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Interstitial acoels (Platyhelminthes: Acoela) from Bermuda

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Abstract.—One new genus, *Antrosagittifera,* and four new species of interstitial acoel flatworms from Bermuda are described, bringing the total number of known acoels from Bermuda to eight. The new species are *Haploposthia vandula, Parahaploposthia velvetum, Antrosagittifera corallina,* and *Proporus bermudensis.* A previously described species, *Pseudaphanostoma opisthorchis,* is reassigned to the genus *Haploposthia.*

Hyman (1939) provided the first taxonomic report of acoels from Bermuda with her descriptions of *Amphiscolops bermudensis* and *A. sargassi,* which were collected from rooted seaweeds and floating Sargassum, respectively. She also reported the presence of *A. langerhansi* which was not found in nature in Bermuda, but was present in aquaria at the Bermuda Biological Station.

A fourth seaweed-dwelling species of Acoela, *Convoluta sutcliffei* (Hanson, 1961) has since been transferred the genus *Pseudohaplogonaria* by Dörjes (1968).

During a 5-day stay at the Bermuda Biological Station in June 1999, we collected and examined interstitial fauna from two locations, North Rock and Castle Roads. We report here our findings of one new genus and four new species of interstitial acoels. Photographs and sketches of some of these species collected by J. P. S. Smith, III and S. Tyler in March 1985 were compared with these new findings.

Methods

Animals were extracted from sediment using magnesium-chloride anesthetization (Sterrer 1971). Squeeze preparations for light microscopic observation were made by placing live specimens on a slide along with a drop of magnesium chloride isotonic to seawater.

For histological study, specimens were relaxed in isotonic magnesium chloride, fixed in phosphate-buffered 2.5% (v/v) glutaraldehyde, washed in phosphate buffer (Millonig's buffer, 0.1 M), fixed in phosphate-buffered 1% (v/v) osmium tetroxide, dehydrated in acetone, and embedded in EMBed/Araldite epoxy resin. For some specimens, steps from aldehyde fixation through dehydration were enhanced by microwave radiation (Samsung oven, two 7-sec irradiations at 650 W separated by a 20-sec hiatus, with specimen-vial on ice and with water ballast of two filled 300-ml beakers; Giberson & Demaree 1995). Serial thick sections (1.25–2 μm) were prepared according to Smith & Tyler (1984) and stained without deresination in toluidine blue. Thin sections for electron microscopy were stained with uranyl acetate and lead citrate.

Whole mounts of individual worms were processed to reveal musculature through staining of their F-actin with fluorescently labeled phalloidin (BODIPY 558/668 or Alexa 488; Molecular Probes, Eugene, OR). The specimens were first relaxed in a magnesium-chloride solution isotonic to sea water, fixed for 1 hr in 4% (w/v) formaldehyde in PBS, rinsed in PBS (phosphate-buffered saline), attached with poly-L-lysine to a coverslip, permeabilized for 1 hr with 0.2% (v/v) Triton X-100 in PBS, stained 40 min with phalloidin-Alexa or

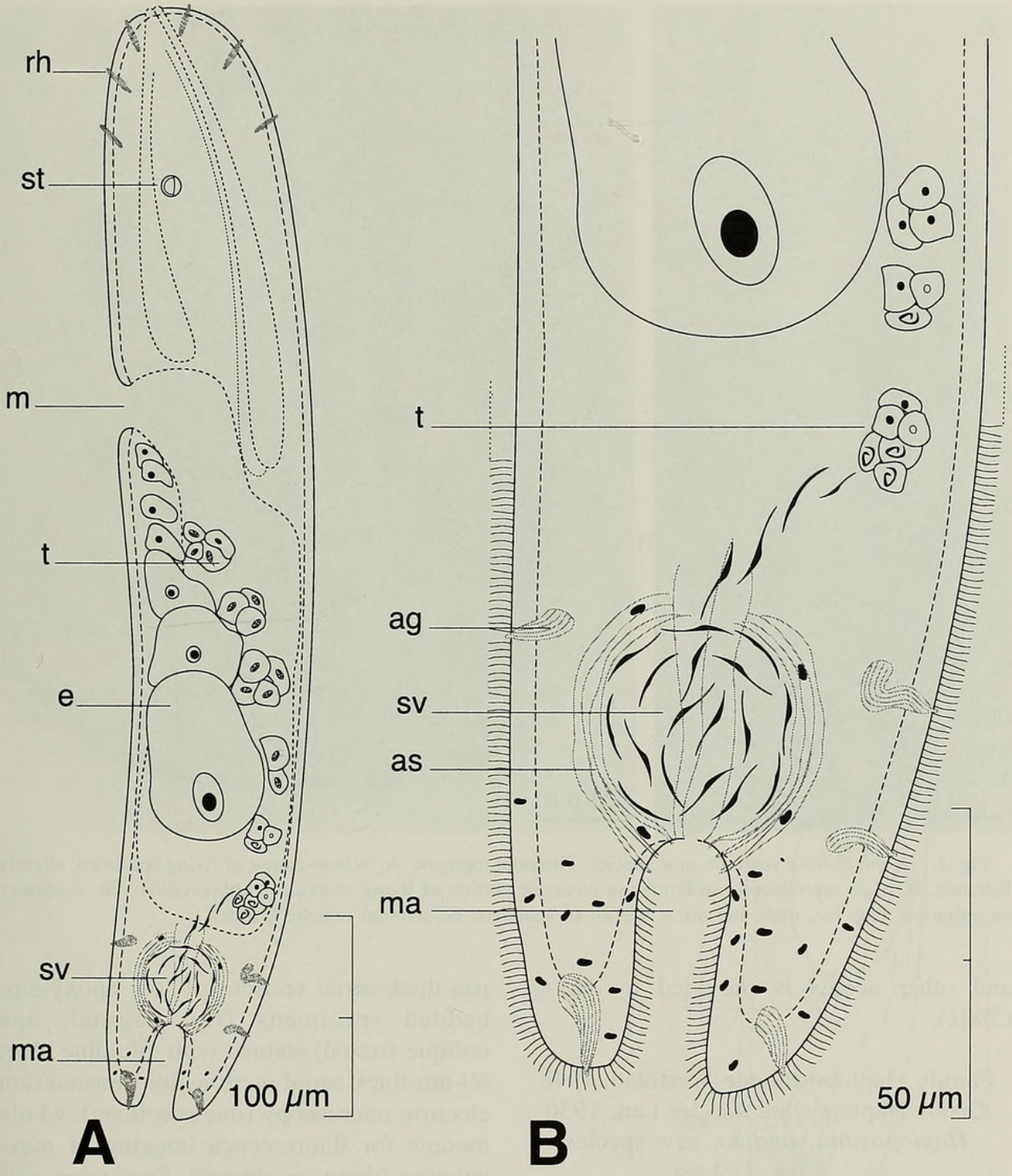

Fig. 1. *Haploposthia vandula,* new species. Sagittal reconstruction to show arrangement of organs. A, Whole organism; B, Reproductive structures in posterior portion of animal. Abbreviations: ag, accessory gland; as, accessory secretions; e, egg; m, mouth; ma, male antrum; rh, rhabdoid; st, statocyst; sv, seminal vesicle; t, testes.

