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Brackish water Plathelminthes from Alaska as evidence for the existence of a boreal brackish water community with circumpolar distribution

Peter Ax and Werner Armonies

Contents

Abstract

The brackish water plathelminth fauna of Alaska is compared to European and Canadian brackish water biotopes. 37 species are presented including descriptions of 18 new species. 13 species (35 % of the total number found in Alaska) also occur in Europe and 6 (16 %) in SE Canada. Most of the common species are confined to brackish waters. *Coronhelmis lutheri*, *Halammovortex nigrifrons*, and 3 marine species are common to Alaska, Canada, and Europe. *Maehrenthalia americana* n. sp. occurs in Canada and Alaska but is unknown from Europe. Results corroborate the hypothesis of the existence of a boreal to subarctic brackish water community of Plathelminthes with a circumpolar distribution.

A. Introduction

Brackisb water biotopes of the European coasts of the Atlantic Ocean and the adjoining seas harbour a multitude of genuine brackish water species of Plathelminthes. A biogeographical comparison of these sites with brackish water habitats of the southern Canadian Atlantic coast yielded a surprisingly high degree of faunal similarity. Almost two thirds of the brackish water plathelminths found in S Canada (37 species) occur on both sides of the Atlantic Ocean in respective habitats (Ax & Armonies 1987).

The term 'brackish water species' is used to deliminate those species which (1) find their ecological optimum in the brackish water range of salinity, and which (2) are unable to permanently survive under either entirely marine or freshwater conditions (Remane 1969). Therefore, the high degree of faunal similarity of brackish water Plathelminthes between the European and Canadian coastlines cannot be explained by accidental crossings of the North Atlantic. This led to the hypothesis of a circumpolar distribution of brackish water Plathelminthes (Ax & Armonies 1987). This circumpolar distribution may be the result of either a still present or a historical connection of American and European populations. The Canadian and European populations may be connected either via the N Atlantic (with Greenland, Iceland, Jan Mayen, and Spitsbergen serving as intermittent stations), or via the coastlines of Sibiria, Alaska, and N Canada. Unlike other hypotheses of faunal distribution – such as continental drift (e. g. Sterrer 1973; Westheide 1977) – the idea of a present or historical continuous circumpolar distribution may be tested and, potentially, falsified by further studies of the plathelminth fauna along the hypothesized routes of connection

This presentation of the brackish water plathelminth fauna found during a 5 weeks stay of the senior author in Seward, Alaska, is a first attempt to test the hypothesis of a circumpolar connection. Alaska is an intermittent station between Europe and Canada along the circumpolar Sibirian route. A priori, the hypothesis of a faunal connection alongside this route was assumed to be rejected if there were no species in common with either European or Canadian brackish waters. Indeed, many of the Alaskan plathelminth species are hitherto only known from the Pacific and seem to belong to a distinctly separated Pacific fauna. However, at least 9 brackish water species are common to Europe and Alaska thus yielding further evidence for the existence of a boreal to subarctic brackish water community of plathelminthes with a circumpolar distribution. More strictly, the results corroborate the idea of a faunal connection along the Sibirian coastline. An Atlantic connection of N America and Europe is nevertheless possible.

Acknowledgements

The senior author thanks Dr. V. Alexander, Professor and Director of the Institute of Marine Science, University of Alaska, Fairbanks, for providing research facilities at the Seward Marine Center. Furthermore he and his wife are most thankful to Dr. A. J. Paul and Dr. J. Paul for their effective support during the stay in Seward.

B. Sample sites

Samples were collected between July 7th and August 13th, 1988. Most sample sites are situated at the Kenai Peninsula (approx. 60° N, 150° W) while a single sampling trip extended as far as Kotzebue beyond the Arctic Circle (approx. 67° N, 162° 30' W; Fig. 1–3).

Most of the sample sites are characterized by a low salinity (refractrometrical measurements). Particularly in some of the beaches salinity showed strong short-term variations (shock-biotopes, cf. Den Hartog 1964) while in salt marshes salinity seems to be less variable (Table 1). Strong salinity variations are also recorded from the open coastal waters such as Resurrection Bay near Lowell Point. Here salinity was 5‰ S on July 27th, 26‰ on August 4th (both at high tide), and only 5–6 ‰ S at the low tide of August 5th. These strong salinity variations are caused by different amounts of melting water from adjacent glacier fields and a variable amount of water exchange with the open sea. Both factors are depending on weather and therefore rather unpredictable. High salinity (> 30‰ S) was only measured at a few intertidal localities. Thus, a strongly varying salinity (mostly) in the brackish water range seems to be a normal summer phenomenon in these subartical coastal waters. Consequently, only salinity tolerant (euryhaline) marine species and brackish water species can be expected.

According to Troll & Paffen (in Blüthgen 1980) the Kotzebue Sound has a subarctic tundra climate. A comparable climate is found at the N Canadian coastline (adjoining to the Beaufort Sea), in the Hudson Bay area (to 70° N), at the SW coast of Greenlad, in the northern part of Iceland, and along the Sibirian arctic coastline. Anchorage and the Kenai Peninsula have an oceanic (cold temperate) boreal climate. In Europe, the same type of climate occurs at the northern coast of Norway.

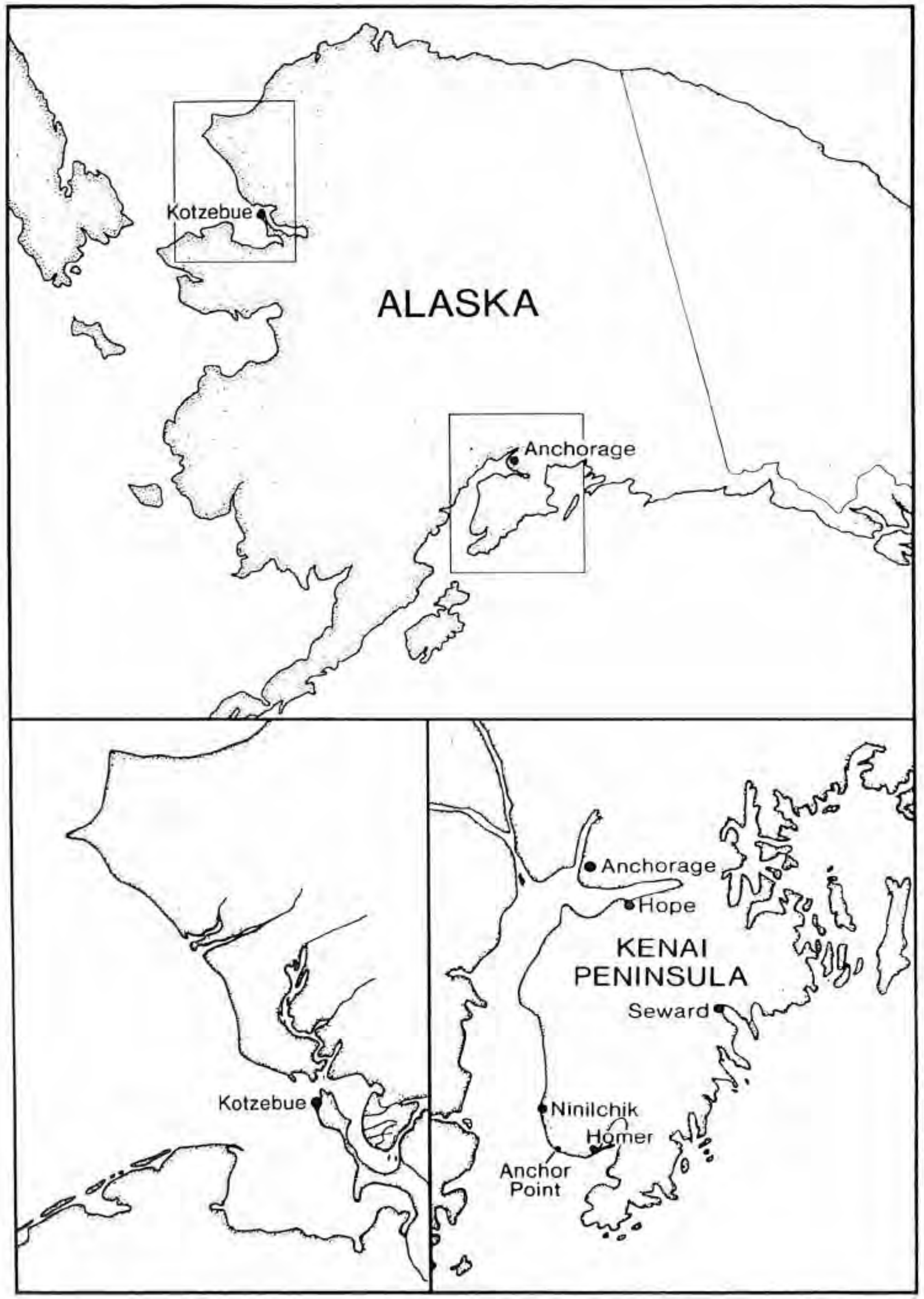

Fig. 1. Location of the sample sites.

