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Anatomy and Systematics of Some Polycystididae (Turbellaria, Kalyptorhynchia) from the Pacific and S. Atlantic

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Paraustrorhynchus gen.n., *P. pacificus* sp.n. (California), *Antiboreorhynchus novzelae* sp.n. (New Zealand) and *Gyratrix proaviformis* sp.n. (Oregon) are described as new taxa. Additional notes are given on *Gyratrix hermaphroditus* Ehrbg. (new localities on the N. American Pacific coast), *Scanorhynchus forcipatus* Karling (new locality in California), *Paraustrorhynchus elixus* (Marcus) comb.n. and *Alcha evelinae* Marcus (new localities in California). The taxonomy of the genera and species is discussed. Viewpoints are presented on evolutionary trends and homologous atrial organs in the family Polycystididae.

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1. Introduction

This paper is in the main a further report from the senior author's turbellarian studies along the N. American Pacific coast in the years 1960 and 1969 (Karling 1962*a*, 1962*b*, 1964, 1966; Schockaert & Karling 1970; Holmquist & Karling 1972). A small material from the Brazilian coast and from New Zealand in the collections of the Swedish Museum of Natural History, Section of Invertebrate Zoology (SMNHI), has also been considered.

The study further belongs to a series of papers (Schockaert 1971, 1974; Schockaert & Brunet 1971; Schockaert & Karling 1970, 1975) intended to result in a monographic review by the junior author on the anatomy and taxonomy of the family Polycystididae.

The senior author is responsible for the main part of this study, but a large part of the studies on serial sections have been elaborated by the junior author.

Drawings without a linear scale have been made freehand. No linear scale has been drawn in the photographs, the size of the pictured animals and organs being evident from the corresponding linear drawings and from the text.

The position of the structures in the longitudinal axis of the animal is determined in per cent of the whole body length beginning from the anterior body tip.

2. Material and methods

The material from the N. American Pacific coast has been collected and studied on live specimens by the senior author. The material for serial sections has been fixed with Bouin's fluid or mercury chloride–formalin–acetic acid solutions. Our general embedding media for whole mounts have been polyvinyllactophenol or Turtox CMCP-9. Sections of 4–5 μm have been stained with Ehrlich's hematoxylin or Heidenhain's ironhematoxylin, eosine or erythrosine being used as counterstains.

The Brazilian material belongs to Dr Ernst Marcus' collection, now in SMNHI (cf. Dörjes & Karling 1975). Its condition makes it difficult to examine, but rather good whole mounts have been achieved by resolving canadabalsam preparations and reembedding the specimens in our general embedding media.

Concerning the material from New Zealand, see the description of *Antiboreorhynchus novzelae*.

All material, including the types, is deposited in SMNHI.

3. Descriptions

Gyratrix hermaphroditus Ehrenberg, 1831

G. arenarius Evdonin, 1971

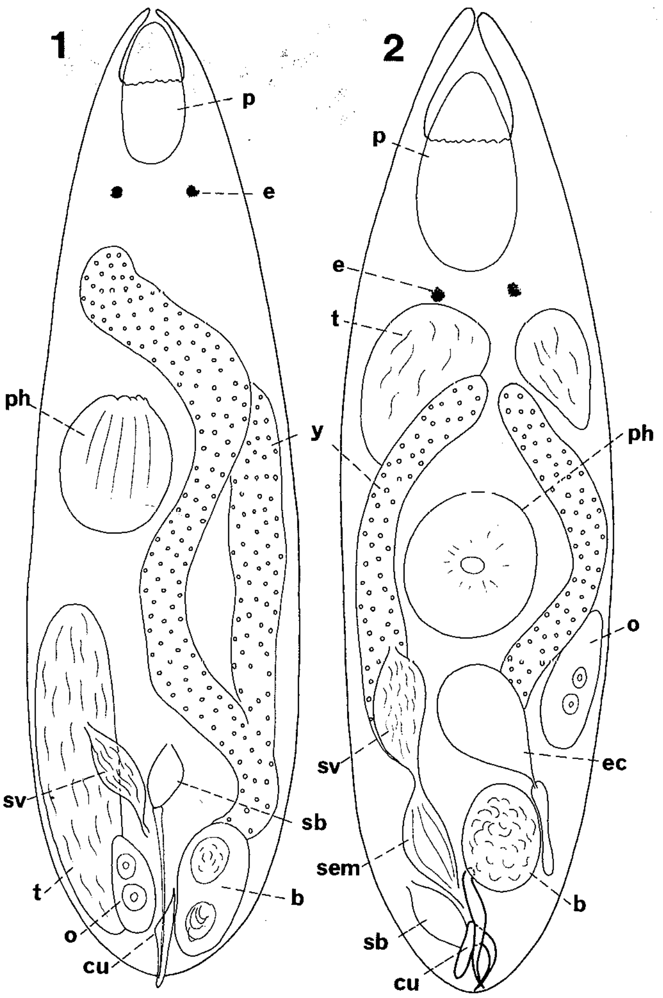
New localities. USA, California, Pacific Grove and Elkhorn Slough, several places in the tidal zone and in tidepools, sand, pebbles, algae (September 1960, March and April 1969); Oregon, Newport, Yaquina head, tidal zone, sand with *Zostera* (1969-04-27).

Other distribution. Cosmopolitan and holeuryhaline. In the Pacific previously reported from the Asian NE area (Evdonin 1971) and Hawaii (Karling et al. 1972).

Material. Live specimens, several whole mounts.

Description and discussion. Among the specific characters of "*G. arenarius*"—paired yolk glands, short distance between male and female genital pores, proportions of the cuticular apparatus (Evdonin 1971)—only that of the yolk glands appears taxonomically acceptable. All these characters are based on live material, which is unreliable in regard to the soft anatomy. The yolk glands of *G. hermaphroditus* form a variable reticulate complex (Meixner 1925, p. 295–297), obviously arisen by fusion of paired gonads. The proportions of the cuticular pieces are in no way exceptional (see below).

No characteristic features have been found in the shape of the cuticular apparatus in the Pacific material. Contrary to *G. proaviformis* (see below) the sheath is about half the length of its stalk and terminally provided with two small teeth enclosing the stylet. The length of the stylet and the sheath+



Figs. 1–2. Squeezed live specimens (free-hand drawings). — *1, Gyratrix proaviformis.* — *2, Scanorhynchus forcipatus* (from California).

stalk vary greatly. The smallest sizes have been recorded in a Hawaiian specimen, stylet 87 μm, sheath 23 μm and its stalk 55 μm (Karling et al. 1972, p. 261). Almost the same measurements have been recorded in a Californian individual (100, 35 and 61 μm respectively) and in "*G. arenarius*" (stylet 89–99 μm, sheath+stalk 95–102 μm, Evdonin, op. cit.), but in another individual from California an exceptionally large apparatus was found (275, 87 and 160 μm respectively).

The morphologically rather homogeneous image of *G. hermaphroditus* remains unchanged after our studies on the Pacific material.

Gyratrix proaviformis **sp.n.** (Figs. 1, 3–5, 10–11)

Locality. USA, Oregon, Boiler Bay, S. of Lincoln City, sand with *Phyllospadix,* low water, 1969-04-02 (type locality).

Material. One specimen studied alive, 3 whole mounts, one of them holotype (No. 2771, leg. Karling).

Derivation of the species name. In allusion to the name of the related species *G. proavus.*

Diagnosis. About 1 mm, faintly yellowish with paired about 30 μm large (max.) eyes, externally highly resembling *G. hermaphroditus.* Yolk glands paired (?), ovary and testis unpaired; large bursa caudally. Stylet 116–117 μm, sheath of stylet unstalked, 65–70 μm (3 measurements). The sheath is proximally obliquely cut off, asymmetrically prolonged to an arched square-cut process.

Discussion. G. proaviformis is evidently closely related to *G. proavus* Meixner from sublittoral mud bottom along the northern part of the European Atlantic coast (Meixner 1929; Karling 1955). A comparison between the two species must be restricted to the features visible on live material and whole mounts, no sections of *G. proaviformis* being available. *G. proavus* is eyeless, its stylet (211–232 μm, Figs. 8–9) about twice as long as in *G. proaviformis,* whereas the sheath of the stylet with 58–75 μm (6 measurements on material in SMNHI) equals that of *G. proaviformis*. The different length-ratio between stylet and sheath in the two species is more important than the absolute figures. The sheath of *G. proavus* is proximally rounded–pointed, not square, and distally provided with a small hook, lacking in the new species.

According to my insufficient material the paired yolk glands seem to be asymmetrically developed in the two species, on one side extending more anteriorly than on the other side.

G. hermaphroditus differs distinctly from *G. proavus* and *G. proaviformis* in its long stalk of the stylet-sheath, and also —at least from *G. proavus*—in some features of the internal anatomy. According to Meixner (1929, p. 788) *G. hermaphroditus* has evolved from a form like *G. proavus*. This holds true also after the discovery of *G. proaviformis,* the level of organization being the same in these two species. To place one of them on a higher evolutionary level than the other is not yet possible.