phalloidin-BODIPY, and mounted under a second coverslip with Fluoromount-G. Epifluorescence images of the preparations from both dorsal and ventral aspects were viewed on a Leitz Ortholux microscope, and digital images were recorded using a Cohu 4915 CCD camera and a Scion LG3 frame grabber card on a Macintosh G3 computer. A brief summary of the body-wall musculature is given for each newly described species. A more detailed description of the body-wall musculature of these

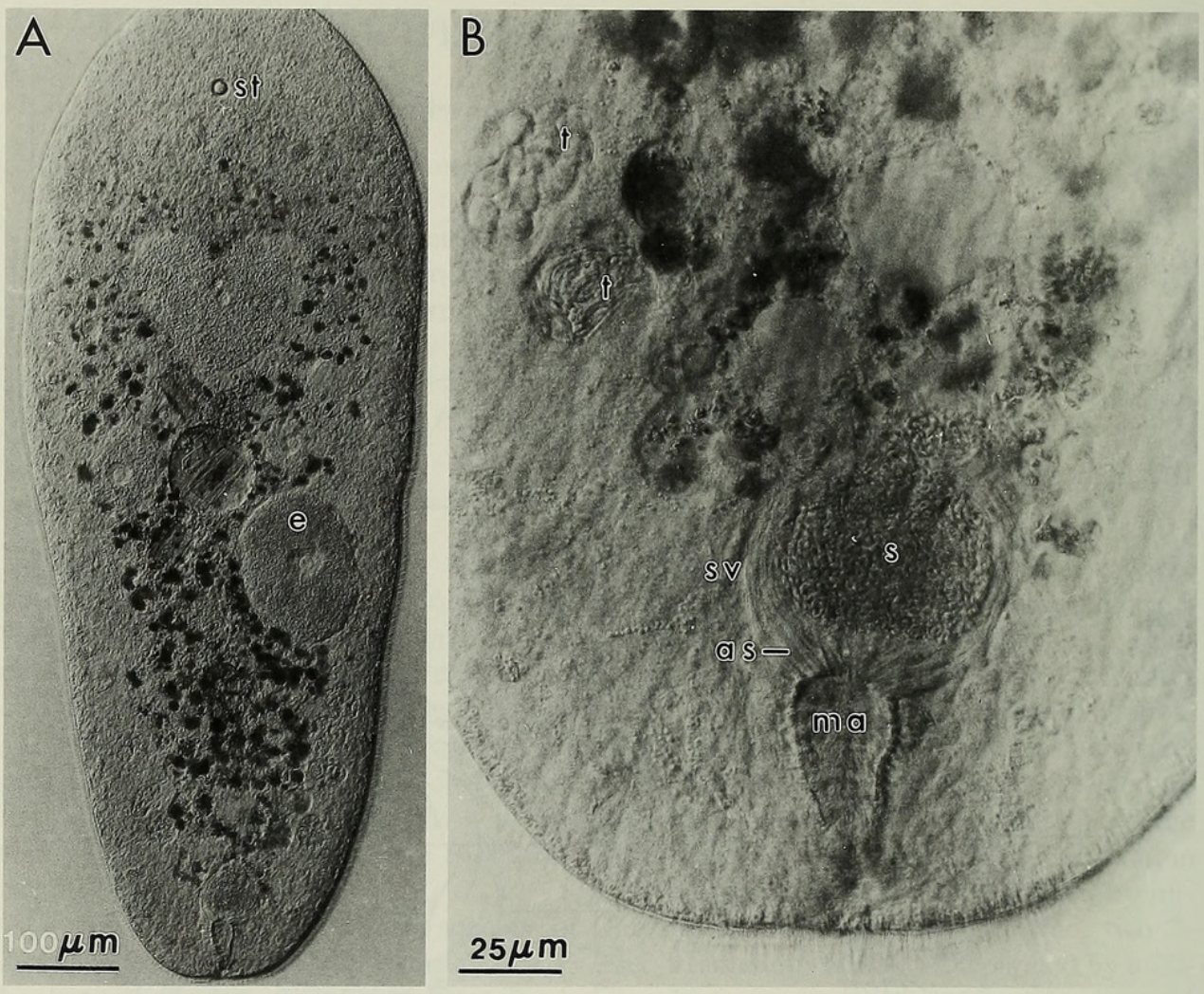

Fig. 2. *Haploposthia vandula,* new species. Photomicrographs. A, Whole-mount of living specimen, slightly flattened. B, Male reproductive structures in posterior portion of living specimen. Abbreviations: as, accessory secretions; e, egg; ma, male antrum; s, sperm; st, statocyst; sv, seminal vesicle; t, testes.

and other acoels is provided by Hooge (2001).

Family Haploposthiidae Westblad, 1948
Genus Haploposthia An der Lan, 1936
Haploposthia vandula, new species
Figs. 1, 2

Holotype.—AMNH 1601, 1.5-μm-thick serial sagittal sections of epoxy-embedded specimen stained with toluidine blue, collected June 1999.

Type locality.—Castle Roads, Bermuda. Subtidal coarse coral sand.

Paratype.—AMNH 1602, epoxy-embedded whole mount, Castle Roads, Bermuda.

Other material examined.—Living specimens in squeeze preparations; sets of 2-μm-thick serial sections of four epoxy-embedded specimens (two sagittal, one oblique-frontal) stained with toluidine blue; 60-nm-thick serial sections for transmission electron microscopy (one specimen); whole mounts for fluorescence imaging of musculature (three specimens). Specimens collected from Castle Roads and North Rock. Nomarski photographs of two specimens collected from Whalebone Bay March 1985 by J. P. S. Smith, III, and S. Tyler.

Description.—Largest adult specimens ca. 1 mm long (Fig. 1A) and ca. 250 μm wide (Fig. 2A). Anterior and posterior ends of body rounded bluntly, anterior more blunt. Body color green. Ocelli absent.