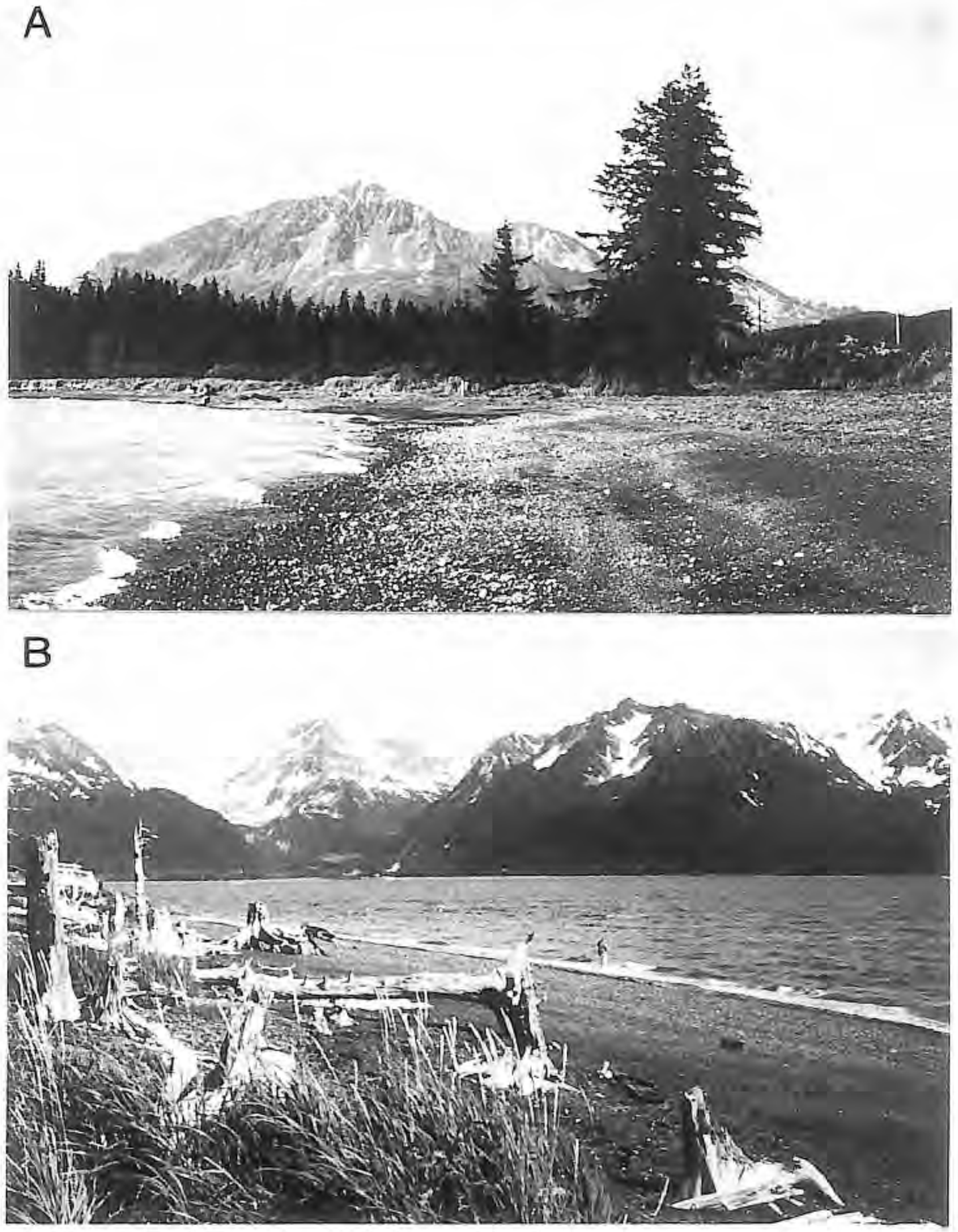

Fig. 2. A. Seward: Fourth of July Beach. Beach with coarse sand, gravel, and boulders. B. Seward: Lowell Point. High energy beach with gravel and boulders.

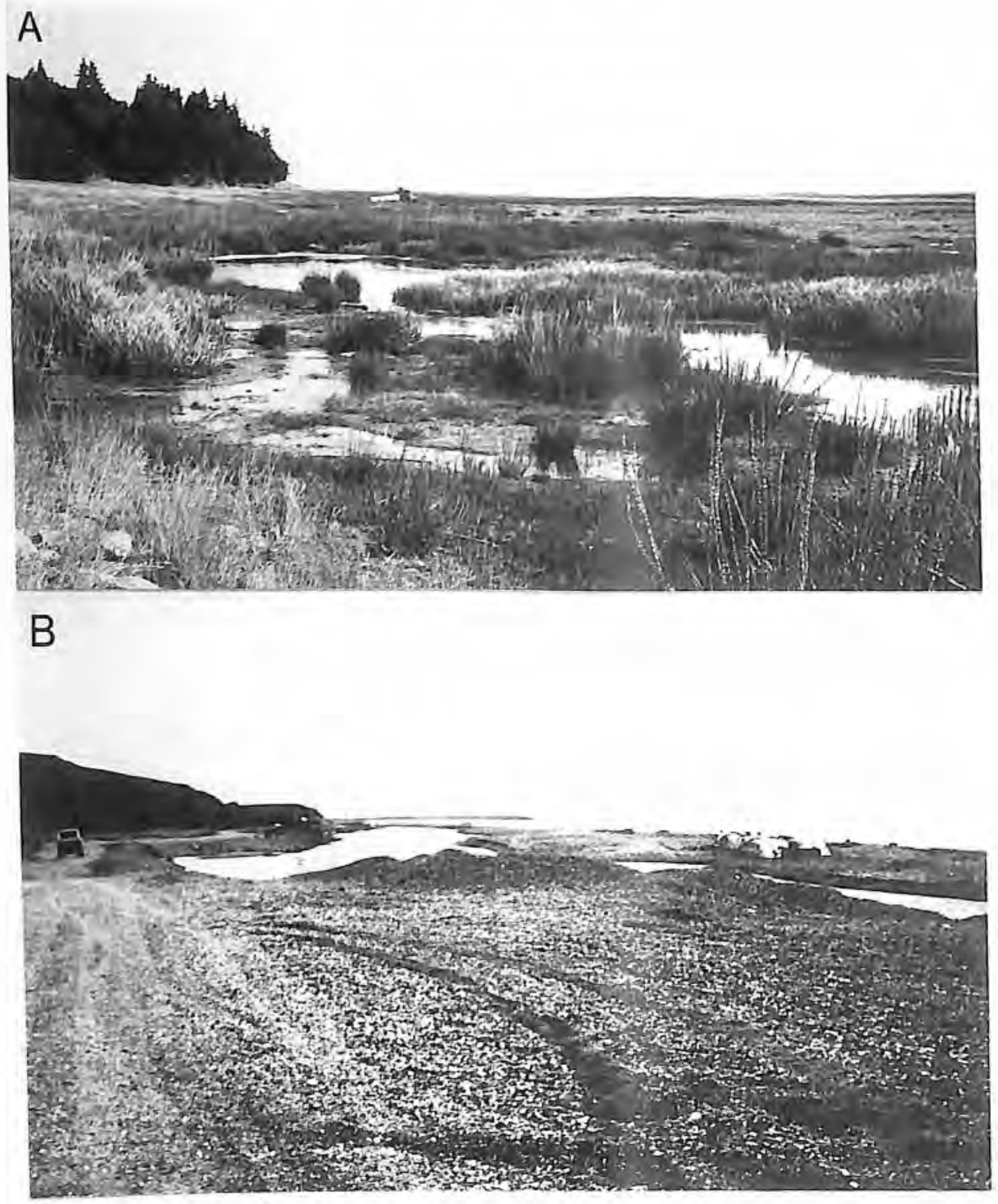

Fig. 3. A. Homer Spit: Salt marsh area with pools. B. Kotzebue: Beach next to the mouth of a small river. Medium to coarse sand with gravel.

Table 1: Alaskan sample sites

Region and site	Sediment properties	Date	Salinity
Kenai Peninsula			
Seward and surroundings	(all sites adjoining to Resurrection Bay)		
– Lowell Point	Beach (coarse sand, gravel, boulders)	7. 7.	12 ‰ S
		27. 7.	5 ‰ S
		4. 8.	26 ‰ S
		5. 8.	5–6 ‰ S
	Fine sand of the lower beach slope	10. 7.	0 ‰ S
		26. 7.	0 ‰ S
	High energy beach with gravel and boulders	2. 8.	13 ‰ S
		5. 8.	21 ‰ S
	Gravel at high tide level	12. 8.	–
	Sand next to a small freshwater outflow	2. 8.	0 ‰ S
		4. 8.	0 ‰ S
– Seward Airport	Salt marsh below the air corridor; mud	12. 8.	7–8 ‰ S
– Fourth of July Beach	Beach with coarse sand, gravel, and boulders	8. 7.	0 ‰ S
		20. 7.	–
		3. 8.	14 ‰ S
	Lower beach slope; coarse sand, gravel and boulders	25. 7.	0 ‰ S
		13. 8.	0 ‰ S
	Upper intertidal muddy sand	8. 7.	0 ‰ S
		11. 7.	–
		13. 8.	0 ‰ S
	Medium to fine intertidal sand	20. 7.	–
	Mudflat adjoining to the salt marsh	8. 7.	–
– Beach N of Industrial Camp	Boulder beach with insular patches of very fine sand	3. 8.	25 ‰ S
– Beach S of Industrial Camp	High energy beach with coarse sand	12. 7.	5 ‰ S
Hope	Mud in front of the salt marsh edge of erosion	19. 7.	12–15 ‰ S
Ninilchik	Medium sand from the shore line	16. 7.	5 ‰ S
	Shore of the Ninilchik River; sand to muddy sand	21. 7.	0 ‰ S
	Mouth of the Ninilchik River into the sandy shore	21. 7.	6–37 ‰ S
Anchor Point	Mouth of the Anchor River into the sandy beach	24. 7.	0 ‰ S
	High energy beach; coarse sediment	24. 7.	–
Homer Spit (eastern side)	Sandy beach slope	16. 7.	–
	Upper intertidal mud with algal cover	16. 7.	38 ‰ S
	Salt marsh pools and creeks	16. 7.	2–35 ‰ S
Anchorage	Muddy salt marsh next to the 5th Avenue	13. 7.	12–13 ‰ S
Kotzebue	Salt marsh; muddy sediment and algae	8. 8.	7–11 ‰ S
	Beach (coarse sand, gravel, boulders) directly opposed to Kotzebue Sound	8. 8.	16 ‰ S
	Medium to coarse sand with gravel, next to the mouth of a small river	8. 8.	10 ‰ S

C. Results

Macrostomida

Macrostomum bicurvistyla Armonies & Hellwig, 1987

(Fig. 4, 5)

Localities: Seward. (1) Fourth of July Beach. Lower beach slope with effluent freshwater; coarse sand, gravel, and boulders (25. 7. 1988). (2) Lowell Point. Sandy sediment with effluent freshwater (2. and 4. 8. 1988).

Material: Live observations on several specimens, including drawings and photographs.