Scanorhynchus forcipatus Karling, 1955 (Figs. 2, 6–7, 12–14)

? S. modestus Evdonin, 1971

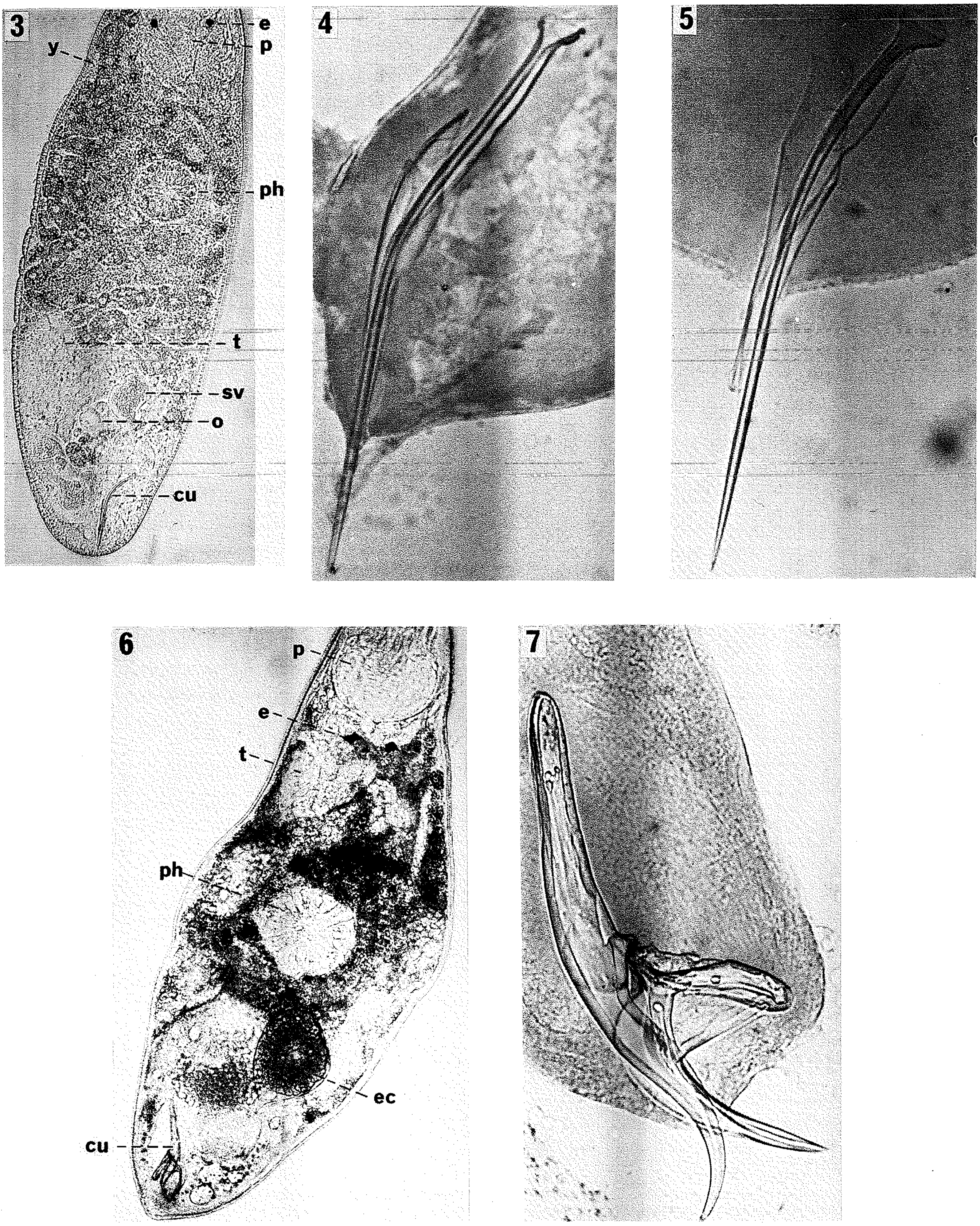
New locality. USA, California, Monterey Bay, fine sand with mud, 2–10 m (1960-09-19 and 1969-04-03).

Other distribution. European Atlantic coast, N. Sea, Skagerrak, Irish Sea, sandy mud, 0–11 m (Karling 1955; Boaden 1966; Schilke 1970). Distribution of *S. modestus:* Sea of Japan and Sea of Okhotsk, sandy bottom in the littoral and the sublittoral zones (Evdonin 1971).

Material. Observations on live material, one whole mount (1969). In 1960 the cuticular apparatus was studied in a crushed specimen.

Description. The description is based mainly on the material from 1969. Length 1.1 mm (in life about 1.5 mm), colourless with paired 29–30 μm large eyes. Proboscis in retracted condition 210 μm (1/6 the body length), pharynx diameter 210 μm. Testes and yolk glands paired but one of the testes smaller than the other; the ovary is unpaired. The male cuticular apparatus is shaped as in the European populations (Karling 1955), thus consisting of a slightly curved, distally pointed, proximally blunt needle and a curved stylet with a triangular basal funnel articulating in a point of its margin with the needle, the opposite part of the edge broadening to a process for muscle attachment. Measurements: needle 174 μm, stylet 87 μm, breadth of basal funnel 58 μm (i.e. about half the length of the stylet). The apparatus is smaller in the 1960 specimen (length of the needle only 72 μm) and the breadth of its stylet base is only about 1/3 of the whole stylet.

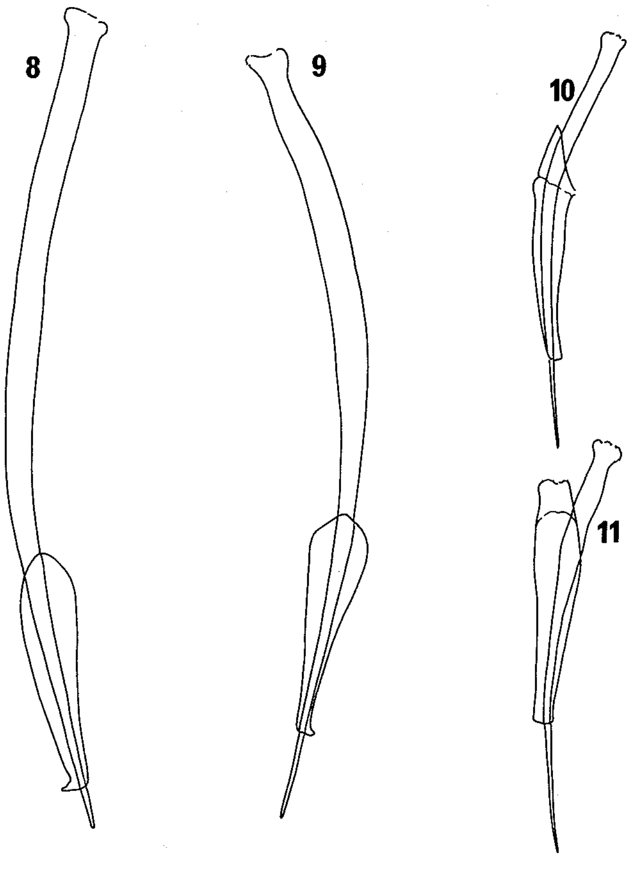
Discussion. The width of the basal funnel in relation to the length of the stylet is markedly greater in the 1969 phenon than in the specimen from 1960, which in this respect agrees



Figs. 3–7. — *3–5, Gyratrix proaviformis* (3, squeezed live specimen; 4–5, male cuticular apparatus, from two whole mounts). — *6–7, Scanorhynchus forcipatus* (from California) (6, squeezed live specimen; 7, male cuticular apparatus, from a whole mount).

with the European form. There is a corresponding difference in the size of the whole apparatus (1969: max. length 174 µm; 1960: 72 µm; European form: 60 µm according to Karling 1955, and 52 µm according to Schilke 1970). The different data from 1960 and 1969, evidently from animals of the same population, does not justify a separation of a Pacific from an Atlantic species on the basis of the cuticular apparatus.

There are two features separating the 1969 phenon from the European form. The ratio proboscis length/body length is about 1/6 in the former, 1/12 in the latter; there are two testes



Figs. 8–11. Male cuticular organs, from whole mounts. — *8–9, Gyratrix proavus* (from Gullmaren, Swedish W. coast, originals). — *10–11, Gyratrix proaviformis.*

—one of them rather small, however—in the former, one single testis in the latter. The ovary is unpaired and the yolk glands are paired in both. Such differences could justify separation on the species level. However, the proboscis is markedly small in the 1960 phenon, according to an observation before the specimen crushed. Further, *S. modestus* Evdonin must be considered in these taxonomic discussions (Evdonin 1971). This species is evidently identical with or at least closely related to *S. forcipatus*. It is true that its cuticular apparatus looks somewhat different, but the picture (Fig. 15) is certainly erroneous in regard to the joint between stylet and needle, the articulation of the two being disregarded. The size of the apparatus is slightly greater (88–98 µm) than in our 1960 phenon, but the proboscis has the same size as in our 1969 phenon.

To sum up, the genus *Scanorhynchus* is represented in the Pacific by (at least) one form, which anatomically closely agrees with *S. forcipatus,* hitherto known only from the European Atlantic waters. The data on the differences between the forms and on the different phena from the Pacific are not unequivocal. The taxonomic state of *S. forcipatus* from the Pacific is thus provisional.

Genus ***Paraustrorhynchus*** gen.n.

Diagnosis. Polycystididae with paired gonads and seminal vesicles and with ventral common genital pore. Large male atrium without copulatory bursa. The male copulatory apparatus consists of a secretory bulb with cuticular outlet (stylet), a complex cuticular organ of two articulating legs with associated muscular non-secretory bulb and of gland bundles closely associated with the seminal duct opening into the male atrium. Female atrial apparatus opens from behind, uterus from the front into the common atrium close to the genital pore. No insemination canals.

Type species: *P. pacificus* sp.n.