Epidermis completely ciliated. Rhabdoid

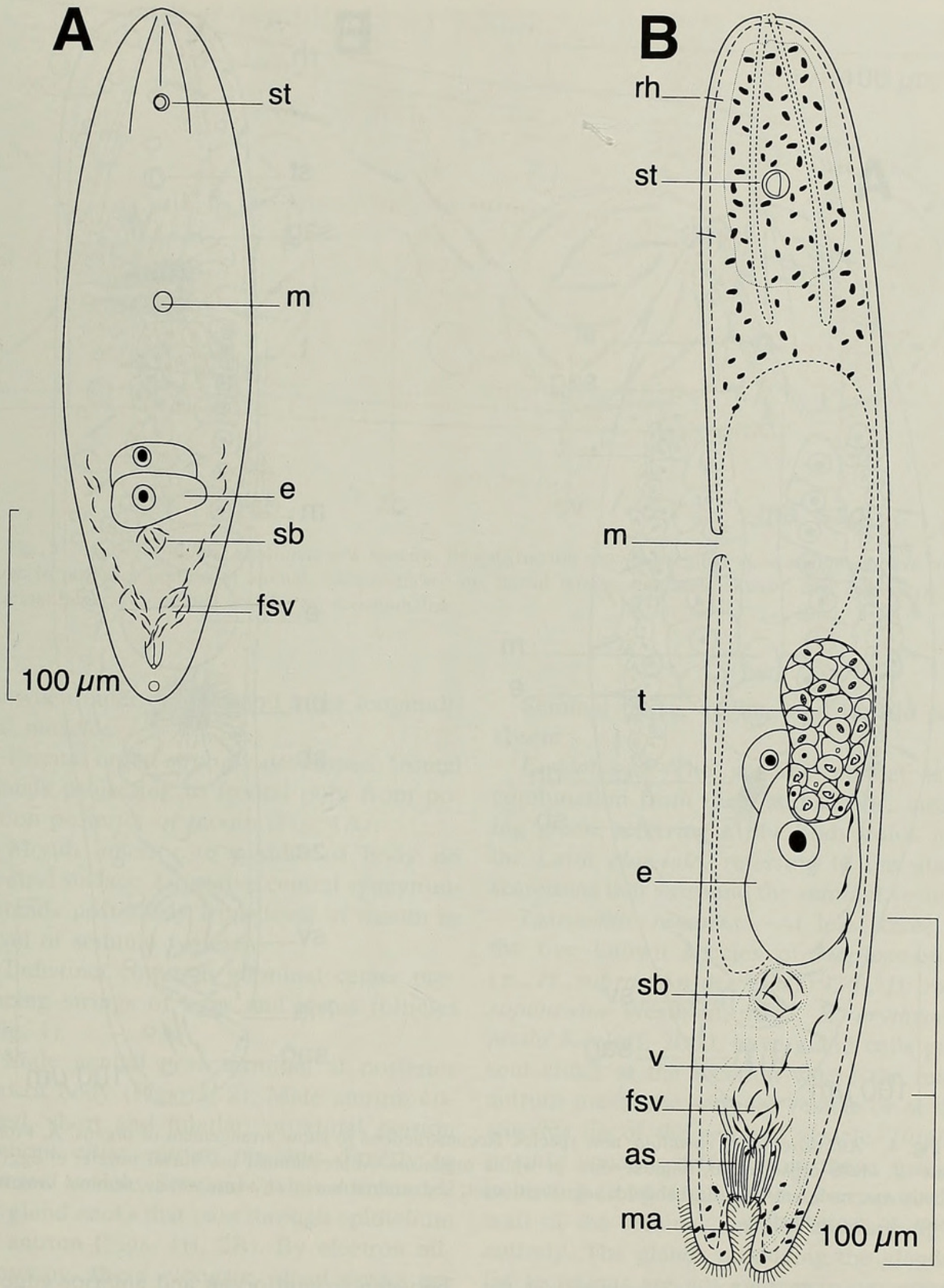

Fig. 3. *Parahaploposthia velvetum,* new species. Reconstructions to show arrangement of organs. A, Frontal view of whole organism. B, Sagittal view of whole organism. Abbreviations: as, accessory secretions; e, egg; fsv, false seminal vesicle; m, mouth; ma, male antrum; rh, rhabdoid; sb, seminal bursa; st, statocyst; t, testes; v, vagina.