Distribution: North Sea (Armonies & Hellwig 1987, Hellwig 1987)

Unpigmented animals with small eye pigmentations close to each other. With densely packed aggregates of rhabdites. Normally about 1 mm long with tubular intestine, but some individuals of both locations 3 to 4 mm long and with an intestine with lateral diverticles. The stylets of large and small individuals are identical: Length 120 to 148 µm (diagonally), with stronger coverslip compression up to 158 µm. Proximal opening 20 to 25 µm, strongly compressed up to 41 µm. Distal opening 6 to 7 µm. Median diameter 8 to 10 µm. The stylet is two-fold flexed in the same direction with an average diameter of 10 (9 to 12) µm

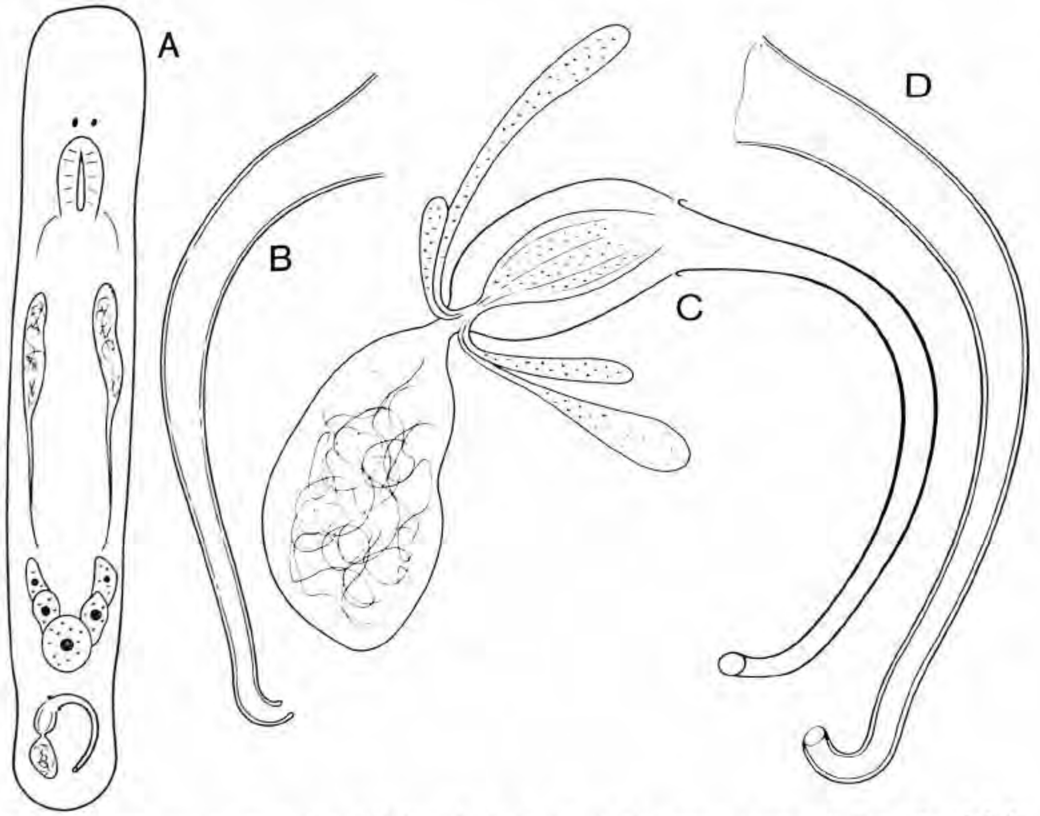

Fig. 4. *Macrostomum bicurvistyla*. A. Habitus. B. Stylet. C. Male organ (Seward: Fourth of July Beach). D. Stylet (Seward: Lowell Point).

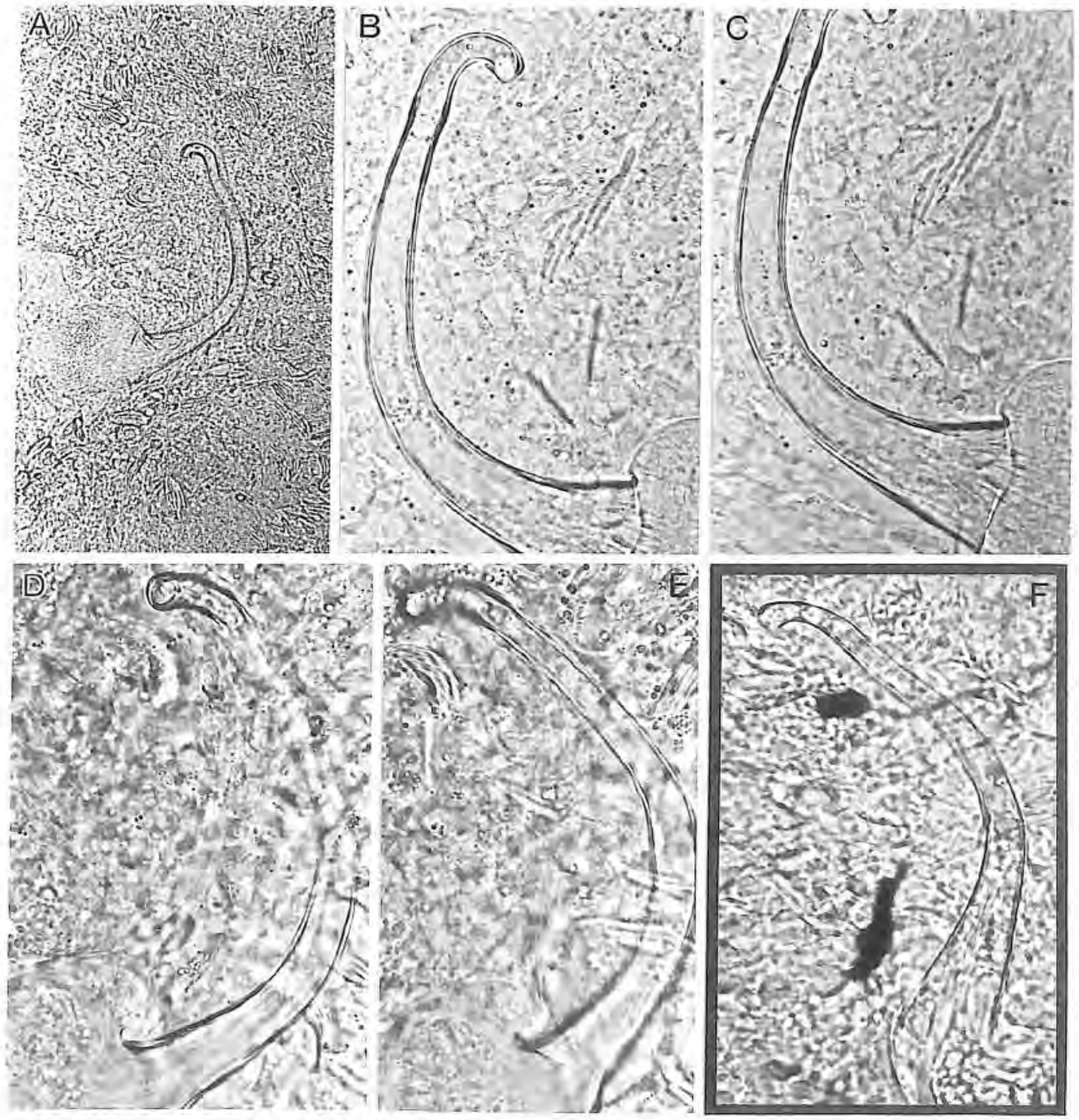

Fig. 5. *Macrostomum bicurvistyla*. A–C. Stylet (Seward: Lowell Point). D, E. Stylet (Seward: Fourth of July Beach). F. Stylet (North Sea: Island of Sylt).

at the first and 6 to 7 µm at the second flexion. At the distal opening the tube is slightly strengthened at one side.

In the North Sea only small (up to 1.5 mm long) specimens have been found up to now. In accordance with the above specimens they have small eye spots and many groups of tightly packed rhabdites. The shape of the stylet is identical, however, the measures of the European animals are slightly smaller: Length 105 to 125 µm, proximal opening 20 µm, diameter 7 µm at the first and 4.5 µm at the second flexion, distal opening 5 µm (only two specimens, cf. ARMONIES & HELLWIG 1987).

Macrostomum curvituba Luther, 1947

(Fig. 6, 7)

Locality: Kotzebue Sound. Medium to coarse sand with gravel at the outlet of a small river. Salinity of the river mouth 10 ‰, Kotzebue Sound 16 ‰ S (8. 8. 1988).

Material: Live observations on five specimens, including drawings and photographs. Additionally five specimens sectioned.

Distribution: North Sea, Baltic Sea (cf. ARMONIES 1987).

Whitish animals 0.7 to 1.2 mm long without pigmented eye spots. Stylet 89 to 91 µm long with a proximal opening of 12 to 15 µm and a distal opening of 4 to 5 µm (21 to 26 and 5 to 7 µm, respectively, in strongly compressed specimens). The shape and size of the stylets conform well with those of European specimens (AX 1951, LUTHER 1960, AX & AX 1970). Examination of the sectioned material states the species identity.

M. curvituba is a brackish water species favouring the oligo- and mesohalinicum. So far, the species has not been found south of 53 ° N, presumably because of its preference for temperatures lower than 10 °C (ARMONIES 1987).

Macrostomum extraculum n. sp.

(Fig. 8, 9)

Locality: Ninilchik. Lagoon near the Cook Inlet River (locus typicus). Medium sand with moderate amounts of detritus from the shore zone. Salinity 5 ‰, regularly found in several samples (16. 7. 1988).

Material: Live observations on several specimens, including drawings and photographs.

About 1.0 to 1.2 mm long unpigmented specimens. With strong bundles of rhabdites, with paired eye pigmentations. Seminal vesicle ovoid, prostatic vesicle ovoid to spherical. The stylet is a tube of 68 to 72 µm height (3 measurements) which is flexed like a cork-screw. The proximal opening is 18 to 22 µm wide and

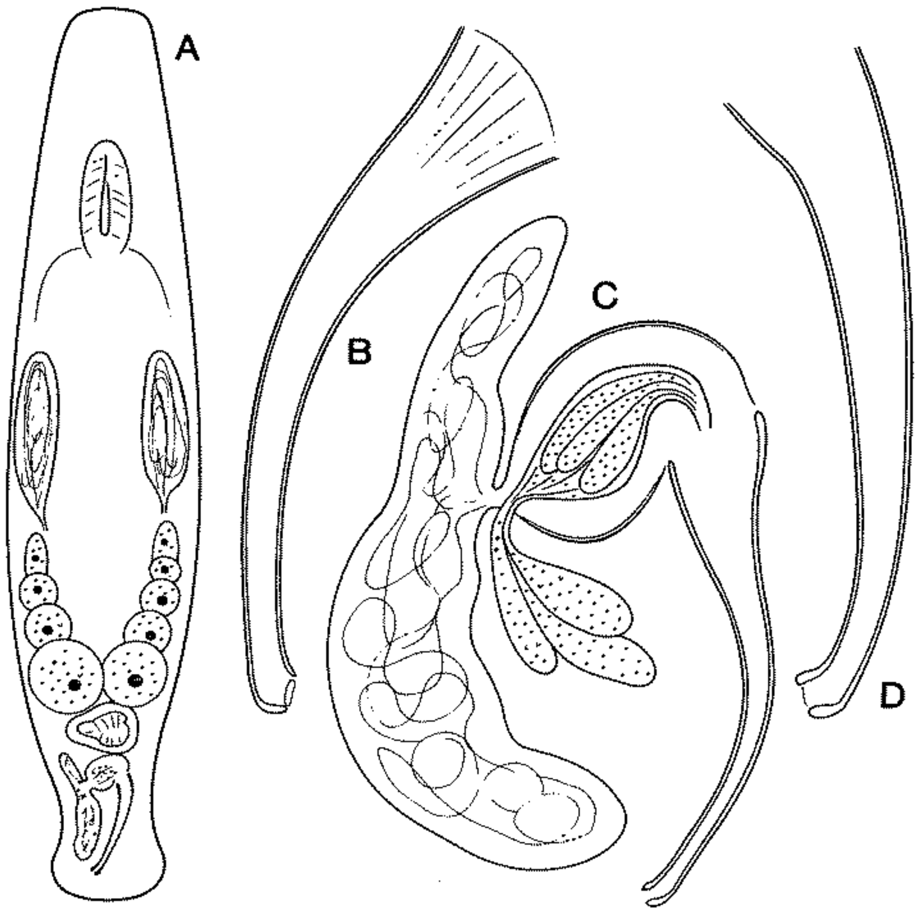

Fig. 6. *Macrostomum curvituba*. A. Habitus and organisation. B. Stylet. C. Male organ. D. Stylet (Kotzebue).

the distal opening 3 µm. There is a solid conical enlargement of about 4 × 6 µm near the distal opening.