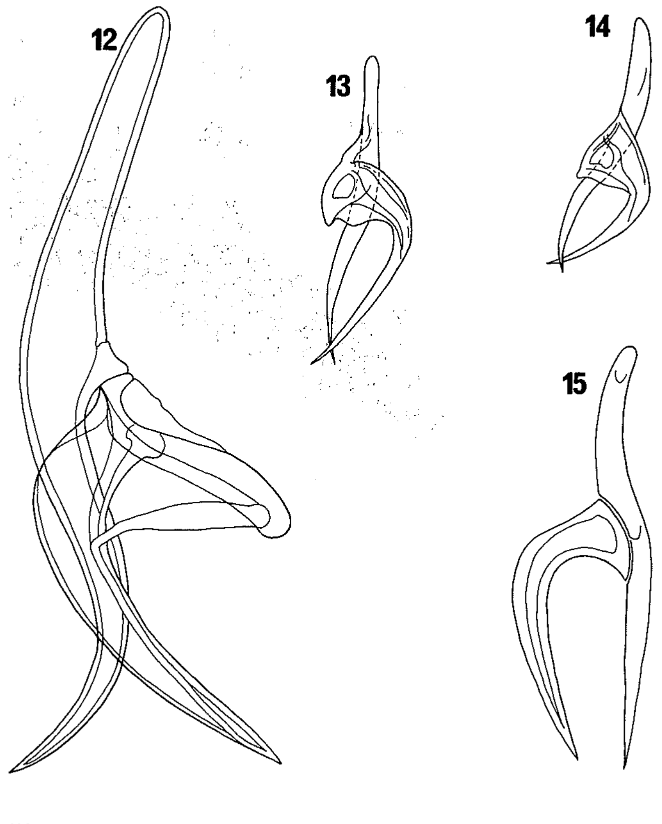
Paraustrorhynchus pacificus sp.n.
(Figs. 16–19, 20, 23, 33)

Localities. USA, California, Monterey Bay, off Fishermens Wharf, fine sand with mud, about 26 m, 1960-09-19 (type locality); Pacific Grove, Point Pinos, "Great tidepool", seaweed and pebbles, March 1969.

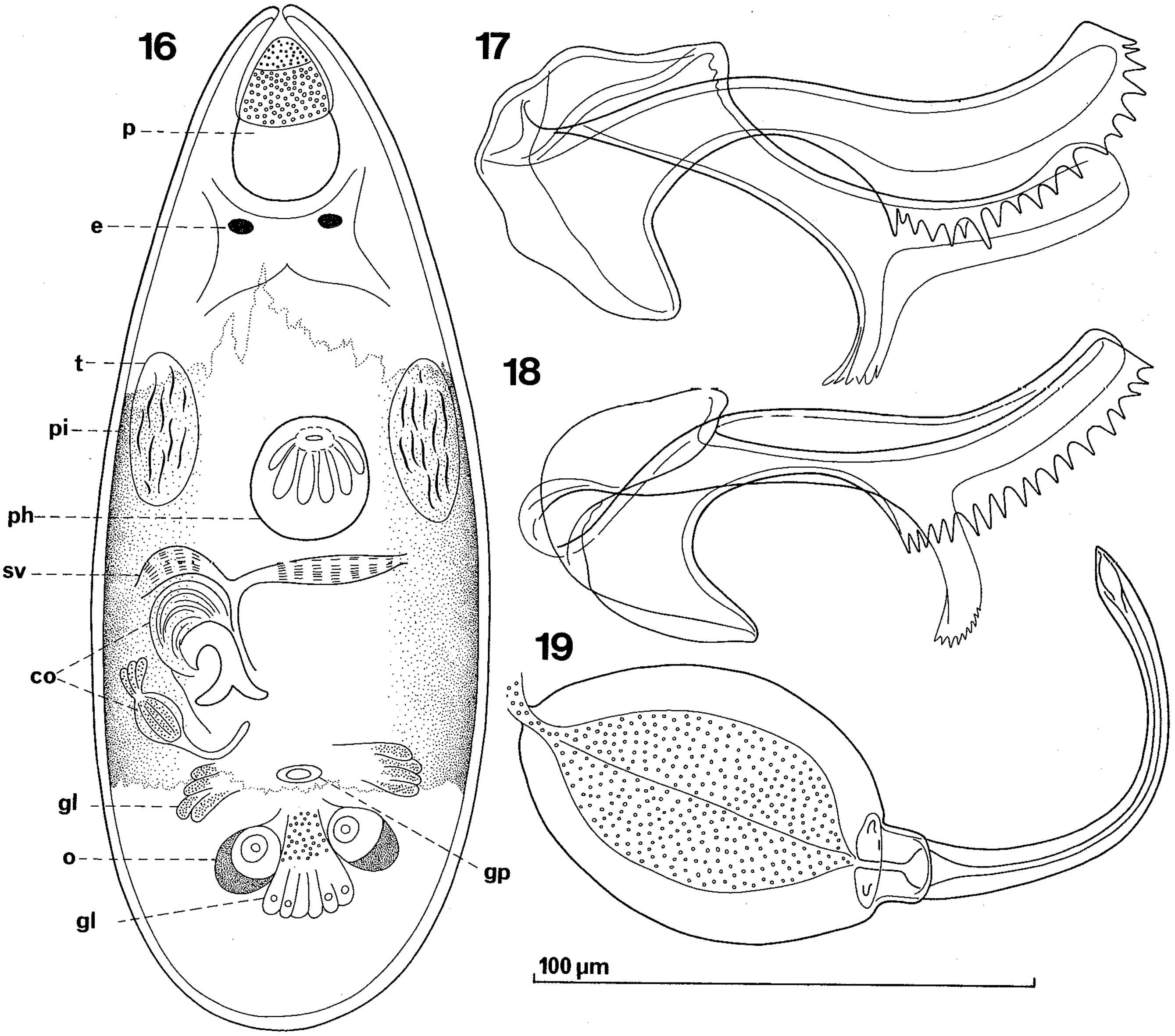
Material. Observations on live material, two whole mounts, one of them holotype (No. 2772, leg. Karling), 8 specimens serially sectioned.

Diagnosis. Stylet of the secretory bulb a 120–130 µm long, fine, curved tube (Fig. 19). Complex cuticular organ about 140 µm (Figs. 17, 18). It consists of two proximally articulating legs of equal length. Both legs broaden distally, one to a comb with short triangular teeth, the other to a pair of lobes, one of them smooth, the other distally finely toothed (see also Fig. 33). The legs are moved by an almost globular muscle arch around the elastic cuticular joint of the legs. Female atrial apparatus without bursa.

Description. Adult live specimens (Figs. 16, 20) 1–1.5 mm, fusiform, anteriorly tapering, caudally rounded, paired almost



Figs. 12–15. Scanorhynchus species, male cuticular organs. — *12–14, S. forcipatus* [12, Monterey Bay, 1969; 13, the same, Monterey Bay, 1960; 14, the same, European form (from Karling 1955)]. — *15, S. modestus* Evdonin (from Evdonin 1971).



Figs. 16–19. Paraustrorhynchus pacificus. — *16,* squeezed live specimen (free-hand drawing). — *17–18,* complex cuticular organ in different aspects, from a squeezed live specimen. — *19,* secretory bulb with stylet from the same specimen.

globular eyes behind the proboscis. Pharynx in about 30%. Mid part of the body dorsally with a brown pigment mantle, which is irregularly delimited, anteriorly with patches of variable length and shape. The pigment consists of small granules under the body wall. The paired ovaries laterally in about 80% are covered proximally with a brownish pigmented tunica. Three cuticular structures, two of them more or less covering each other, can be seen in about 60%. They belong to the male copulatory apparatus.

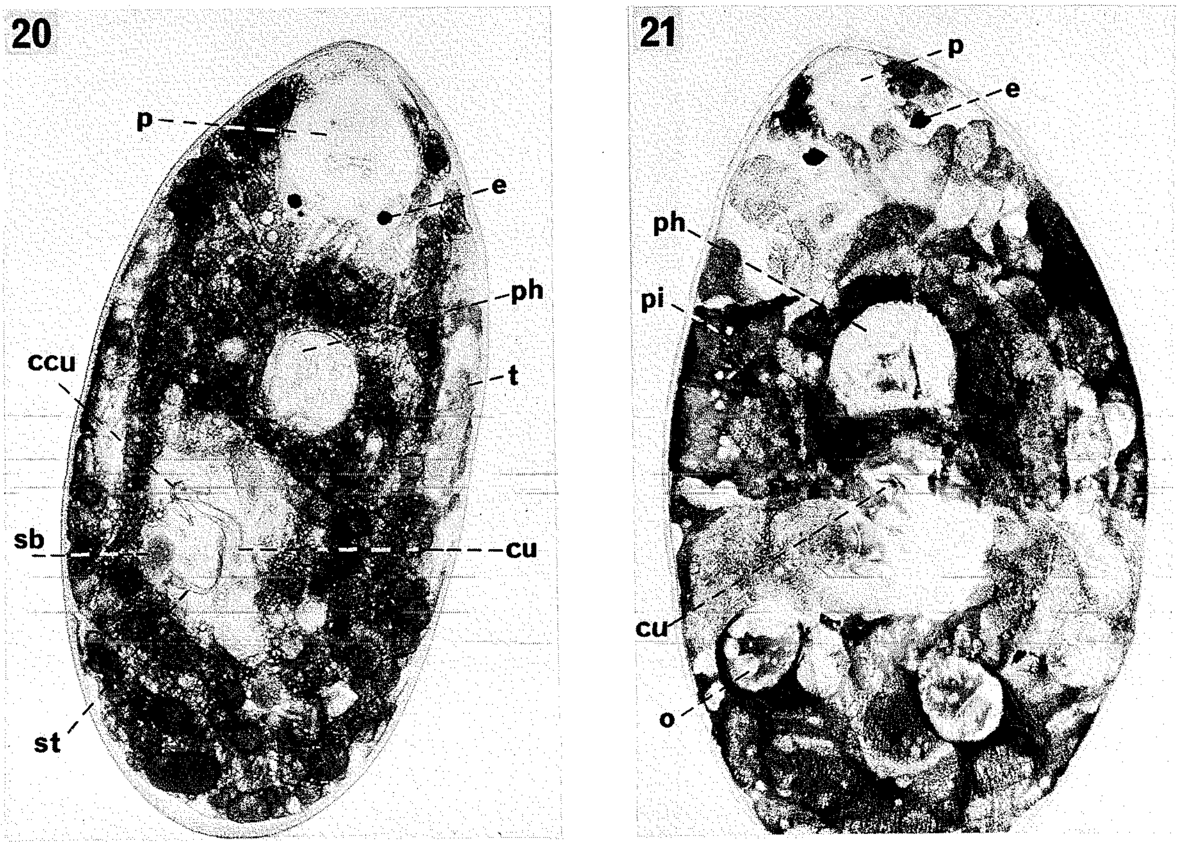
Here only genital organs will be described in detail. The gonads are paired, the testes laterally situated beside the pharynx, the yolk glands forming a dorsal mantle when fully developed.