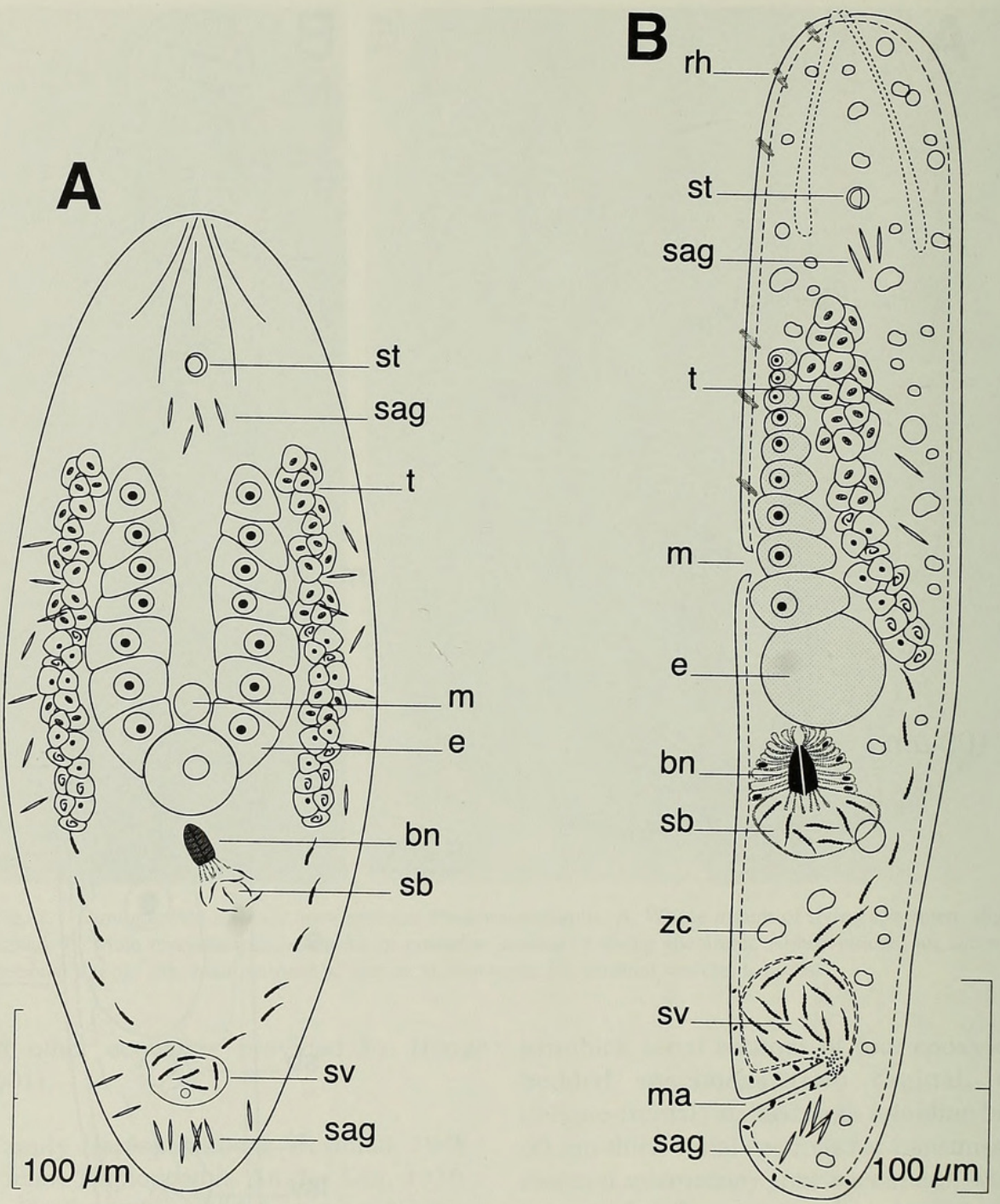

Fig. 4. *Antrosagittifera corallina,* new species. Reconstructions to show arrangement of organs. A, Frontal view of whole organism. B, Sagittal view of whole organism. Abbreviations: bn, bursal nozzle; e, egg; m, mouth; ma, male antrum; rh, rhabdoid; sag, sagittocyst; sb, seminal bursa; st, statocyst; sv, seminal vesicle; t, testes; zc, zooxanthellae.

glands few (Fig. 1A), concentrated at the anterior tip. Accessory glands present in region around male copulatory apparatus (Fig. 1B).

Musculature with circular fibers that encircle the body along entire length of animal; straight longitudinal muscles present between frontal organ and anterior edge of mouth; longitudinal muscles that have a longitudinal orientation anteriorly, but bend medially to cross diagonally over the body (longitudinal-cross-over fibers), present in both dorsal and ventral body wall; anterior with ventral diagonal muscles positioned

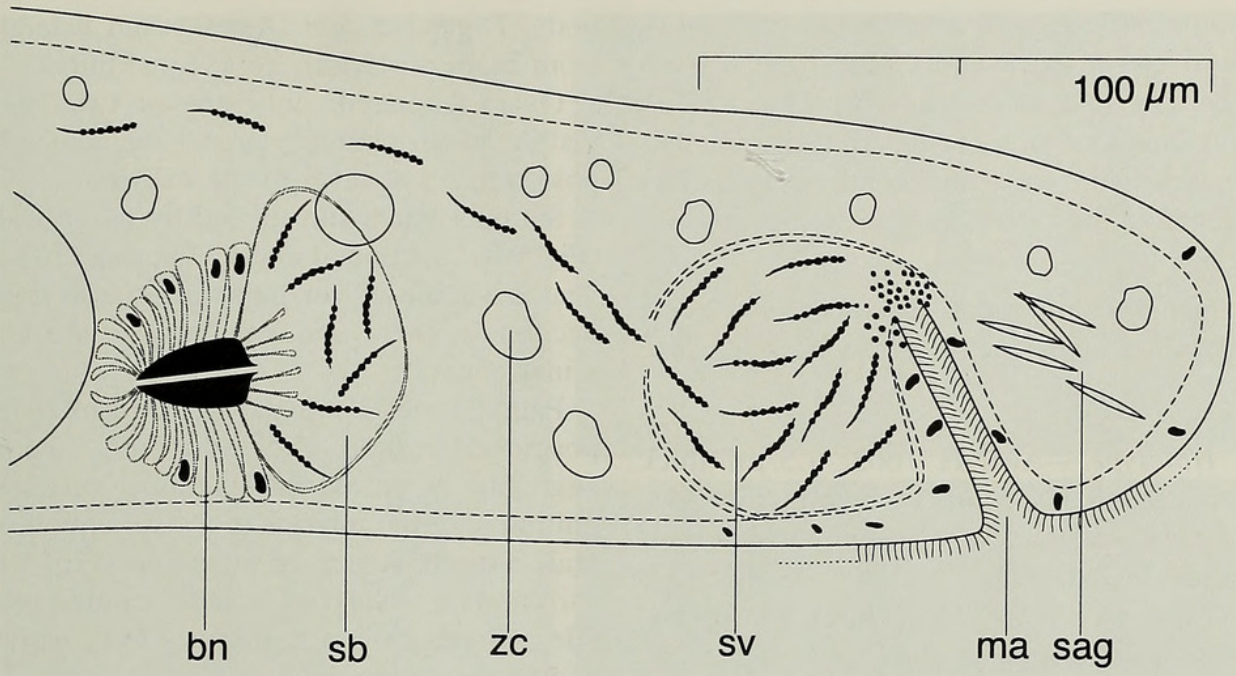

Fig. 5. *Antrosagittifera corallina,* new species. Reconstruction showing sagittal view of reproductive structures in posterior portion of animal. Abbreviations: bn, bursal nozzle; ma, male antrum; sag, sagittocyst; sb, seminal bursa; sv, seminal vesicle; zc, zooxanthellae.

between outer circular and inner longitudinal muscles.

Frontal organ strongly developed; frontal glands projecting to frontal pore from position posterior of mouth (Fig. 1A).

Mouth anterior to middle of body on ventral surface. Digestive central syncytium extends posteriorly from level of mouth to level of seminal vesicle.

Indistinct common germinal center producing strings of eggs and testes follicles (Fig. 1).

Male genital pore terminal at posterior end of body (Figs. 1, 2). Male antrum ciliated, short and tubular; proximal portion without cilia; antrum opening directly to seminal vesicle. Seminal vesicle surrounded by gland necks that pass through epithelium of antrum (Figs. 1B, 2B). By electron microscopy, these elongate gland necks are seen to contain thin rhabdiform granules that stain metachromatically (pink) with toluidine blue. Thin parenchymal muscles extend anteriorly from proximal end of male antrum, terminating slightly anterior to seminal vesicle.

Seminal bursa, vagina, and female pore absent.

Etymology.—The specific epithet is a combination from the Latin *viridis,* meaning green, referring to the body color, and the Latin *glandula,* referring to the gland secretions that surround the seminal vesicle.

Taxonomic remarks.—At least three of the five known species of *Haploposthia,* i.e., *H. rubra* (An der Lan, 1936), *H. rubropunctata* Westblad, 1945, *H. erythrocephala* Kozloff, 2000, have gland cells present either at the location where the male antrum meets the seminal vesicle or at the anterior tip of the seminal vesicle. *Haploposthia vandula* differs from these species in having elongate gland necks compose the wall of the seminal vesicle, enwrapping it entirely. The glands producing the glandular secretions are not evident in our epoxy serial sections; however, the secretions appeared similar in color of staining and in density to the secretions contained within the epidermal accessory glands (Fig. 1B) in the posterior end of the animal.