Discussion. A stylet formed like a cork-screw and with a distal conical enlargement is unique in the taxon *Macrostomum*. Cork-screw formed stylets also occur in *M. reynoldsi* Ferguson, 1939, and *M. retortum* Papi, 1951. A lateral clubshaped enlargement of the distal part of the stylet is also found in *M. mediterraneum* Ax, 1956.

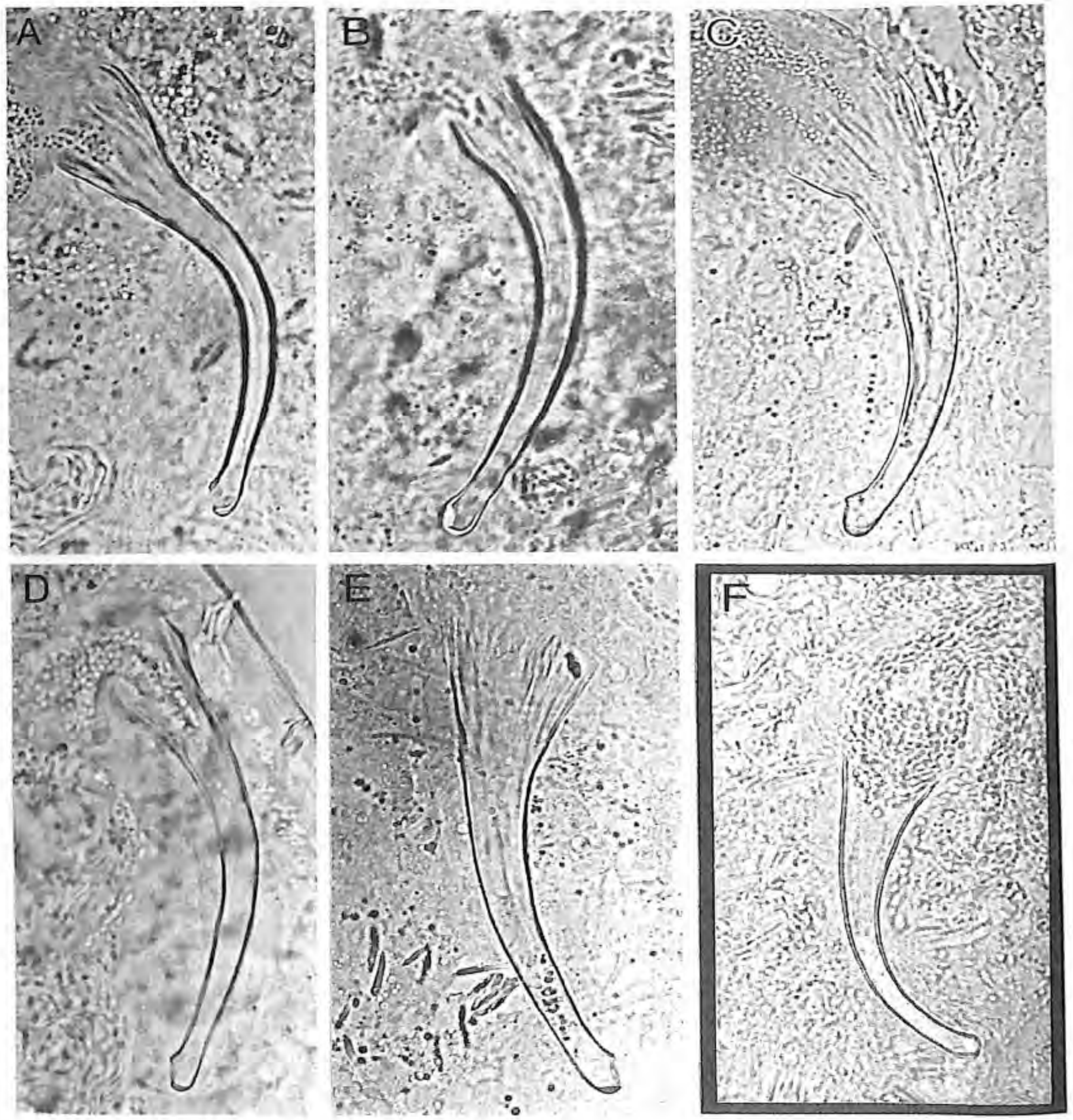

Fig. 7. *Macrostomum curvituba.* A–E. Stylets of different individuals (Kotzebue). F. Stylet (North Sea: Island of Sylt).

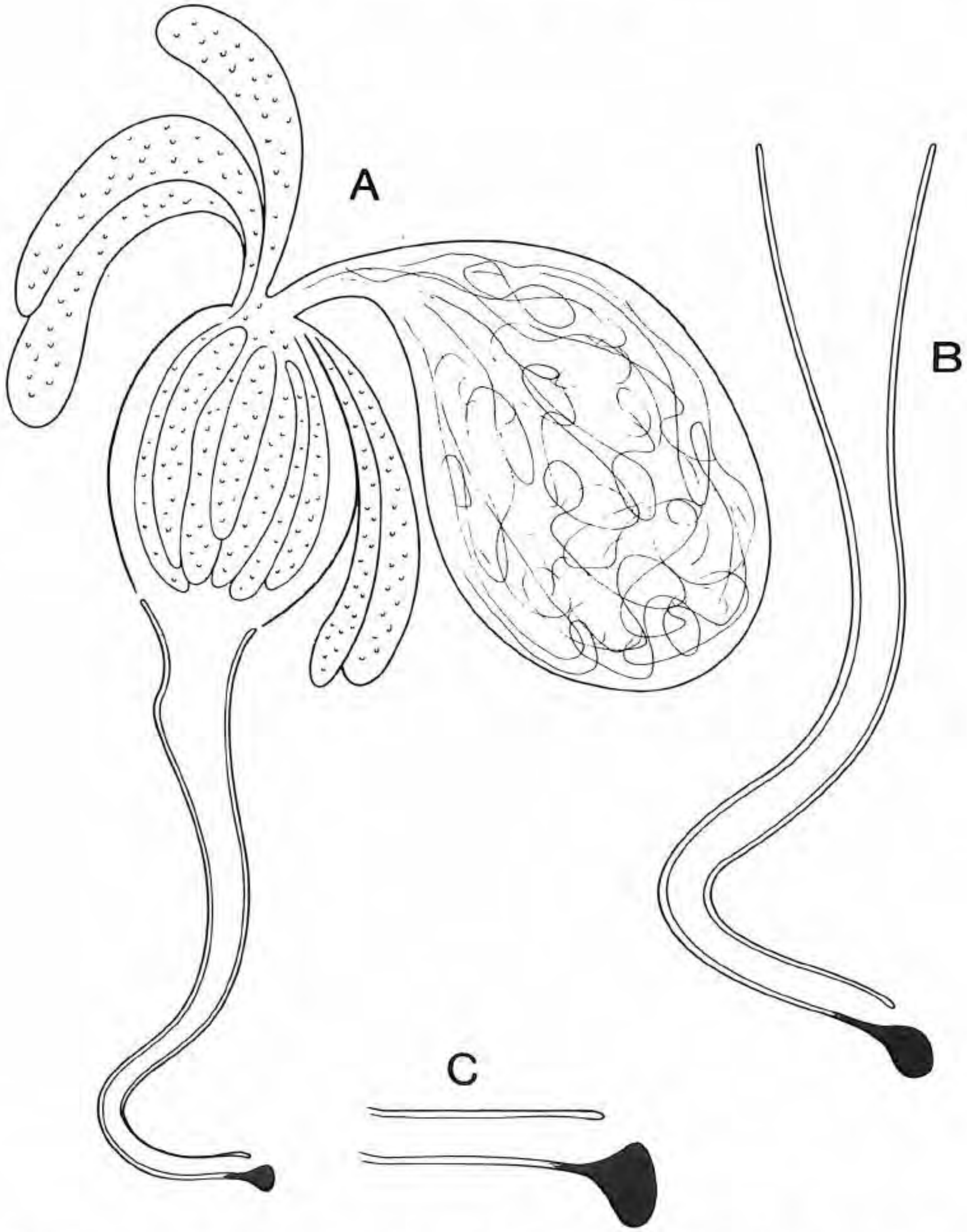

Fig. 8. *Macrostomum extraculum.* A. Male organ. B. Stylet. C. Tip of the stylet, enlarged (Kenai Peninsula: Ninilchik).