The genital pore in about 70% opens into a small common atrium receiving anteriorly the uterus stalk, posteriorly the female genital canal, and enlarges dorsally to the male genital atrium (Fig. 23).

The female canal is divided by a sphincter into a narrow distal duct and a small proximal cavity, which laterally receives the paired ovovitelloducts and from behind a large bundle of glands. The cavity can contain sperm but is not differentiated to a real bursa.

In the sections the spacious male atrium is more or less folded with its epithelium in part transformed to pseudocilia and its basement membrane caudally and dorsally strengthened to a pseudocuticle, indicating a function as copulatory bursa of this atrial part. Here also (alien) sperm and secretion could be found. A tubiform diverticle of varying length enclosing a curved stylet opens into the male atrium from the left side in front of the "bursa". Anteriorly the male atrium branches into two wide diverticles, one for the complex cuticular apparatus, the other the seminal diverticle. A strong two-layered muscular mantle encloses the male atrium. The course of the muscle fibers is rather regular around the distal funnel-shaped part of the male atrium, in the internal layer circular, in the external layer longitudinal. Proximally the course of the fibers is irregularly spiral in both layers.

The stylet is fixed with its proximal cylindrical base to a secretory bulb. It is double-walled, groove-shaped with



Figs. 20–21. Squeezed live specimens. — *20, Paraustrorhynchus pacificus.* — *21, Alcha evelinae* from California.

slightly enlarged distal pore. The bulb is short, fusiform with a thick muscle mantle of spiral fibers. It contains three strands of fine eosinophil secretion of one single sort. It is fixed to the globular muscle arch (see diagnosis) by muscle fibers evidently functioning as retractor of the bulb. Complex cuticular apparatus, see diagnosis.

The seminal diverticle is cut off from the main part of the male atrium by a broad sphincter, proximally thinned out to a single layer of fibers around the diverticle. The short seminal duct from the paired seminal vesicles and two bundles of gland ducts with different secretion open into the diverticle, which thus functions as an ejaculatory duct. Coarse secretion, intensely stained by hematoxylin, accumulates in an ampulla with its own membranous wall. Another bundle consisting of some (five?) strands with fine eosinophil secretion somewhat protrudes into the diverticle in the shape of a cushion of irregular papillae, evidently a result of the contraction of the circular fibers enclosing the bundle.

Discussion, see chapter 4.

Paraustrorhynchus elixus (Marcus, 1954) comb.n.
(Figs. 25–28)

Austrorhynchus elixus Marcus, 1954

Locality. Atlantic, Brazil, Bay of Santos, São Vicente, tide pools with shell gravel (type locality); Ilha de São Sebastião (Marcus 1954).

Material. One slide with several sectioned specimens of different taxa, two whole mounts prepared from material in alcohol, one of them designated lectotype (No. 2780, leg. E. Marcus).

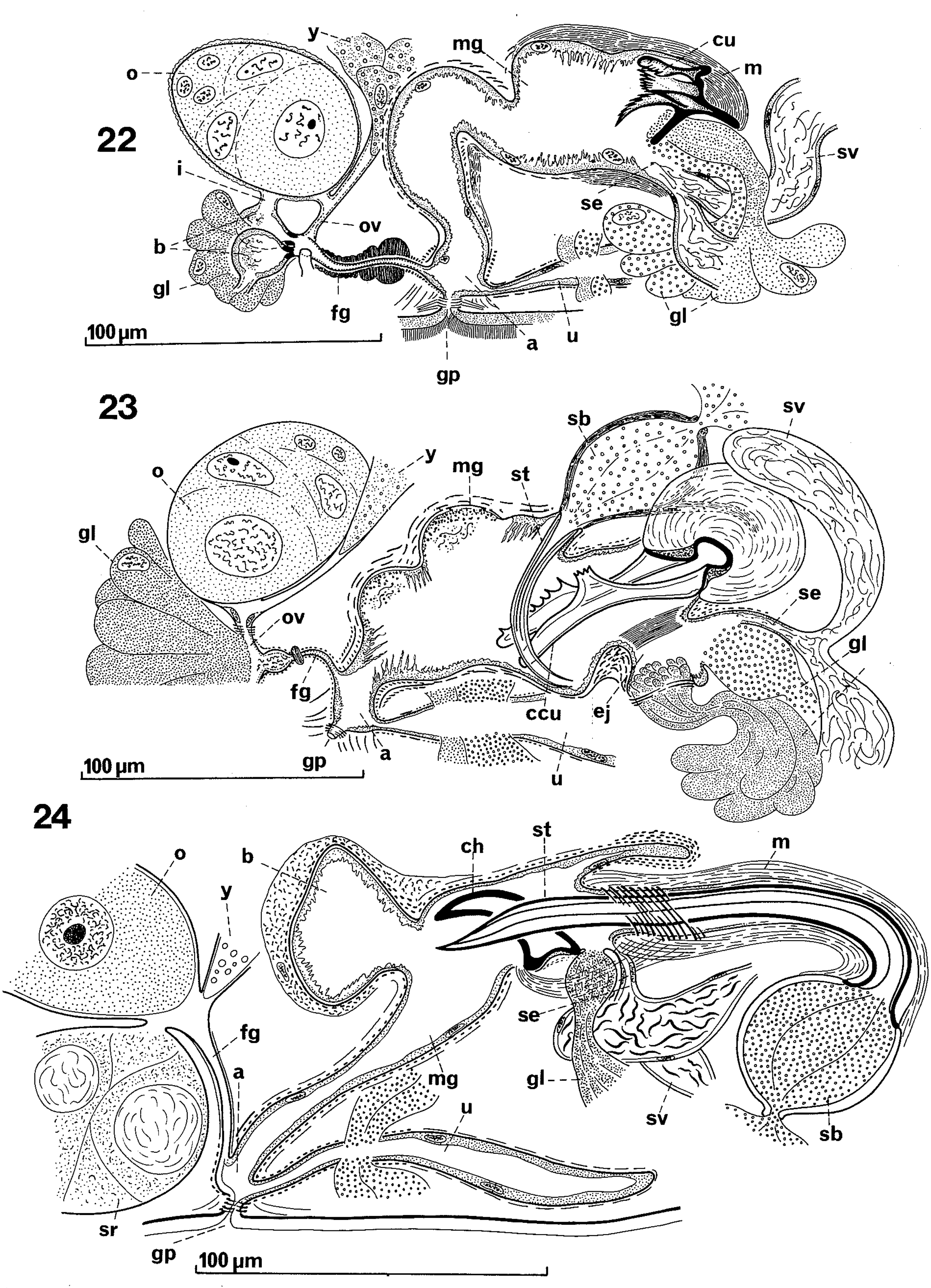
Diagnosis. Stylet of the secretory bulb a short hook (Marcus, 15–30 μm; lectotype, 30 μm). Complex cuticular apparatus of two distally pointed S-shaped flattened pieces (Marcus, 50 μm; lectotype 80 μm). The shorter piece is distally hook-shaped and at half its length, where the two pieces articulate with each other, provided with a short, pointed tooth (Figs. 25–26). Female atrial apparatus with a bursa communicating with the intestine.

Description. Some additional and correcting notes will be given to Marcus' description (1954) of the male copulatory apparatus. The bent needle of the complex cuticular organ encloses, according to Marcus, the seminal (ejaculatory) duct. We have found that the two pieces of the complex organ articulate at a joint at approximately half their length and that the common seminal duct opens freely into the male atrium beside the base of the needle. The pointed tooth emerges at the joint of the two pieces. A bundle of glands open close to the pore of the seminal duct. An almost globular muscle arch encloses the basal parts of the two pieces and bundles of muscle fibers run from the arch to the secretory vesicle (Figs. 27–28).

Discussion, see chapter 4.

Genus ***Alcha*** Marcus, 1949

New diagnosis (cf. Marcus 1949, p. 32). Polycystididae with paired gonads and seminal vesicles and with ventral common genital pore. Large male atrium without copulatory bursa. Male copulatory apparatus with a cuticular organ (40–53 μm long in *A. evelinae*) consisting of several (3?) distally comb-shaped lamellae based on a common triangular frame. The seminal duct and a bundle of glands open into the male



Figs. 22–24. Sagittal reconstructions of the atrial organs, from the right side. — *22, Alcha evelinae.* — *23, Paraustrorhynchus pacificus.* — *24, Antiboreorhynchus novzelae.*

atrium close to this organ. No secretory bulb, no tubular stylet. Female atrial apparatus opens from behind, uterus from the front into the common atrium close to the genital pore. Female atrial apparatus with paired globular bursae together functioning as insemination canals.