Haploposthia vandula was the most

common acoel in our sediment collections from North Rock and Castle Roads. Even after we had extracted most of the adult specimens of *H. vandula* from our buckets of sediment, we could continue to extract numerous immature specimens.

Genus *Parahaploposthia* Dörjes, 1968
Parahaploposthia velvetum, new species
Fig. 3

Holotype.—AMNH 1603, 1.5-μm-thick serial sagittal sections of epoxy-embedded specimen stained with toluidine blue, collected June 1999.

Type locality.—North Rock, Bermuda. Subtidal coarse coral sand.

Paratype.—AMNH 1604, epoxy-embedded whole mount, North Rock.

Other material examined.—Living specimens in squeeze preparations; two sets of 1.5–2-μm-thick serial sagittal sections of epoxy-embedded specimens stained with toluidine blue (one sagittal, one frontal); whole mounts for fluorescence imaging of musculature (14 specimens). Specimens collected from North Rock.

Description.—Adult specimens ca. 350 μm long and 100 μm wide (Fig. 3); maximum width at middle of body and narrower at the posterior and anterior ends. Pale-yellow body color.

Epidermis completely ciliated. Rhabdoid glands absent, or only two or three present on ventral side of anterior end (Fig. 3B).

Musculature with circular fibers that encircle the body along entire length of animal; straight longitudinal muscles present between frontal organ and anterior edge of mouth; longitudinal muscles that have a longitudinal orientation anteriorly, but bend medially to cross diagonally over the body (longitudinal-cross-over fibers), present in both dorsal and ventral body wall.

Frontal organ weakly developed; frontal glands projecting to frontal pore through brain from position just posterior to it.

Mouth opening anterior to middle of body. Digestive central syncytium extends from brain posteriorly to seminal bursa.

Ovary unpaired; only one or two eggs visible in specimens; largest egg extends posteriorly past level of seminal bursa.

Seminal bursa surrounded by tissue wall (Fig. 3B). Sectioned material appears to reveal a vagina as an indistinct tissue connection from the seminal bursa to the terminal gonopore.

Paired testes compact, ca. 60 μm long, positioned behind level of mouth. Sperm aggregate as paired false seminal vesicles, uniting slightly anterior to proximal end of male antrum. A ring of secretions (Fig. 3B) surround the distal end of false seminal vesicles; glands extend posteriorly to proximal end of male antrum.

Ciliated male antrum ca. 20 μm long, tubular, with weak musculature; opens terminally at common gonopore.

Etymology.—The specific epithet is from the Latin *velvetum,* meaning velvet, referring to "softness" of the epidermis due to the sparseness of obvious rhabdoids and accessory glands.

Taxonomic remarks.—The four known species of *Parahaploposthia* share weakly developed frontal glands, unpaired ovaries, paired testes, ciliated male antrum bearing proximal glands, and the lack of a seminal vesicle or penis. The addition of *P. thiophilus* Fegley et al., 1984, to this genus expanded the diagnosis to include haploposthiids having a seminal bursa and a vagina that is a "tissue connection indistinct in sectioned material." Due to this expanded diagnosis, *P. velvetum* seems to fit well within the genus; although the presence of a vagina may be more questionable in *P. velvetum* than in *P. thiophilus. Parahaploposthia velvetum* also resembles *P. thiophilus* in having compact testes, but differs in having fewer rhabdoids and a less muscular male antrum without accessory glands associated with the gonopore. The male antrum of *P. velvetum* appears to more resemble that of *P. avesicola* Dörjes, 1968, and *P. cerebroepitheliata* Dörjes, 1968.

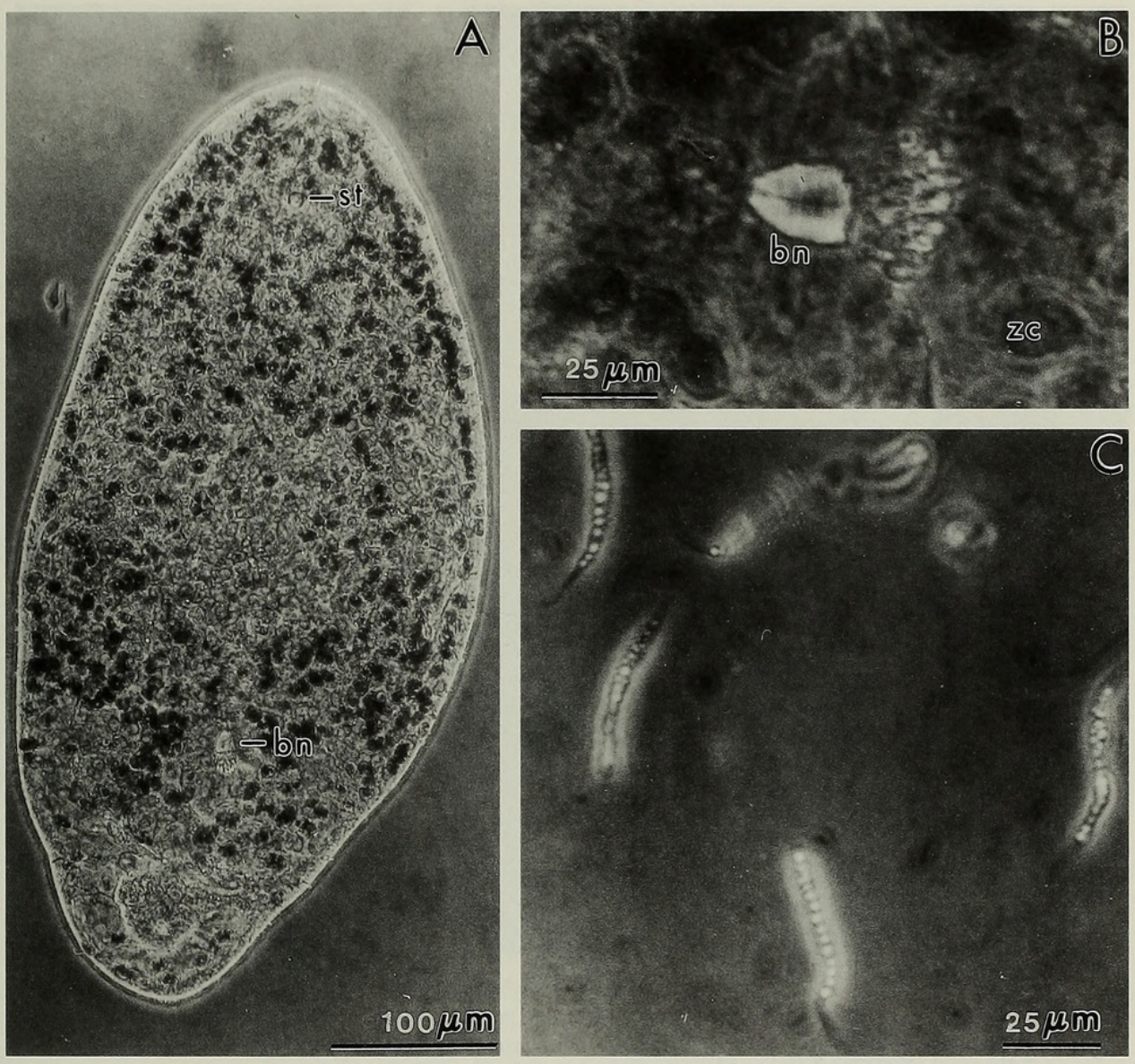

Fig. 6. *Antrosagittifera corallina,* new species. Photomicrographs. A, Whole-mount of living specimen, moderately flattened. B, Bursal nozzle. C, Sperm. Abbreviations: bn, bursal nozzle; st, statocyst; zc, zooxanthellae.