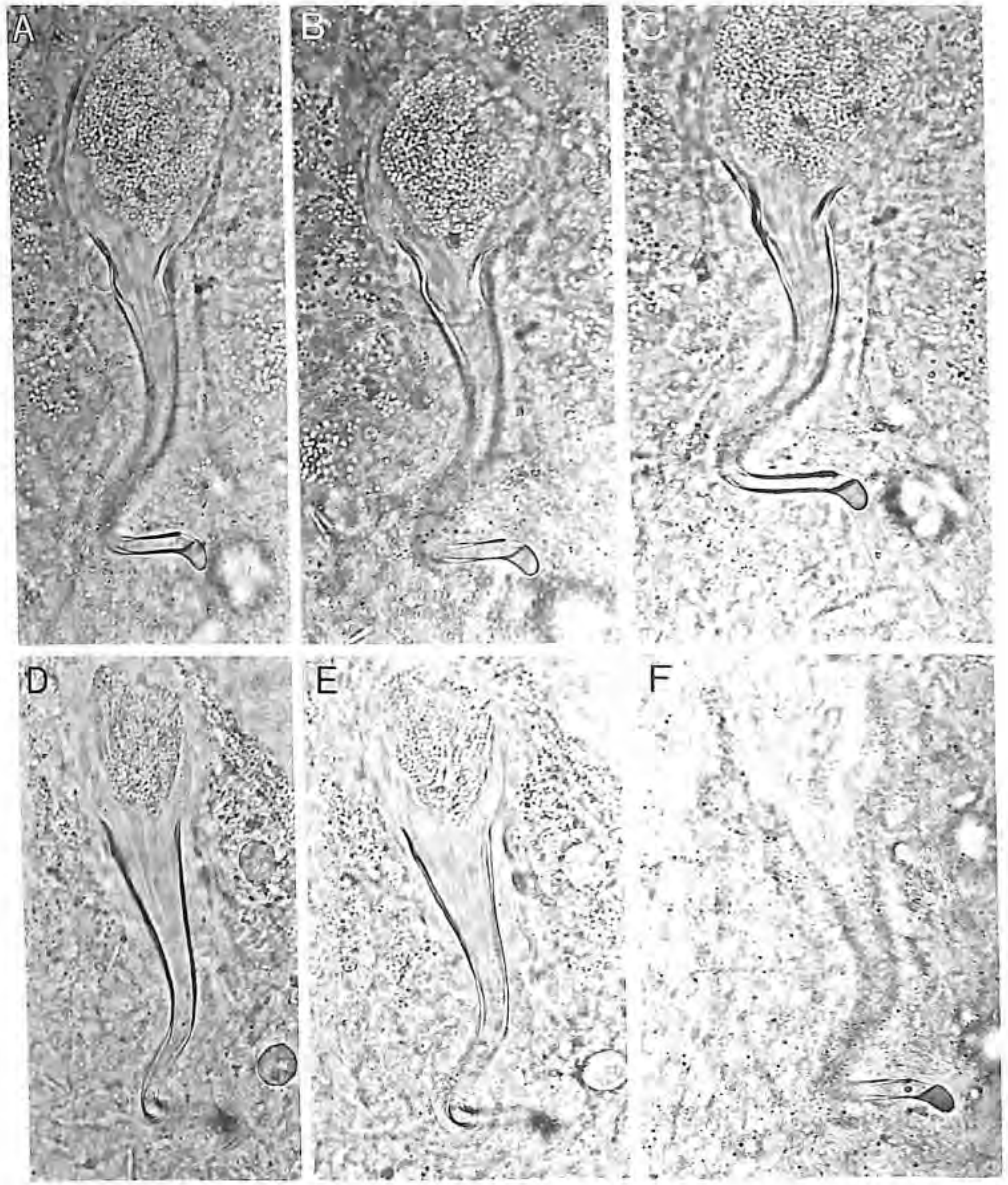

Fig. 9. *Macrostomum extraculum.* A–C. Stylet of one specimen, different focus. D–F. Stylet of another specimen, different focus (Kenai Peninsula: Ninilchik).

Macrostomum pusillum Ax, 1951

(Fig. 10 A)

Locality: Homer Spit. Intertidal sandflat behind a dune wall (16. 7. 1988).

Material: Live observations on a few specimens, including photographs.

Distribution: North Sea, Baltic Sea, Atlantic coast of Norway, Mediterranean, Black Sea; SE Canada (Ax & Armonies 1987).

The shape of the stylet conforms well with European and Canadian specimens. Length of the stylet: Alaska 26 to 27 µm, Canada 23 to 25 µm, Europe up to 26 µm. Diameter of the proximal opening: Alaska 16 to 17 µm, Canada 10 to 15 µm, Europe 14 to 17 µm (see Ax & Armonies 1987).

Macrostomum spirale Ax, 1956

(Fig. 10 B, C, 11)

Locality: Kotzebue. Salt marsh east of the village, salinity 7 to 11 ‰ (8. 8. 1988).

Material: Live observations on two specimens, including drawings and photographs.

Distribution: North Sea, Baltic Sea, Mediterranean; in poly- to mesohaline habitats without strong currents (Ax 1951, 1956 a, Den Hartog 1977, Armonies 1987).

About 1.5 mm long specimens with weakly developed eye pigmentations. The vaginal pore with its conspicuous strengthening and the surrounding voluminous glands, the shape of the seminal and prostatic vesicles and the stylet all conform well with European animals.

Macrostomum tenuicauda Luther, 1947

(Fig. 10 D–F, 12)

Localities: (1) Seward. Lowell Point, fine sand of the lower beach slope with effluent freshwater (10. 7. 1988). (2) Homer Spit. Lower beach slope behind a dune dam (16. 7. 1988).

Material: Live observations on several specimens, including drawings and photographs.

Distribution: North Sea, Baltic Sea, and a salt lake in N-Germany (Luther 1947, 1960, Rixen 1961, Karling 1974, Den Hartog 1977, Armonies 1987). Most localities are in meso- to oligohaline salt marshes.

Animals 0.7 to 0.8 mm long, some with and some without pigmentation of the eye spots. The stylet is a tube of 55 to 65 µm tapering distally. At the distal opening one side is elongate, the wall stregthened and curved, thus causing the distal opening to lie in a line with the shorter wall of the stylet. The stylets of

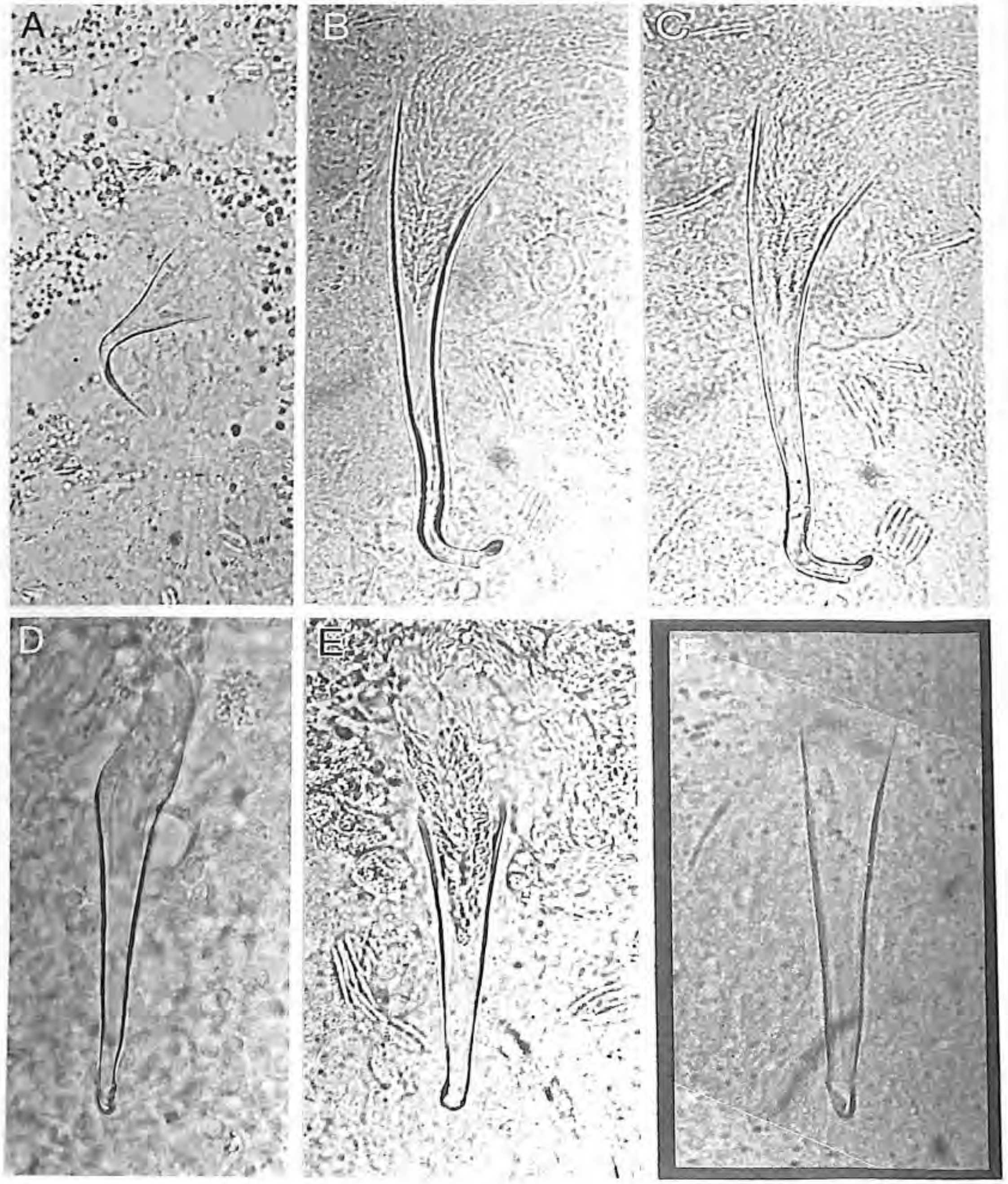

Fig. 10. A. *Macrostomum pusillum.* Stylet (Kenai Peninsula: Homer Spit). B, C. *Macrostomum spirale.* Stylet (Kotzebue). D, E. *Macrostomum tenuicauda.* Stylet (D Seward: Lowell Point, E Kenai Peninsula: Homer Spit). F. *Macrostomum tenuicauda* (North Sea: Island of Sylt).

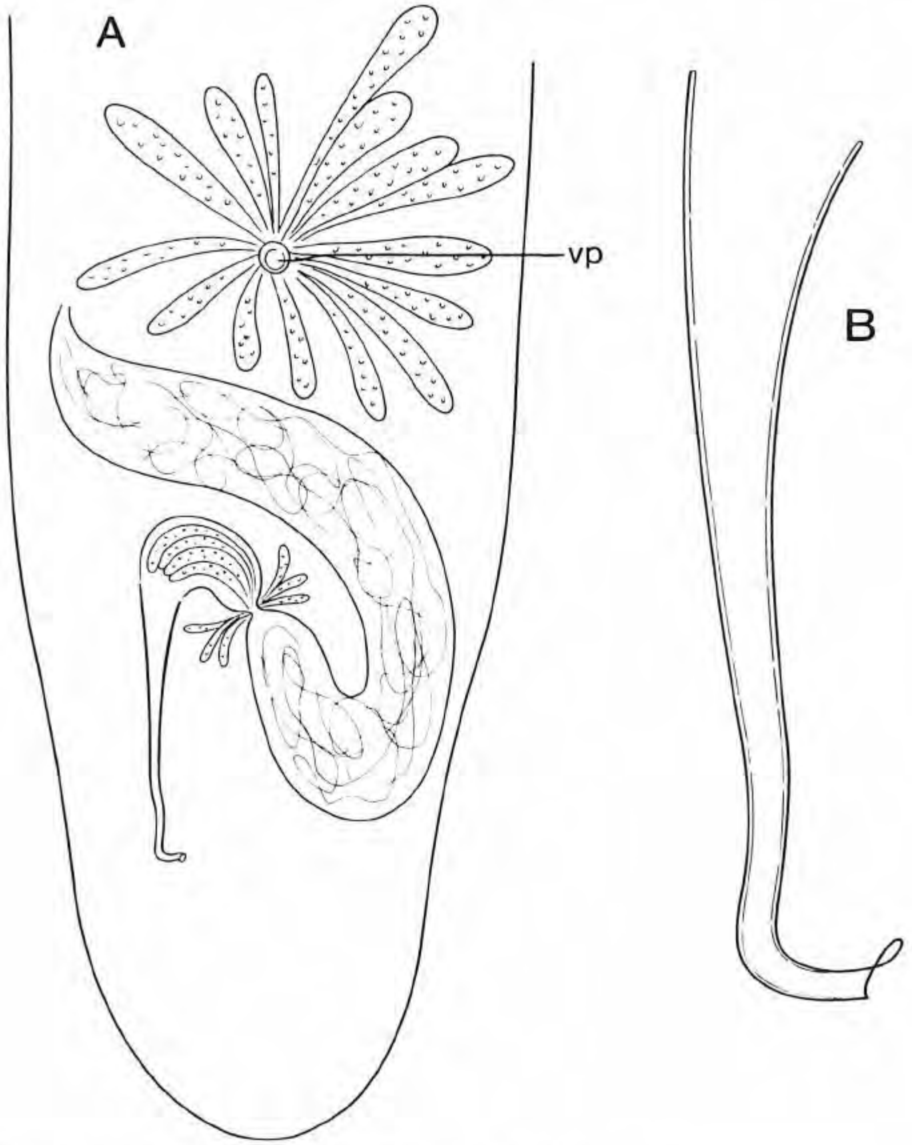

Fig. 11. *Macrostomum spirale.* A. Male organ. B. Stylet (Kotzebue).