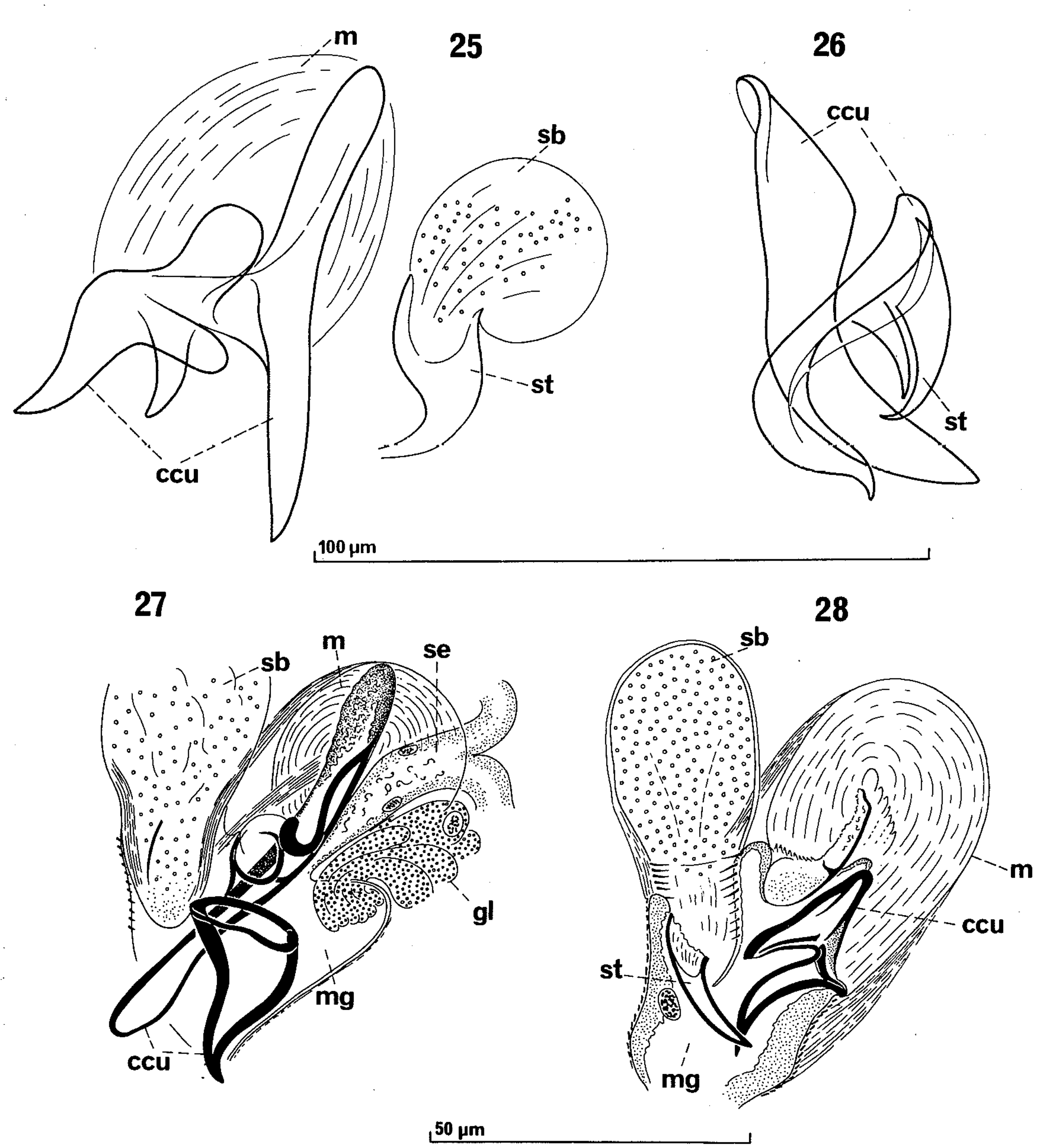
Type species: *A. evelinae* Marcus, 1949.

Alcha evelinae Marcus, 1949 (Figs. 21, 22, 29–32, 34, 35)

New localities. USA, California, Pacific Grove, Hopkins Marine Laboratory, tidepools (September 1960), and Point Pinos, "Great tidepool", seaweed and gravel (March 1969).

Other distribution. Atlantic, Brazil, Bay of Santos, Ilhas das Palmas and de São Sebastião, seaweed in the eulittoral zone (type locality, Marcus 1949).

Material. Marcus' material, consisting of one slide with sagittal



Figs. 25–28. Paraustrorhynchus elixus. — *25,* male copulatory apparatus from a whole mount. — *26,* male cuticular apparatus from another whole mount. — *27–28,* male copulatory apparatus from serial sections.

sections, evidently the basic material for Figs. 39–41 in Marcus (1949), and three whole mounts (new preparations in polyvinyllactophenol), one of which designated lectotype (No. 2664, leg. Marcus). The Californian material, consisting of two whole mounts and six specimens sectioned serially. Our description is based on the Californian material in regard to the internal anatomy and on the whole mounts from both collections in regard to the male cuticular apparatus.

Diagnosis, provisionally as for the genus, see above.

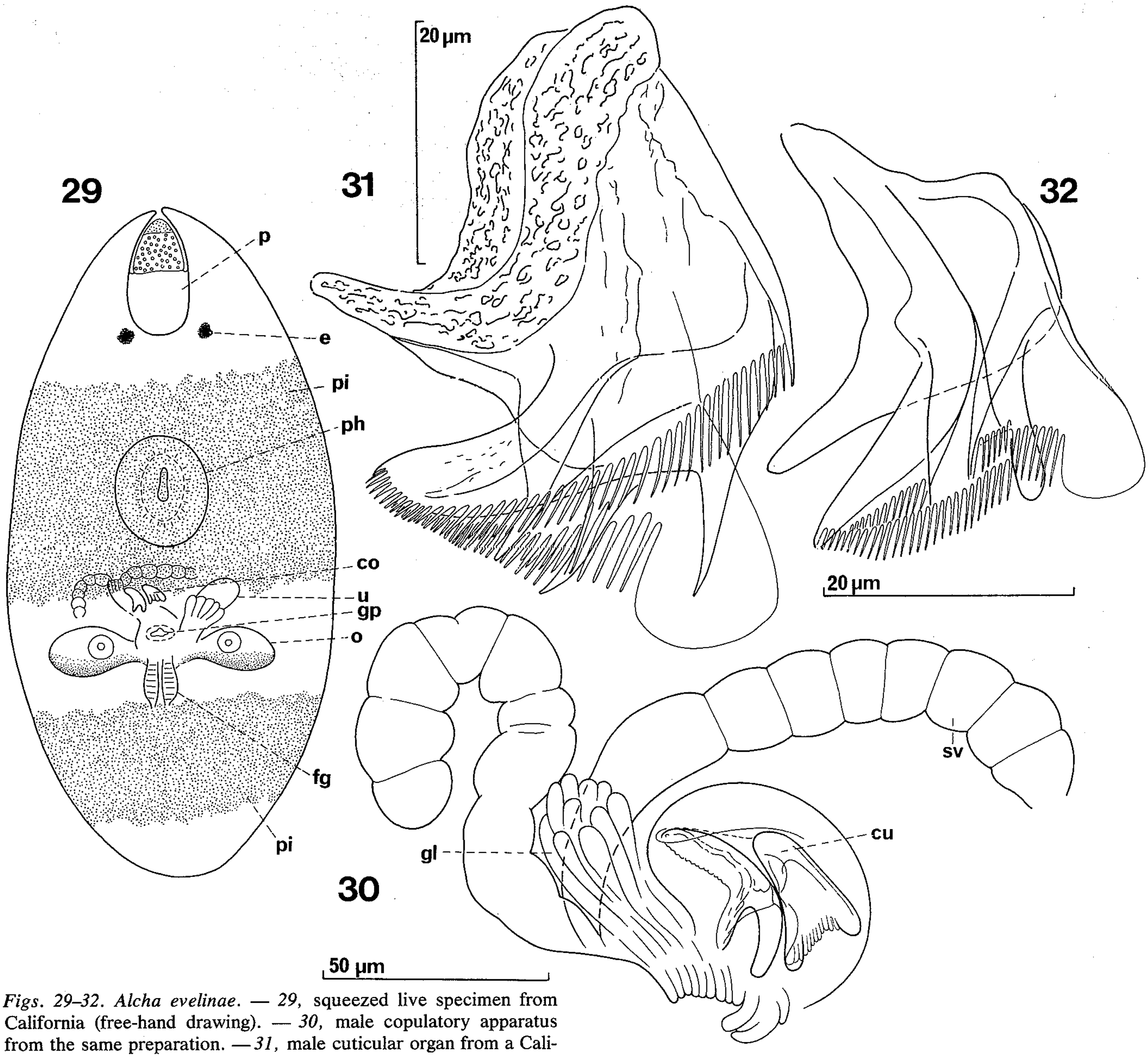
Description. Marcus' observations of the shape and colour of the animal are principally in accordance with our own observations (Figs. 21, 29).

The animal is about 1 mm, fusiform, anteriorly tapering, caudally rounded. Most characteristic is the pattern of pigmentation, two broad dark-blue dorsal mantles against a (brown-) yellowish background. The yellowish colour is bound to the perivisceral fluid, the blue to a layer of fine granules under the body wall. The blue mantles are irregularly delimited and sometimes split up to smaller areas. In young animals they are incomplete, the posterior mantle sometimes lacking. The ovaries are yellowish pigmented to a varying degree. The paired black eyes behind the rather small proboscis (1/8 of the body length) are about 25 µm large. The pharynx in about 40% is also rather small. Slightly behind the pharynx the small male cuticular apparatus can be seen.

Contrary to Marcus' information, no cellular membranes can be seen in the epidermis. As reported by Marcus, there are four cuticular knobs at the proximal pharynx pore, a feature highly characteristic in the fam. Polycystididae.

Six radial rows of fixators can (contrary to Marcus) be separated from the protractors of the proboscis. We have found one single pair of integument retractors (ventrally) but cannot say anything definitely about the proboscis retractors. Two pairs of glands open in the apex of the proboscis and one pair of frontal glands beside the aperture of the proboscis pocket.

Marcus' observations on the paired gonads can be verified. Additional and correcting notes will be given on the atrial organs.