Family Sagittiferidae Kostenko & Mamkaev, 1990
Subfamily Sagittiferinae Gschwentner et al., 1999
Antrosagittifera, new genus

Diagnosis.—Sagittiferidae with long, narrow ciliated antrum, the wall of which does not contain sagittocysts. Seminal vesicle surrounded by tissue wall. Sagittocysts and symbionts are present. Does not reproduce asexually by fission.

Etymology.—*Antrosagittifera* (Latin, f.); prefix derived from the Latin *antrum.*

Type species.—*Antrosagittifera corallina,* new species

Antrosagittifera corallina, new species
Figs. 4–6

Holotype.—AMNH 1605, 2-µm-thick serial sagittal sections of epoxy-embedded specimen stained with toluidine blue, collected June 1999.

Type locality.—North Rock, Bermuda. Subtidal coarse coral sand.

Other material examined.—Living specimens in squeeze preparations; one

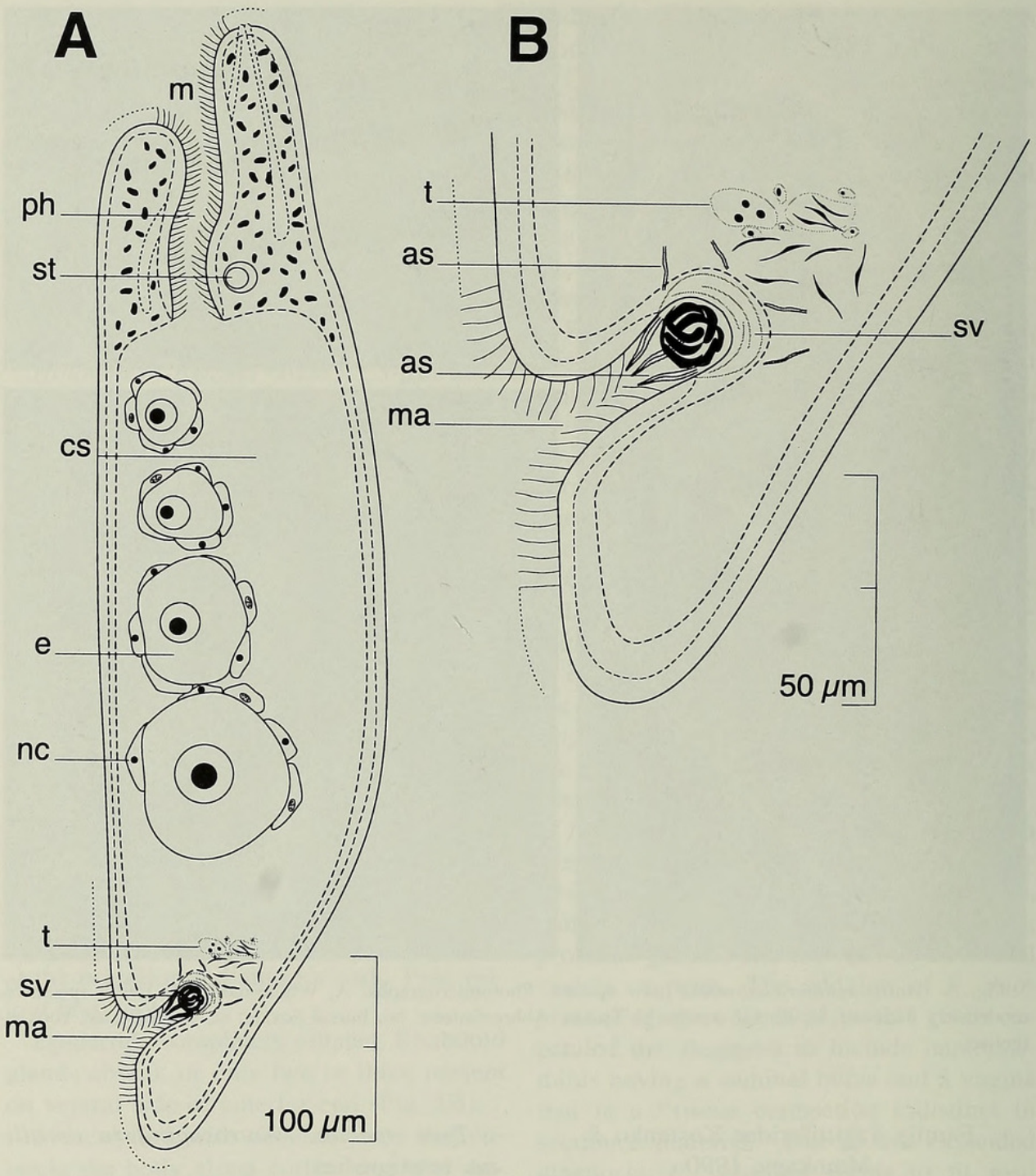

Fig. 7. *Proporus bermudensis,* new species. Sagittal reconstruction to show arrangement of organs. A, Whole animal; B, Male reproductive structures in posterior portion of animal. Abbreviations: as, accessory secretions; cs, central digestive syncytium; e, egg; m, mouth; ma, male antrum; nc, nurse cell; ph, pharynx; st, statocyst; sv, seminal vesicle; t, testes.

set of 2-μm-thick sagittal serial sections of epoxy-embedded specimens stained with toluidine blue; whole mounts for fluorescence imaging of musculature (12 specimens). Specimens collected from North Rock.

Description.—Adult specimens ca. 600 μm long and 200 μm wide (Figs. 4A, 6A). Anterior and posterior ends rounded, posterior less blunt. Greenish-brown color conferred by conspicuous zooxanthellae.

