae (Cannon 1982). Thus, the absence of a secondary uterus in *Parafallacohospes* also distinguishes this genus from *Fallacohospes*. The uterine duct of *Parafallacohospes* is probably homologous to the secondary uterus of *Fallacohospes*. Descriptions of the secondary uterus have not been detailed enough to establish whether the secondary uterus differs in histology from the uterine duct of closely related species that do not retain egg capsules (i.e., that lack a secondary uterus). It is possible that retention of egg capsules by *Fallacohospes* is a purely behavioral phenomenon, and that the secondary uterus of *Fallacohospes* does not differ in morphology from the uterine duct of *Parafallacohospes*.

*Parafallacohospes* differs most conspicuously from *Desmote*

and *Bicladus* in the lobed shape of the body, in the small size of the intestinal ceca, and in the midlateral position and branched form of the testes (see Table 1).

#### *Parafallacohospes* gen. n.

##### *Diagnosis*

Body flattened, with two broad lobes protruding from each side. Pharynx small, intestinal ceca unlobed, shorter than one third the total length of the adult body. Single gonopore located on ventral midline, near posterior end of body. Common genital atrium gives rise dorsally to an elongate bursal canal, receives the male antrum on the right side, and receives the uterine canal anteriorly. Anterior end of bursal canal narrow and "sclerotized," connected to the "sclerotized" posterior end of the seminal receptacle. A single, laterally directed "sclerotized" branch of the bursal canal connects to the seminal bursa. Two ovaries, each subdivided into anteriorly directed terminal branches. Vitellaria highly ramified; branches long, thin, radiating to near all margins of the body. Ductus communis extends from anterior end of seminal receptacle to mid-dorsal side of the spherical uterus. Uterine duct long; secondary uterus lacking. Two testes. Testes elongate, branched, located in midlevel of body, lateral to ovaries. Shaft of penis stylet straight or curved but posterior end straight and extended into a point on one side.

TYPE SPECIES: *Parafallacohospes bransfieldensis* from the 20-rayed antarctic crinoid, *Promachocrinus kerguelensis*.

##### Discussion

The bursal canal – seminal bursa – seminal receptacle complex provides some of the principal characters used in umagillid systematics. We have a tenuous understanding of umagillid phylogeny because we lack adequate descriptions of these organs for many species and we do not understand the