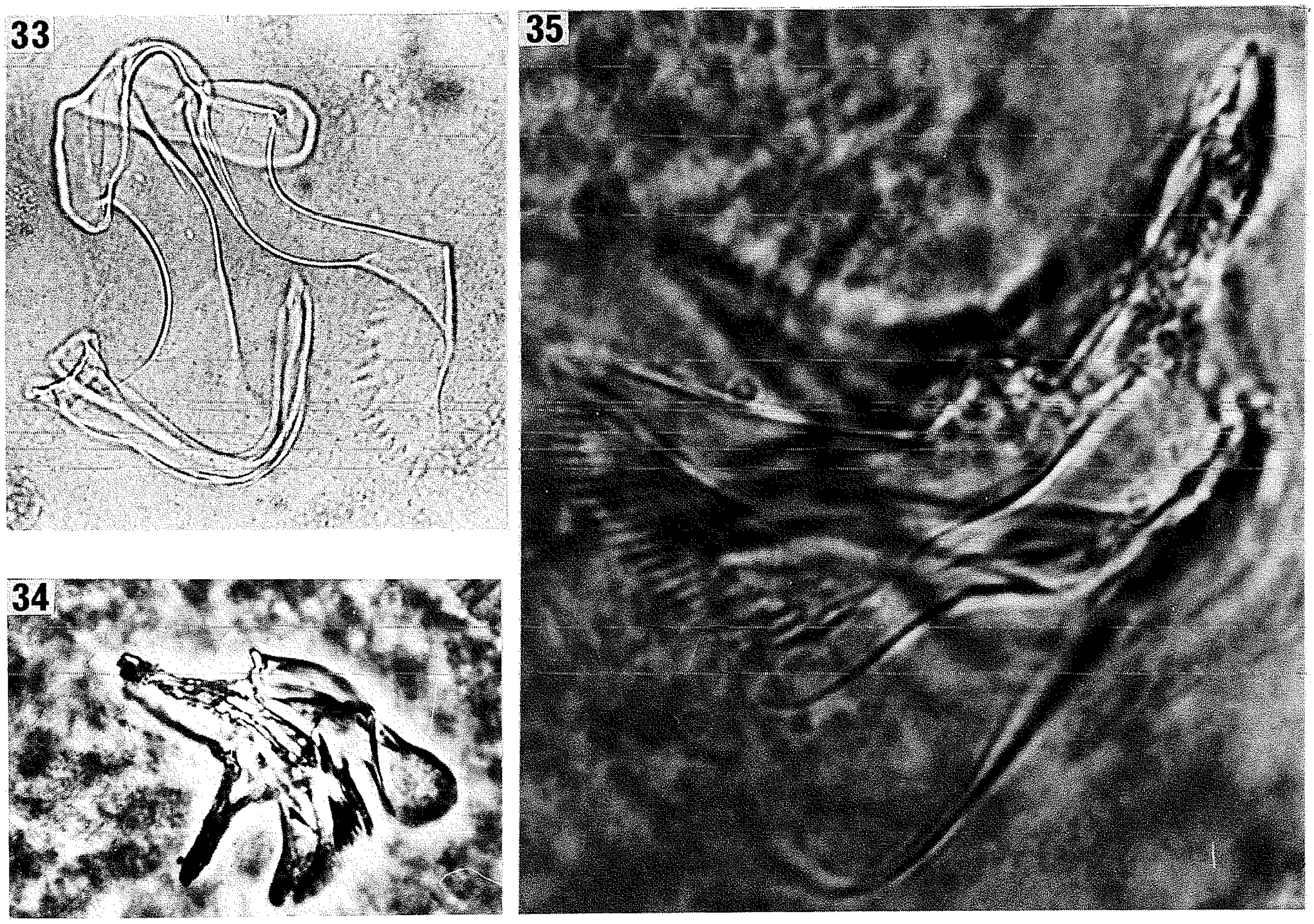


Figs. 29–32. Alcha evelinae. — *29,* squeezed live specimen from California (free-hand drawing). — *30,* male copulatory apparatus from the same preparation. —*31,* male cuticular organ from a Californian specimen, whole mount. — *32,* the same from a Brazilian specimen, whole mount (=Fig. 35).

The two small bursae with their cuticular "mouthpieces" and the strong sphincter around the female genital canal are similar in the Brazilian and the Californian material (Fig. 22). However, contrary to Marcus, the bursae are not closed proximally but communicate with the ovaries through short plasmatic ducts, being thus dilatations of paired insemination canals. The ovocytes are evidently discharged together with the yolk cells through paired canals, the oviducts s.lat., not through the bursae, where the mouthpieces are efficient obstructions, but the oviducts s.str., i.e. the pores from the ovaries to the vitelloducts, were not distinctly seen in our slides (Marcus has drawn them in his Figs. 39–40).

Marcus describes the male atrium as consisting of a large external vesicle enclosing an internal one. This is a misinterpretation due to the fact that the spacious male atrium is more or less folded in preserved animals, in its posterior part enlarged and thus functioning as copulatory bursa. The condition of the epithelium in the male atrium varies, evidently owing to the state of sexual maturity, sometimes normal with big nuclei, sometimes transformed to pseudocilia, sometimes degenerated upon a pseudocuticle. The main part of the thick muscular mantle around the male atrium consists of protractors evidently functioning in protrusion of the complex structures in the proximal end of the male atrium including the cuticular apparatus.

The short wide seminal duct from the paired seminal vesicles opens together with an ampulla filled with secretion into the anterior end of the male atrium. The ampulla consists of the enlarged ducts of two kinds of glands differing in the coarseness of their secretion. The cuticular apparatus is situated beside this complex. Marcus describes it from sections (1949, Figs. 39, 41) as three curved pointed blades. Our material makes a more detailed description of the organ possible, but misinterpretations are not excluded, due to its complicated construction and small size. In gently squeezed live animals it appears as a distally bifurcated curved hook basally united with an almost triangular distally fringed piece (Figs. 30, 34). In whole mounts and with high magnification the



Figs. 33–35. Male cuticular organs, whole mounts. — *33, Paraustrorhynchus pacificus.* — *34, Alcha evelinae,* Californian specimen. —*35,* the same, Brazilian specimen (=Fig. 32).

organ is revealed as one single structure consisting of a system of membranes—here called the skirt—based on an irregularly triangular frame (Figs. 31, 32, 35). It is possible that the skirt consists of three (see above, Marcus) irregularly folded plates with some ridges resembling hooks. The "hem" of the skirt is laterally drawn out to a "tongue" and on the opposite side to a rounded "blade". The rest of the hem is differentiated to combs with fine teeth. Two combs begin with short teeth on the tip of the tongue, a third comb with long teeth beside the blade. A break in the rim (system of combs) indicates a slit in the skirt.

The cuticular organ described here has the same shape and consists of the same parts in the Brazilian and the Californian material. It is a little smaller in the former (40 μm, three specimens) than in the latter (53 μm, two specimens) and the teeth are accordingly a little different in size. These differences appear to be taxonomically unimportant.

Discussion, see chapter 4.

Genus **Antiboreorhynchus** Karling, 1952

Diagnosis (modified from Karling 1952). Polycystididae with paired gonads and seminal vesicles (testes and seminal vesicles not known from *A. torquatus*) and with ventral common genital pore. Large male atrium with stalked copulatory bursa. The male copulatory apparatus consists of a secretory bulb with curved (spiral) cuticular stylet, a simple cuticular piece of varying shape, and of gland bundles closely associated with the seminal duct opening into the male atrium (not seen in *A. torquatus*). Female atrial apparatus opens from behind, uterus from in front into the common atrium close to the genital pore. No insemination canals.

Type species: *A. torquatus* Karling, 1952.

Antiboreorhynchus novzelae sp.n.
(Figs. 24, 36–38)

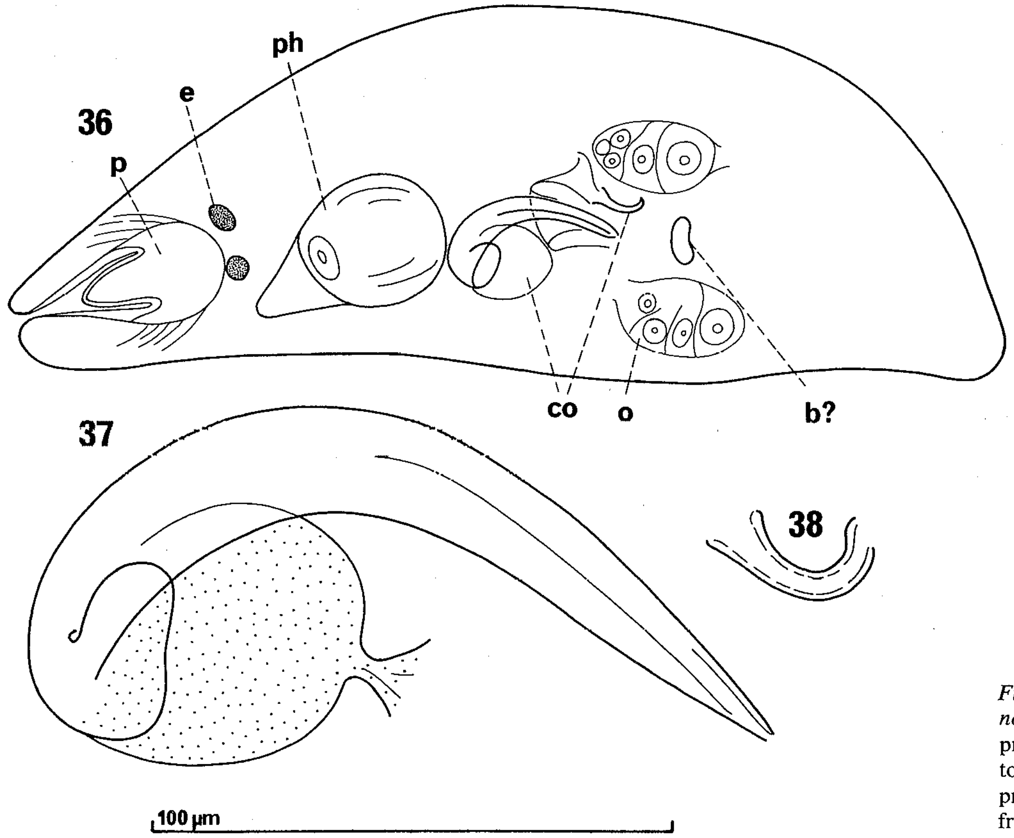
Locality. New Zealand, Little Papanui near Dunedin, on shells of living *Perna (Mytilus) canaliculus* Gmelin, Nov. 1953 and Febr. 1954 (type locality, the sample contained two specimens, one of them a plagiostomid).