Epidermis completely ciliated. Rhabdoid

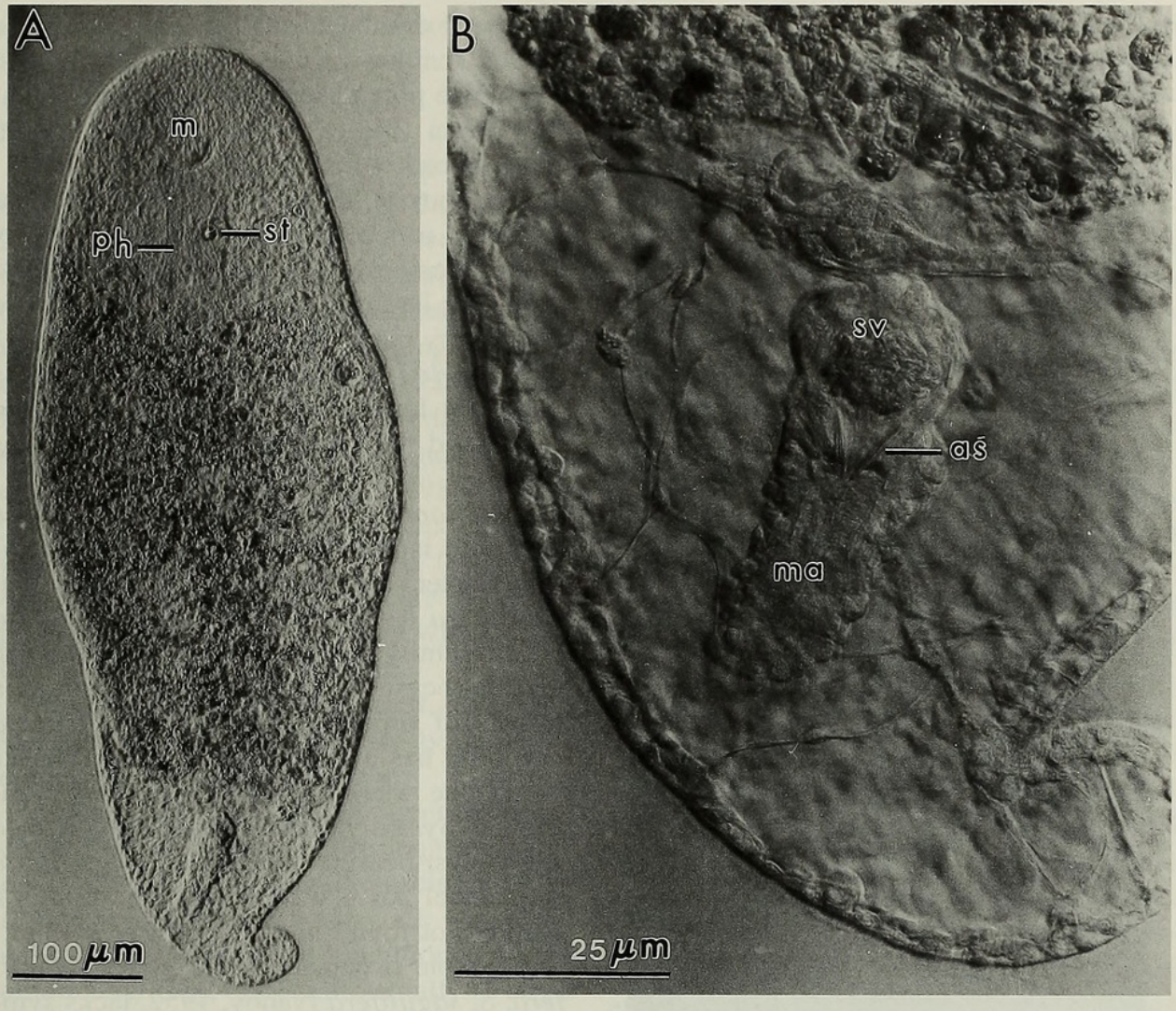

Fig. 8. *Proporus bermudensis,* new species. Photomicrographs. A, Whole-mount of living specimen, slightly flattened, ventral view. B, Male reproductive structures in posterior portion of living specimen. Abbreviations: as, accessory secretions; m, mouth; ma, male antrum; ph, pharynx; st, statocyst; sv, seminal vesicle.

glands (Fig. 4B) few and concentrated at the anterior end on the ventral side.

Musculature with circular fibers that encircle the body along entire length of animal; straight longitudinal muscles present between frontal organ and anterior edge of mouth; longitudinal muscles that have a longitudinal orientation anteriorly, but bend medially to cross diagonally over the body (longitudinal-cross-over fibers), present in both dorsal and ventral body wall; anterior with ventral diagonal muscles positioned between outer circular and inner longitudinal muscles.

Frontal organ weakly developed; frontal glands projecting to frontal pore through brain from position just posterior to statocyst.

Mouth opening at middle of body. Digestive central syncytium extends from brain, past reproductive organs, to posterior tip of body.

Germinal cells in paired strings behind statocyst (Fig. 4B); ovary ventral, testes dorsal. Mature sperm present posteriorly from level of largest egg. Mature sperm like a "string of beads" (Fig. 6C). Paired strings of developing eggs lead to a single large egg located slightly behind mouth.

Male genital pore subterminal at posterior end (Fig. 5). Male antrum long (ca. 40 μm long), with cluster of granules present