European animals have the same shape and size (62 to 66 µm LUTHER 1960; unpubl. own data). In salt marshes of the Island of Sylt in the North Sea, specimens with and without eye pigmentations may be mixed in a single population as was the case in the Alaskan populations.

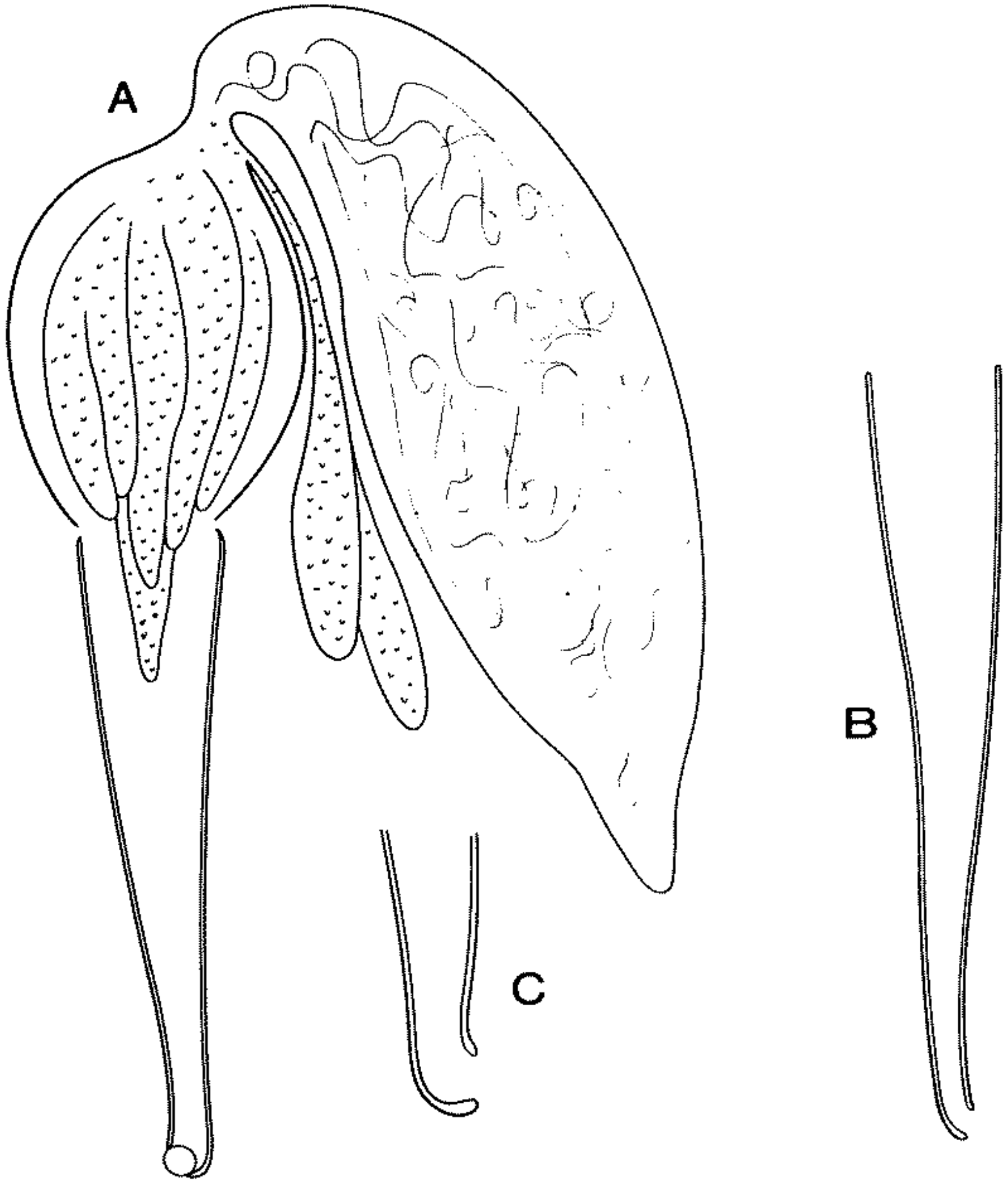

Fig. 12. *Macrostomum tenuicauda.* A. Male organ (Kenai Peninsula: Homer Spit). B. Stylet. C. Tip of the stylet, enlarged (Seward: Lowell Point).

Seriata

Coelogynopora falcaria Ax & Sopott-Ehlers, 1979

(Fig. 13 B)

Localities: (1) Seward. Lowell Point, lower beach slope (26. 7. 1988, 0 ‰ S; 2. 8. 1988, 13 to 14 ‰ S). (2) Ninilchik. Mouth of the Ninilchik River (salinity 0 ‰) into the sandy beach (6 to 37 ‰ S; 21. 7. 1988).

Material: Live observations on several specimens, including drawings and photographs.

Distribution: US Pacific coast, San Juan Island (Ax & Sopott-Ehlers 1979).

Specimens with spherical epidermal glands with a pore and an adjacent finely granuled field. The glands empty by evagination. The prostatic glands form a paired lateral package behind the copulatory apparatus. With regard to the shape, arrangement and number of spines in the various groups, the copulatory apparatus confirms with the original description. However, all measures are about 20 % less.

Coelogynopora scalpri Ax & Sopott-Ehlers, 1979

(Fig. 13 C, D)

Locality: Homer Spit. Lower slope of the sandy beach (16. 7. 1988).

Material: Live observations on several specimens, including drawings and photographs.

Distribution: US Pacific coast, Washington (Ax & Sopott-Ehlers 1979).

About 1 cm long animals with ovoid yellowish epidermal glands. Germaries rather far in front of the pharynx, vitellaries in paired lateral rows of distinctly separated follicles. Sclerotic copulatory apparatus consisting of a central group and paired lateral spines of 105 µm. Central spines separated into two symmetrical groups of 3 elements each: an outer bristle of 115 µm with a lateral projection about 55 µm from the slightly curved tip, a median bristle of about 85 µm with a projection 15 µm from the tip, and the innermost elements of 130 µm. Proximally the three elements of each side are closely placed together. Closer examination of the innermost elements reveales that they are composed of three slender spines each which decrease in size towards the center of the group (about 130, 120, and 110 µm long). The structure of the copulatory apparatus and the shape of each element agrees well with *C. scalpri*. However, all elements are about 20 % longer than in specimens from San Juan Island (Washington, USA).

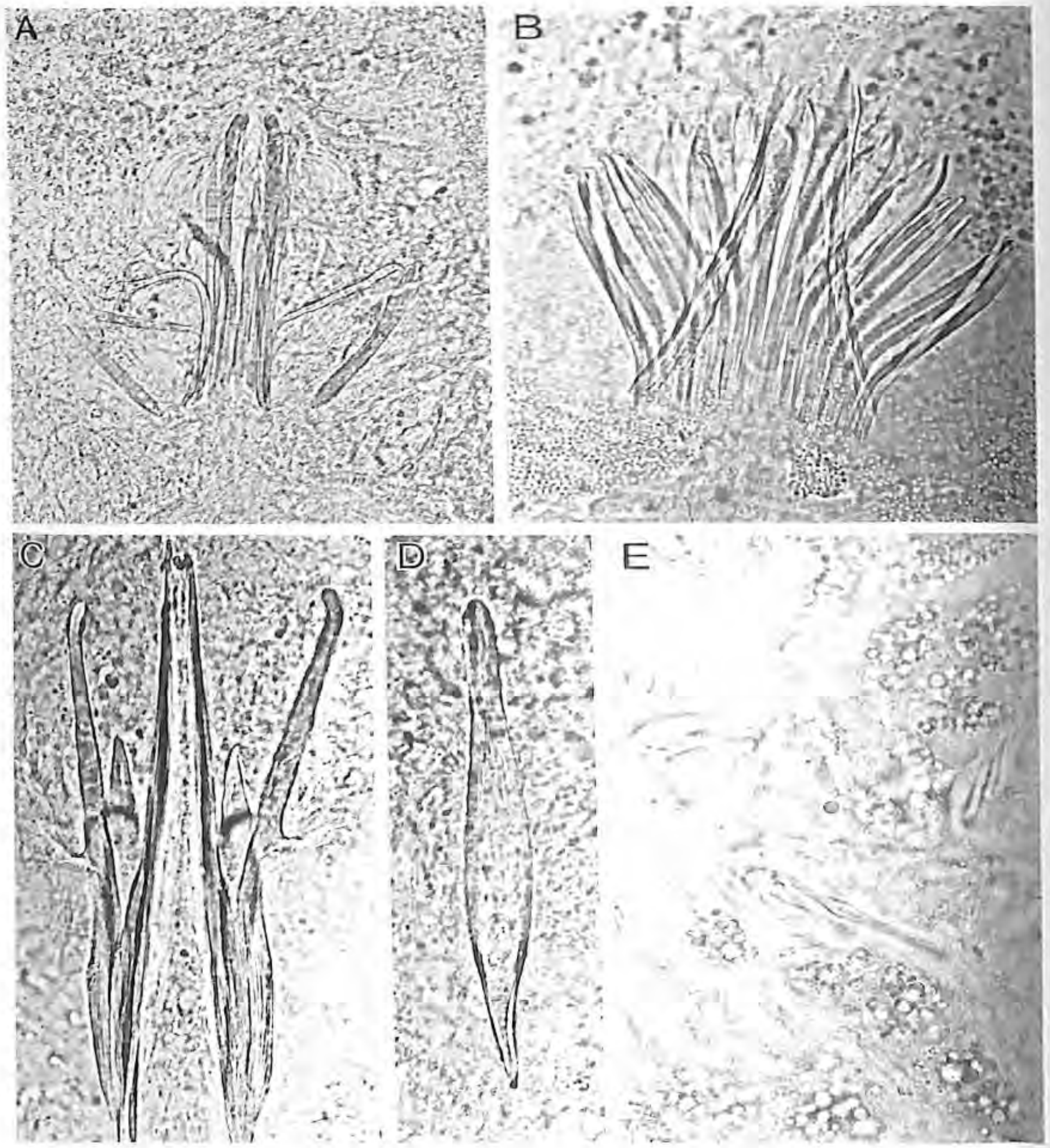

Fig. 13. A. *Coelogynopora sewardensis*. Sclerotic apparatus (Seward: Fourth of July Beach). B. *Coelogynopora falcaria*. Sclerotic apparatus (Kenai Peninsula: Ninilchik). C. *Coelogynopora scalpri*. Central spines of the sclerotic apparatus. D. *Coelogynopora scalpri*. Lateral spine (Kenai Peninsula: Homer Spit). E. *Invenusta paracnida*. Dermal glands (Seward: Lowell Point).