Material. One specimen fixed in "Susa", at first slightly squeezed (Fig. 36), then sectioned longitudinally, one slide (holotype No. 2779, leg. E. J. Batham). The specimen is sexually mature with well developed male and female genital organs.

Derivation of the species name. The name "novzelae", abbreviated from novaezealandiae, regarded as an unpractical name.

Diagnosis. Stylet of the secretory bulb an approx. 140 μm long, curved, distally tapering and pointed tube (Fig. 37). The simple cuticular piece an approx. 28 μm long hook with square tip (Fig. 38). Female atrial apparatus with separate seminal receptacle.

Description. Fixed 0.8 mm long, colourless with paired eyes. Proboscis in front of the eyes, pharynx behind the eyes. At



Figs. 36–38. Antiboreorhynchus novzelae.— *36,* a slightly squeezed preserved specimen.— *37,* secretory bulb with stylet from the same preparation.— *38,* cuticular hook from the same preparation.

half the body length two cuticular structures belonging to the male copulatory system.

Here the genital organs only will be considered in detail. The gonads are paired, the testes situated laterally behind the pharynx, the ovaries laterally behind the atrial complex and the yolk glands dorsolaterally extending from the brain to the rear end.

The genital pore in about 60% opens into a small common atrium receiving anteriorly the uterus stalk, dorsally the male and behind it the female genital canal (Fig. 24). The fine, weakly muscular female canal can be followed in dorsolateral direction to a small cavity into which the paired oviducts open. (The vitelloducts were not distinctly seen.) The cavity communicates on its ventral side with the globular seminal receptacle of vesicula resorbiens type.

The male genital canal is also directed dorsolaterally but on the opposite body side in relation to the female canal. It is distally tubular, proximally enlarged to a strongly folded cavity with a caudal sac-shaped diverticle interpreted as copulatory bursa. Anteriorly a cylindrical stylet pouch opens into the cavity. The male canal has a thin, in part nucleated epithelium, a basement membrane, which in the copulatory bursa is strengthened to a pseudocuticle, and a strong muscular mantle. The paired seminal vesicles open through a short seminal duct into the male genital canal between the hook and the stylet pouch.

Two cuticular organs, the stylet and a small hook (Figs. 37, 38, see also diagnosis), are enclosed in the cavity of the male genital canal.

The stylet discharges secretion from the almost globular secretory vesicle. The hook, according to the rather defective observation on the squeezed specimen, is shaped as a tube with enlarged base and square tip. Our sections do not give a clear impression of the relation between the hook and the bundle of glands opening in the area of the hook base and the adjacent pore of the seminal duct. This topography and the shape of the hook (drawn pointed in our sagittal scheme, Fig. 24) can not be taken for granted, due to the folded condition of the atrial wall and the splitting of the cuticular structures in the single available specimen. The shape of the hook as drawn from the squeezed specimen indicates discharging of secretion through the hook.

Discussion, see chapter 4.

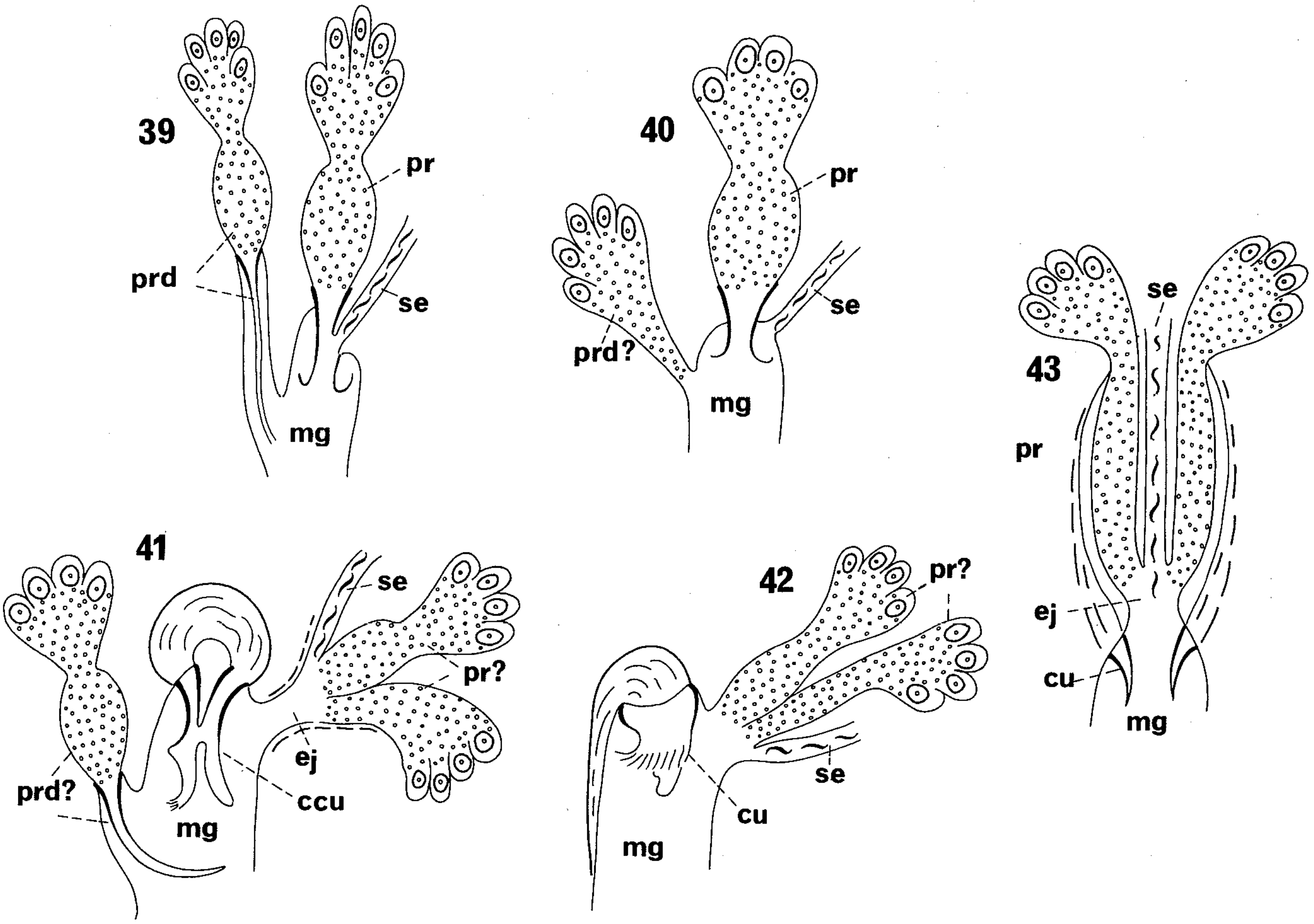
4. On the systematics in the family Polycystididae

For the systematic viewpoints presented below only the senior author is responsible. A broad approach to the systematics in Polycystididae is planned by the junior author.

4.1. *Evolutionary trends and homologous organs in the atrial apparatus*

Phylogenetic considerations based on supposed homology of anatomical structures are often complicated by evolutionary trends, especially frequent in animal groups on a low evolutionary level (cf. Karling 1963*b*). Such trends can be demonstrated in most parts of the atrial apparatus in Polycystididae.

In the female apparatus alien sperms can be stored in a part of the common oviduct (female genital canal), as in *Paraustrorhynchus pacificus.* A seminal receptacle (sometimes paired), such as that in *Antiboreorhynchus novzelae,* is a derivative of this structure. Paired insemination canals,



Figs. 39–43. Schemes of the male copulatory apparatus. — *39, Phonorhynchus helgolandicus.* — *40, Polycystis naegelii.* — *41, Paraustrorhynchus pacificus.* — *42, Alcha evelinae.* — *43, Utelga* sp. Cf. the text.

known e.g. in *Porrocystis* and *Austrorhynchus* (Karling 1952), have evolved to paired bursae in *Alcha evelinae.* A comparison of the female organs in *Alcha* and *Gemelliclinus flavidus* Evdonin (Evdonin 1970, Fig. 4) may exemplify this situation. Both taxa have small paired seminal receptacles [*G. flavidus* also an unpaired female (?) bursa]. In the latter species they have been described as parts of the paired oviducts; in *Alcha* they were originally described as diverticles of the female canal, but have now been revealed as transformed insemination canals. In phylogenetic weighting of such structures, not ~~only parallelism~~ must be considered but also our insufficient knowledge of these often subtle structures, more or less dependent on the sexual maturity.

The male atrium is a conspicuous muscular sac in *Alcha, Paraustrorhynchus* and *Antiboreorhynchus* as well as in many other polycystidids. Stored alien sperm and secretion in a part of this sac, the wall of which is often strengthened by a pseudocuticle, indicate its function as copulatory bursa. *Alcha evelinae, Paraustrorhynchus pacificus, Antiboreorhynchus novzelae* and *A. torquatus* demonstrate steps in the evolution of this atrial part to a stalked bursa. A similar evolution is known e.g. in the genus *Acrorhynchides* (cf. Karling 1963 *a*, pp. 17–18) demonstrating the low taxonomic value of a separate male bursa.