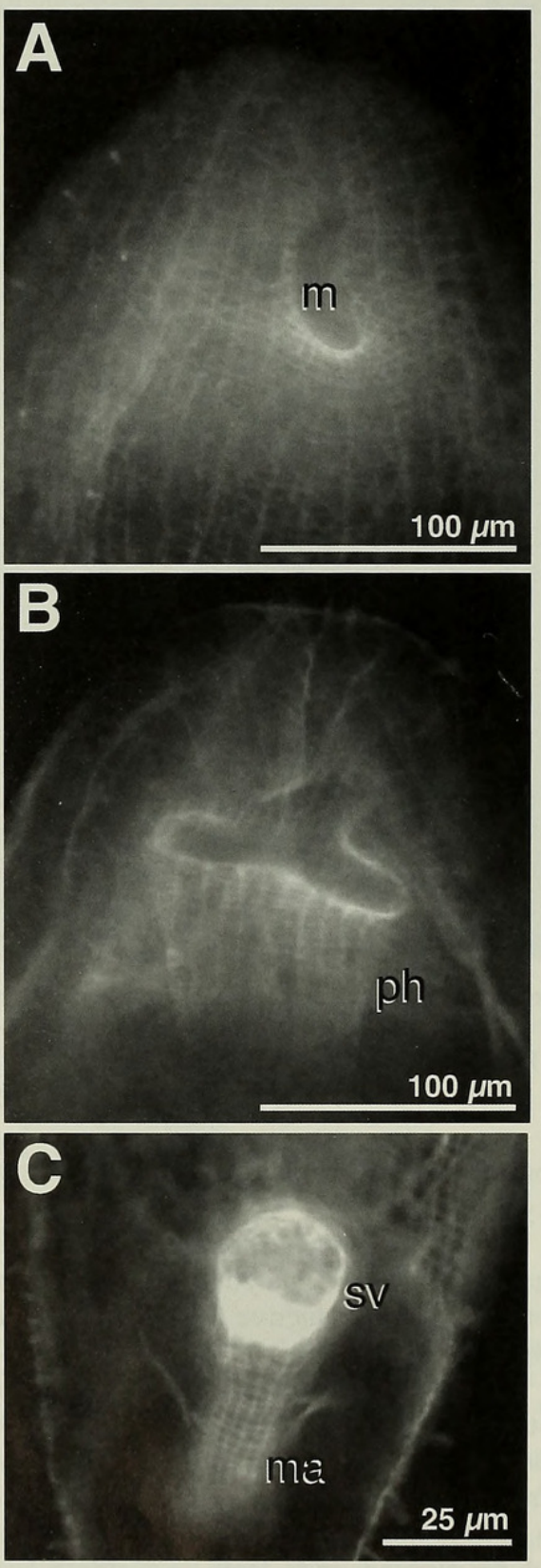

Fig. 9. *Proporus bermudensis,* new species. Whole mounts stained with Alexa-488-labeled phalloidin and viewed with epifluorescence microscopy. A, Ventral view of mouth pore. B, Inner-body musculature of anterior portion of animal, focus on pharynx. C, Inner-body musculature of posterior portion of animal, focus on male copulatory apparatus. Abbreviations: m, mouth; ma, male antrum; ph, pharynx; sv, seminal vesicle.

at its proximal end where it opens into a walled seminal vesicle.

Female pore absent. Weakly walled seminal bursa (Fig. 5), with a large (25 μm long) bursal nozzle (Figs. 5, 6B).

Sagittocysts (Figs. 4, 5) typically less than 20 μm long, scattered infrequently along lateral edges of the body and behind statocyst; largest concentration behind male copulatory organ.

Etymology.—The specific epithet is based on Latin *corallium,* referring to the coral-sand habitat in which this acoel was found.

Taxonomic remarks.—*Antrosagittifera corallina* is united with the genera *Sagittifera* Kostenko & Mamkaev, 1990, and *Symsagittifera* Kostenko & Mamkaev, 1990, in the subfamily Sagittiferinae by the presence of sagittocysts and the lack of fission as a means of reproduction. *Antrosagittifera corallina* has a long ciliated antrum that is unlike the weakly pronounced ciliated antrum of *Symsagittifera* and the complicated sagittocyst-bearing antrum of *Sagittifera.* This acoel has a walled seminal vesicle, a feature not found in the other two genera.

The sole occupant of the genus *Sagittifera, S. sagittifera* Ivanov, 1952, lacks symbionts but has a robust bursal nozzle similar to that of *Antrosagittifera corallina. Antrosagittifera corallina* lacks a female pore and vagina; although this condition is not uncommon among acoel taxa, it is possible that the pore and vagina are present in earlier developmental stages of *A. corallina* but are lost once the seminal bursa is filled with donor-sperm.

Family Proporidae Graff L v, 1882
Proporus bermudensis, new species
Figs. 7–9

Holotype.—AMNH 1606, 1.5-μm-thick serial frontal sections of epoxy-embedded

specimen stained with toluidine blue, collected June 1999.

Type locality.—North Rock, Bermuda. Subtidal coarse coral sand.

Other material examined.—Living specimens in squeeze preparations; three sets of 2-μm-thick serial sections of epoxy-embedded specimens stained with toluidine blue (one sagittal, two oblique-sagittal); whole mounts for fluorescence imaging of musculature (seven specimens). Specimens collected from North Rock, Bermuda. Nomarski photographs of single specimen collected from Castle Roads, March 1985.

Description.—Adult specimens 430–800 μm long and ca. 150 μm wide (Figs. 7A, 8A). Anterior and posterior ends rounded; posterior much narrower. Body without distinct coloration. Ocelli absent.

Epidermis completely ciliated and of the same thickness throughout body. Without epidermal rhabdoid glands.

Musculature with circular fibers that encircle the body along entire length of animal; straight longitudinal muscles present in dorsal and ventral body wall; longitudinal muscles that have a longitudinal orientation anteriorly, but bend medially to cross diagonally over the body (longitudinal-cross-over fibers), present in ventral body wall; dorsal body wall with diagonal muscles interior to circular muscles.

Frontal organ weakly developed; frontal glands projecting to frontal pore from position slightly anterior to statocyst.

Mouth opening sub-terminal at anterior end of body (Figs. 7A, 8A, 9A). Long ciliated pharynx (Fig. 7A), a direct infolding of body wall, with longitudinal and circular muscle fibers (Fig. 9B). Digestive central syncytium extends posteriorly from mouth opening to position behind male copulatory apparatus.

Female and male reproductive structures contained within the digestive central syncytium (Fig. 7A).

Ovaries unpaired. Single string of eggs, each surrounded by nurse cells (Fig. 7A). Without female accessory organs.

Testes unpaired, follicular, restricted to small region immediately anterior to seminal vesicle. Sperm form a small false seminal vesicle immediately outside of the seminal vesicle. Male antrum ciliated (Figs. 7, 8B), a direct infolding of body wall including longitudinal and circular muscle fibers (Fig. 9C). Male antrum capped with a muscular seminal vesicle (Figs. 7, 8B, 9C) with unordered sperm. Rhabdoid-like accessory secretions (Figs. 7B, 8B) that surrounded the posterior portion of seminal vesicle sperm and extended into the male antrum. Additional rhabdoid secretions were present outside of the seminal vesicle in the region of the testes (Fig. 7B).

Taxonomic remarks.—As detailed in Dörjes (1971), Proporidae is composed of a single genus, *Proporus,* and four species. Our animal most resembles *P. venenosus,* which is composed of three subspecies, differing primarily in their body color. The morphology of the male antrum, seminal vesicle, and accessory secretions is very similar in *P. venenosus* and *P. bermudensis.* However, *P. venenosus* has distinct eyespots at the anterior end of its body, as well as paired testes and ovaries. Eyespots are absent in *P. bermudensis,* and its ovary and testis are unpaired.

Reassignment of *Pseudaphanostoma opisthorchis* (Mamkaev, 1967) to the genus *Haploposthia*

The male copulatory apparatus of *Pseudaphanostoma opisthorchis* (Mamkaev, 1967) bears a striking resemblance to that of *Haploposthia vandula* in the way the seminal vesicle is surrounded by gland necks. Although Mamkaev (1967) originally classified *P. opisthorchis* in the genus *Haploposthia,* Dörjes (1968) moved it to *Pseudaphanostoma,* an assignment that seems questionable given the fact that *P. opisthorchis* lacks the muscular seminal vesicle that is diagnostic of the genus *Pseudaphanostoma.* We therefore return this

species to its original placement as *Haploposthia opisthorchis,* n. comb.

Acknowledgments

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