Coelogynopora sewardensis n. sp.

(Fig. 13 A, 14)

Localities: Seward. (1) Fourth of July Beach (locus typicus). Lower beach slope with coarse sand and gravel (20. 7. 1988, 25. 7. 1988). (2) Lowell Point. Sandy beach slope with effluent freshwater (2. 8. 1988, 4. 8. 1988).

Material: Live observations on several individuals, including drawings and photographs.

Animals 7 to 8 mm long. Tightly packed testis follicles forming a median row in front of the pharynx. Vitellaries in lateral rows of distinctly separated follicles, some follicles also behind the pharynx. Paired germaries about one body diameter in front of the pharynx. In adhering specimens the tail end is irregularly lobed. Tubular glands with fine grained secretions occur all over the body wall. The end of these glands may knob-like project over the epidermis. The shape of the glands varies as the animals move. The glands empty by tubiform elongation (initiated by coverslip compression).

The sclerotic apparatus consists of ten spines in a central group and a pair of strong lateral spines (96 µm long). Two median spines of the central group (92 to 100 µm long) are separated from the remaining 4 spines on each side, which are proximally tightly packed together, possibly partially fused. The two most lateral spines of these groups are 100 to 110 µm long, the central ones 130 and 155 to 168 µm, respectively. All spines of the central group have a curved pointed tip and a triangular projection about 16 µm from the tip.

Discussion. With regard to the number and shape of the genital spines, *Coelogynopora hangoensis* Karling & Kinnander, 1953, *C. poaceaglandis* Riser, 1981, and *C. gallica* Sopott-Ehlers, 1976 are the most similar species. Of these, only *C. gallica* has an unpaired short median spine. The lateral spines of the new species are clearly stronger than the spines of the central group, as is the case in *C. hangoensis* (cf. KARLING 1958). However, the tip of the lateral spines is less complicated than in *C. hangoensis*, without additional dentiform projections, and *C. hangoensis* has 12 spines in the central group. The lateral spines of *C. gallica* and *C. poaceaglandis* are not stronger than the central spines. The shape of the tips is specific for each species.

In *Coelogynopora sewardensis* the ten central spines have all a triangular projection about 16 µm from the tip. At least one pair of the largest spines lacks such a projection in the other species. The size of the penial spines differs as well: *C. gallica* 45 to 90 µm (range of all spines), *C. poaceaglandis* 60 to 120 µm, *C. hangoensis* 80 to 140 µm, and *C. sewardensis* 92 to 168 µm. Thus, the sclerotic apparatus of *C. sewardensis* differs from all other species. With regard to the size of the spines and the shape of the lateral spines, *C. sewardensis* is most similar to

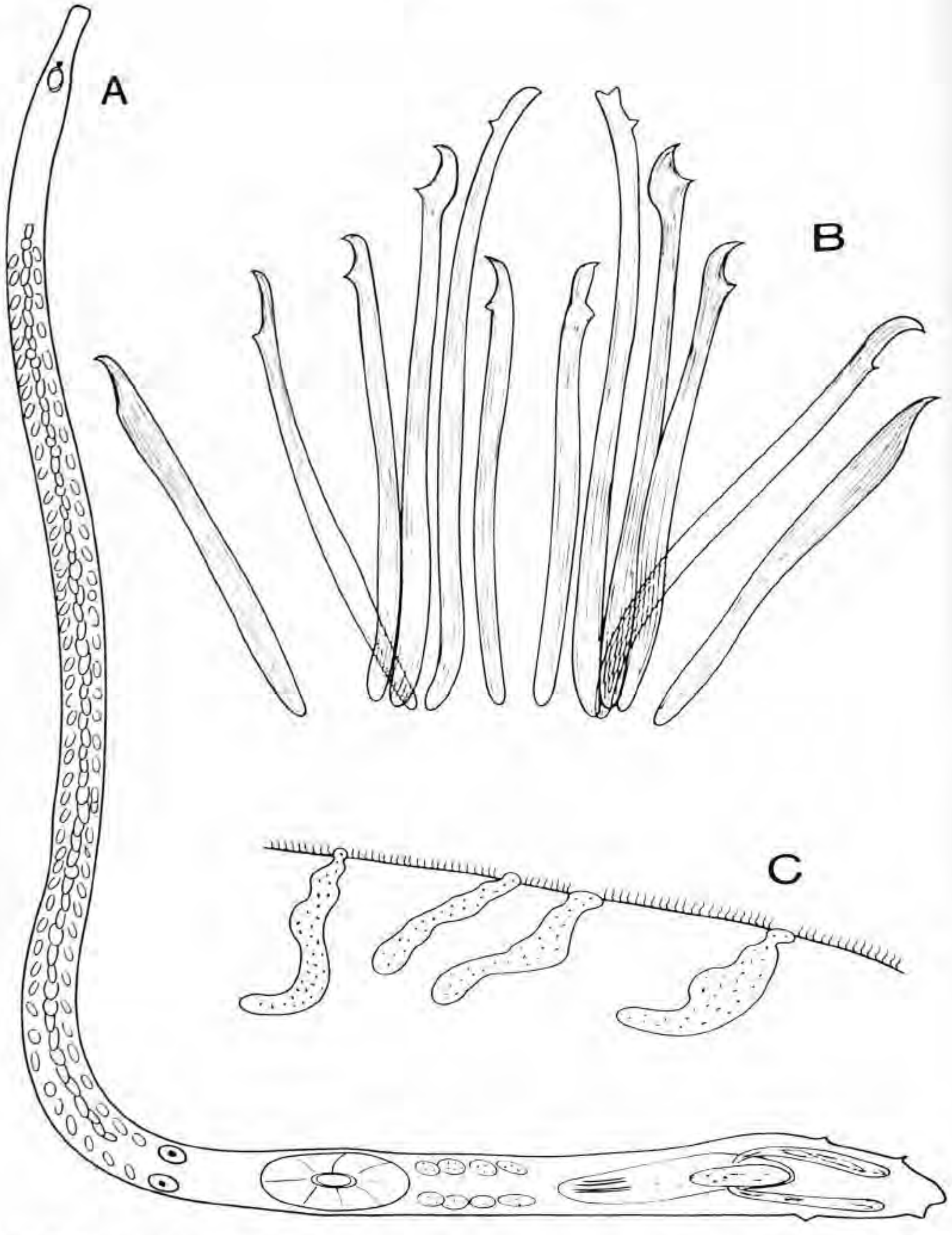

Fig. 14. *Coelogynopora sewardensis*. A. Habitus and organisation. B. Sclerotic apparatus. C. Tubular epidermal glands (Seward: Fourth of July Beach).

C. hangoensis; they could be sister species. Both species occur in coarse grained beaches with a low salinity caused by melting water (cf. Karling 1958).

Invenusta paracnida (Karling, 1966)

(Fig. 13 E)

Localities: (1) Seward. Lowell Point, beach with coarse sand, gravel and boulders, high tide level (7. 7. 1988, salinity of ambient water 12 ‰, 5. 8. 1988, salinity at low tide 21 ‰; 11. 8. 1988). (2) Seward. Extended high energy beach behind the Industrial Camp; lower beach slope near a freshwater outflow (12. 7. 1988, very abundant; ambient salinity at low tide = 5 ‰ S). (3) Ninilchik. Mouth of the Ninilchik River (freshwater) into the sandy slope of the beach (salinity 6 to 37 ‰; 21. 7. 1988). (4) Anchor Point. High energy beach near the mouth of the Anchor River (24. 7. 1988).

Material: Live observations on numerous specimens, including photographs.

Distribution: US Pacific coast, Bodega Bay (Karling 1966), San Juan Island (Ax in Sopott-Ehlers 1976). Japan, Daikoku Island (Tajika 1981).

Animals 3 to 4 mm long, with conspicuous epidermal glands (paracnids) containing a coiled eversible tube of up to 100 µm and small barbs at the outer side. Testis follicles in a single median row in front of the pharynx. Vitellaries in lateral rows of distinctly separated follicles, also behind the pharynx. Seminal vesicles rather short, length about 2 to 2.5 times the diameter of the copulatory bulb.

Archotoplana macrostylis n. sp.

(Fig. 15–18)

Localities: Seward. (1) Lowell Point. Beach near the mouth of a small river; sand from the lower beach slope with freshwater outflow (2. 8. 1988, ambient salinity at low tide 0 ‰; 4. 8. 1988 dominant species, in several samples very abundant). (2) Fourth of July Beach (locus typicus). Coarse sand with gravel and boulders (8. 7. 1988, numerous); lower part of the beach with effluent freshwater (20. 7., 25. 7. and 13. 8. 1988, abundant).

Material: Live observations on numerous specimens, including drawings and photographs. Nineteen animals sectioned; one animal sectioned sagittally = holotype No. P 2141, 9 paratypes No. P 2142 to P 2150, Zoological Museum of the University of Göttingen.

Up to 4 mm long animals, anteriorly evenly tapering from the middle of the body. Anterior tip squarely blunt with slightly marked corners and weak sensory bristles; no prominent tactile hairs. Two pairs of adhesive papillae dorsolaterally before and behind the pharynx. Caudal end triangular with lateral rows of flat adhesive papillae. Pharynx at the beginning of the rear half of the body. Copulatory organ close to the caudal end. Compared to other otoplanids *A. macrostylis* moves relatively slowly and steadily.