Phonorhynchus helgolandicus (Meczn.) is the first sufficiently described polycystidid with two secretory bulbs in the male apparatus provided with their own cuticular outlets, "stylets" (Fig. 39, cf. Karling 1956, with references). The seminal duct (common sperm duct) opens together with one of the bulbs through a complicated stylet, the whole complex demonstrating a copulatory organ of "divisa" type (Karling op. cit.), a feature previously regarded as an exclusive characteristic of the fam. Polycystididae. The secretory bulb of this copulatory organ has been regarded as the "prostatic" vesicle (Kornsekretblase, vesicula granulorum), its stylet as the prostatic stylet, the other bulb+stylet being an accessory apparatus, a "prostatoid" (Hyman 1951, p. 117).

In many polycystidids with a single cuticular stylet associated with a secretory bulb (e.g. *Polycystis,* type genus of the family Polycystididae) this complex has been homologized with the prostatic apparatus of *Phonorhynchus,* due partly to its close association with the seminal duct (Fig. 40: cf. Karling 1956, Figs. 39, 40). A bundle of glands discharging their secretion freely into the male genital canal is perhaps a kind of prostatoid (not found in all *Polycystis* species). In some species with a simple pointed stylet, not distinctly associated with the seminal duct, e.g. *Progyrator mamertinus* (Graff) (cf. Meixner 1925) and *Mesorhynchus terminostylis* Karling, the true homologies are more obscure (see below). The case is complicated when there are two or more cuticular structures, one of them tubular and associated with a secretory bulb, the other (others) not tubular, sometimes aberrant. Then the single bulb+stylet has been regarded as the prostatic organ, the other cuticular pieces as accessory.

This interpretation may be true in many cases, e.g. in *Gyratrix* (Karling 1956, Fig. 18*g*) and *Cincturorhynchus ruber* Evdonin (Evdonin 1970), resembling *Phonorhynchus* and *Polycystis* in the close association of seminal duct and the bulb+stylet. In *Porrocystis assimilis* (Levinsen), *Antiboreorhynchus torquatus* Karling and the genus *Austrorhynchus* Karling the single bulb+stylet has been homologized with the prostatic organ of *Phonorhynchus*, no other secretory organs being found and the orifice of the seminal duct being indistinct (Karling 1952). Observations on the new material of polycystidids make this interpretation somewhat doubtful, and the possibility must be considered that the secretory bulb+stylet in these taxa are homologous with the prostatoid in *Phonorhynchus* and the accessory structures with the prostatic stylet of this taxon. This reassessment of the cuticular structures is based on the following anatomical facts (the true function of the different parts in the male apparatus being almost unknown). The single tubiform stylets in *Antiboreorhynchus novzelae, Paraustrorhynchus pacificus* and *P. elixus* are needles or hooks without distinct relation to the seminal duct, quite in accordance with the stylet of the prostatoid in *Phonorhynchus*. They are rather uncomplicated without "holdfast" structures. Their function as sexual stimulators or weapons is supposed but not ascertained. The seminal duct and a complex of glands (often two kinds as in many prostatic bulbs) are more closely associated with the "accessory" cuticular structures (at least in the species studied on satisfactory material), which evidently function as holdfasts in copulation, as also must be assumed for the single hook in *Porrocystis assimilis* and the complex "accessory" cuticular structures in *Austrorhynchus*, though a sexually stimulating function is not excluded. The collar-like structures in the prostatic stylets of *Phonorhynchus helgolandicus* and *Polycystis naegelii* are evidently also holdfast structures. Even in cases with only non-tubular cuticular pieces, a homologization of the latter (or part of them, see below *Alcha*) with the prostatic stylet of *Phonorhynchus* appears possible. The theory of the evolution of tubular stylets from cuticular hooks ("Hakenstilette", Karling 1956, pp. 204–206) must perhaps be somewhat modified. Non-tubular cuticular structures can be very differently shaped, and it is possible that the evolution from hooks to tubular stylets involves lamellar pieces such as those in *Alcha* or *Austrorhynchus*. Of course, an evolution in the opposite direction is in no way excluded, i.e. a transformation of tubular stylets to pieces of different shape.

The copulatory apparatus in *Paraustrorhynchus pacificus* is of special interest in regard to the interpretation of the male structures (Fig. 41). The seminal diverticle, including the seminal duct and the bundles of (prostatic) glands, can be regarded as a "conjuncta" bulb with weakly differentiated wall (diaphragm, septum, cf. Karling 1956, p. 190) and a short wide ejaculatory duct, i.e. a common outlet for sperms and prostatic secretion. This whole complex and the non-tubular cuticular apparatus are situated close together. The secretory bulb with its tubiform stylet has an isolated position. In accordance with previous interpretations, e.g. on *Austrorhynchus*, it could be regarded as the prostatic vesicle with its prostatic stylet. However, a comparison with *P. helgolandicus* (Fig. 39) makes its homologization with the prostatoid of this species more probable. Consequently the non-tubular cuticular structure can be interpreted as a homologue to the prostatic stylet of *P. helgolandicus*.

In the male apparatus of *Alcha evelinae* (Fig. 42) there is a marked topographical similarity with *Paraustrorhynchus*, apart from the lack of a secretory bulb+stylet. In the genus *Rogneda* there are species with a separate cuticular apparatus, as in *Alcha* and *Paraustrorhynchus*, others with a copulatory apparatus resembling a conjuncta organ with the cuticular pieces enclosing the secretory bulb+seminal duct (cf. Karling 1953). The function of these cuticular pieces as holdfasts is indisputable (Karling 1956, p. 209).

The construction types of the male copulatory apparatus in *Paraustrorhynchus, Alcha* and *Rogneda* can be compared with the conjuncta organs in other kalyptorhynchians (e.g. *Utelga* species, fam. Koinocystididae, cf. Karling 1954) with cuticular hooks outside the ejaculatory duct (Fig. 43).

It seems that the extreme manifoldness in the construction of the male copulatory apparatus in the family Polycystididae is due to the loose association of seminal duct, cuticular organs and different kinds of glands and secretory vesicles. All these structures can be combined in different ways, giving rise to trends and making the interpretation of homology extremely difficult. Besides the cases related here the "seminal bulb" and other types of "interposed" secretory vesicles must be considered in a broader review of the male atrial organs in the family Polycystididae (see also Karling 1956, pp. 212–218; and Schockaert 1974).

4.2. *On the taxonomy of the polycystidids described in the present paper*

The genus *Alcha* was placed into the fam. Koinocystididae by Marcus (1949), but its natural position is in the fam. Polycystididae (Karling 1952, p. 28). In this genus, as well as in the genus *Rogneda*, secretion is discharged into the male atrium without any kind of tubular stylet, and the cuticular apparatus consists of two or more non-tubular pieces. The assumption that *Alcha* is nothing but a *Rogneda* (Karling 1953, p. 362) has not been verified; the cuticular apparatus is principally different in the two genera and the female atrial organs are higher differentiated in *Alcha* (paired insemination canals). In *Rogneda* a stalked copulatory bursa opens from behind into the male atrium, whereas in *Alcha* the posterior part of the wide male atrium evidently functions as bursa. As shown above, this difference is taxonomically rather unimportant, however.

In *Antiboreorhynchus novzelae*, as well as in *A. torquatus*, the male atrial apparatus consists of a large male atrium provided with a stalked bursa, of a secretory vesicle with curved stylet (a "prostatoid", see above) and of another cuticular structure—at least in *A. novzelae* closely associated with the seminal duct—and glands interpreted here as prostatic (see above). The shape of the stylet of the "prostatoid" in *A. novzelae* lies almost within the variability of this organ in the insufficiently known, perhaps polytypical species *A. torquatus* (see Karling 1952, Fig. 12). *Porrocystis assimilis* resembles the two *Antiboreorhynchus* species in the construction of the male atrial apparatus (see Karling 1952). It has no bursa associated with the male atrium, its "prostatic" cuticular structure is a single hook and its female atrial apparatus is characterized by paired insemination canals.

Paraustrorhynchus elixus was brought by Marcus into the genus *Austrorhynchus* Karling, which he regarded as a "morphologically natural" taxon, though he himself describes the aberrant feature, that sperms are ejaculated through a "seminal stylet" (1954, p. 483). Our observation that the seminal duct opens directly into the male atrium brings *P. elixus* closer to the genus *Austrorhynchus* (see Karling 1952) but this genus is a closed natural entity without a place for *P. elixus*. *P. elixus* and *P. pacificus* have a somewhat similar prostatic cuticular apparatus of scissor type. However, their anatomical differences are considerable, and the nomination of separate genera for the two species could be justified as well.

Parenthetically it must be pointed out that a male cuticular apparatus of scissor or tong typus is realized in several polycystidid taxa phylogenetically apart from the genus *Paraustrorhynchus* (e.g. *Scanorhynchus* and *Psammopolycystis*, cf. Karling 1956).

The phylogenetic relations of the genera *Gyratrix* and *Scanorhynchus*, known from previous studies (Karling 1955), will not be discussed here.

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Abbreviations in the figures

a	common atrium
b	bursa
ccu	complex cuticular apparatus
ch	cuticular hook
co	male copulatory apparatus
cu	male cuticular apparatus
e	eye
ec	egg capsule
ej	ejaculatory duct
fg	female genital canal
gl	glands
gp	genital pore
i	insemination canal
m	muscles (muscular bulb)
mg	male genital canal (atrium)
o	ovary
ov	common oviduct
p	proboscis
ph	pharynx
pi	pigment
pr	prostatic vesicle (glands)
prd	prostatoid
sb	secretory bulb
se	common seminal duct
sem	seminal bulb
sr	seminal receptacle
st	stylet
sv	seminal vesicle
t	testis
u	uterus
y	yolk glands

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