Testis follicles in an unpaired median row in the forebody, caudally followed by the paired germaries. In a fully developed specimen the yolk glands already started in front of the testis follicles and streched backward to the beginning of the copulatory organ. Only beside the pharynx the paired lateral rows were separated by a small gap forming a frontal and caudal partition. However, in sectioned specimens no yolk follicles were found in front of the pharynx.

The epidermis has intraepithelial nuclei throughout the body but in some regions nuclei are scarce, possibly partly depressed. Except of the frontal and caudal end and the adhesive discs the entire body is ciliated. The ventral cilia are slightly longer than the lateral and dorsal ones, thus forming a creeping sole. However, the body ciliation is only well seen in smaller organisms and continuously worse in larger ones. It is not clear if this refers to a decrease in the density of cilia with increasing body size, or to an artifact of preservation. Adhesive discs contain 6 to 8 adhesive papillae each. Rhabdoids are scattered over the entire body wall.

In sections the anterior tip of the body is seen to be retracted to a pit by strong longitudinal muscles split up from the subepidermal musculature. Further ventrally the frontal glands also open in a small pit (both pits as in *A. dillonbeachensis*, see KARLING 1964). The subepidermal musculature is generally weak, except strongly strengthened longitudinal muscles in the ventral praepharyngeal region. The brain capsule is feebly developed. One pair of photoreceptors anterior dorsally in the brain.

The pharynx is cylindrical, in preserved specimens about twice the long as wide. Except the most distal border it is entirely ciliated. Longitudinal pharyngeal muscles next to the epithelium. In the proximal half of the pharynx the inner circular muscles are arranged in 2 to 3 layers. Intestine with weakly developed lateral diverticles, strongly narrowed above the pharynx.

Female organs. The vitellaries form a paired lateral row from about the middle of the pharynx backwards to the copulatory organ. Paired germaries in front of the pharynx. The paired germo-vitello-ducts pass the pharynx ventrolaterally and continue below the vitellaries. At the beginning of the copulatory organ they unite to form a single (left sided) duct which enters the common atrium genitale from dorsally. Numerous shell glands empty into a small pocket-like enlargement between the genital atrium and the unpaired oviduct. Cement glands empty into the distal part of the genital atrium. The common atrium is longish, with a high epithelium containing nuclei.

Male organs. The copulatory organ consists of a seminal vesicle, prostatic vesicle, and a sclerotic apparatus with a median stylet and numerous spines. In live observation the seminal vesicle is piriform. Its caudal musculature is weakly developed while the frontal part is surrounded by strong circular muscles. When

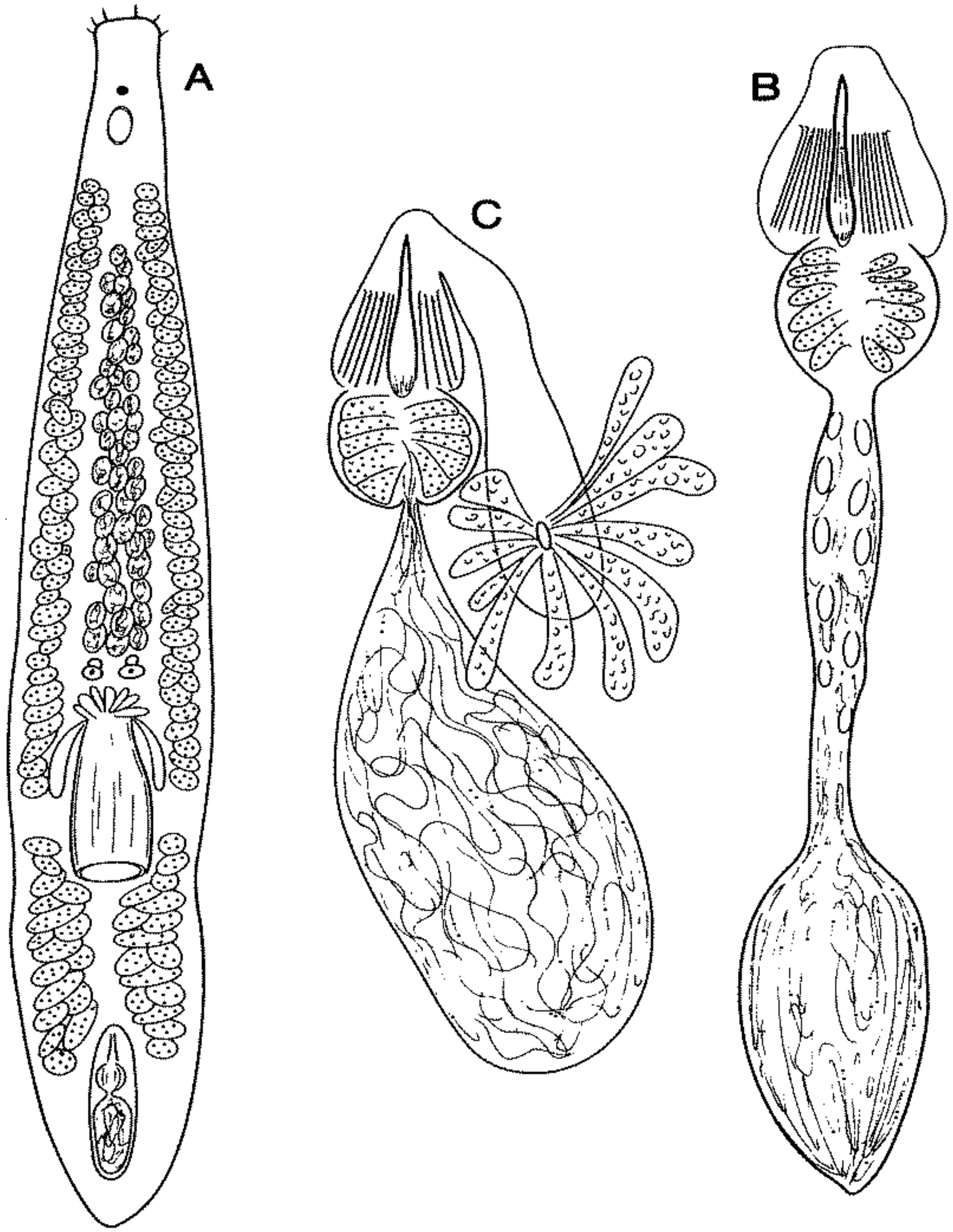

Fig. 15. *Archotoplana macrostylis*. A. Habitus and organisation. B. Copulatory organ. C. Copulatory organ, atrium, cement glands. Frontal part of the seminal vesicle contracted (Seward: Fourth of July Beach).

contracting they form a long intervesicular duct between the caudal part of the seminal vesicle and the prostatic vesicle. The seminal vesicle has a very thin inner epithelium in the distal part which becomes higher in parallel with the outer muscle cover. A few nuclei are scattered in the frontal part which also bears a few cilia. The prostatic vesicle is filled with a high epithelium containing finely granuled secretions and there is only a small ciliated inner cavity.

The stylet (78 to 83 µm long) is not tubiform but an open groove. It is fixed in a muscular pin projecting into the male genital atrium. 40 to 52 spines of 45 to 50 µm surround the stylet in two cycles. The spines insert in a muscular pocket between the median pin with the stylet and the outer musculature of the copulatory organ. The spines are weakly curved and the pointed tip is bent outward. About 6 µm from the tip the spines bear a lateral clasp of 6 µm. The tip

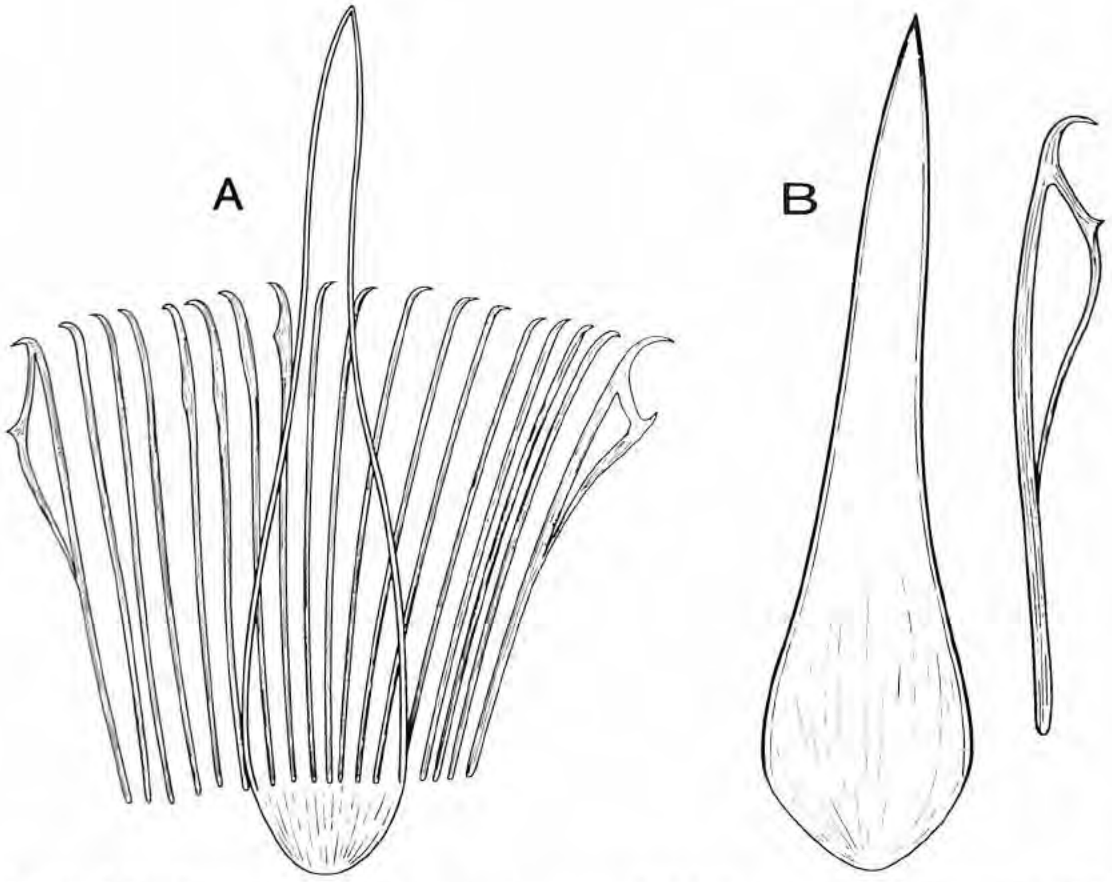

Fig. 16. *Archotoplana macrostylis*. A. Sclerotic apparatus. B. Median stylet and one spine of the sclerotic apparatus (Seward: Fourth of July Beach).

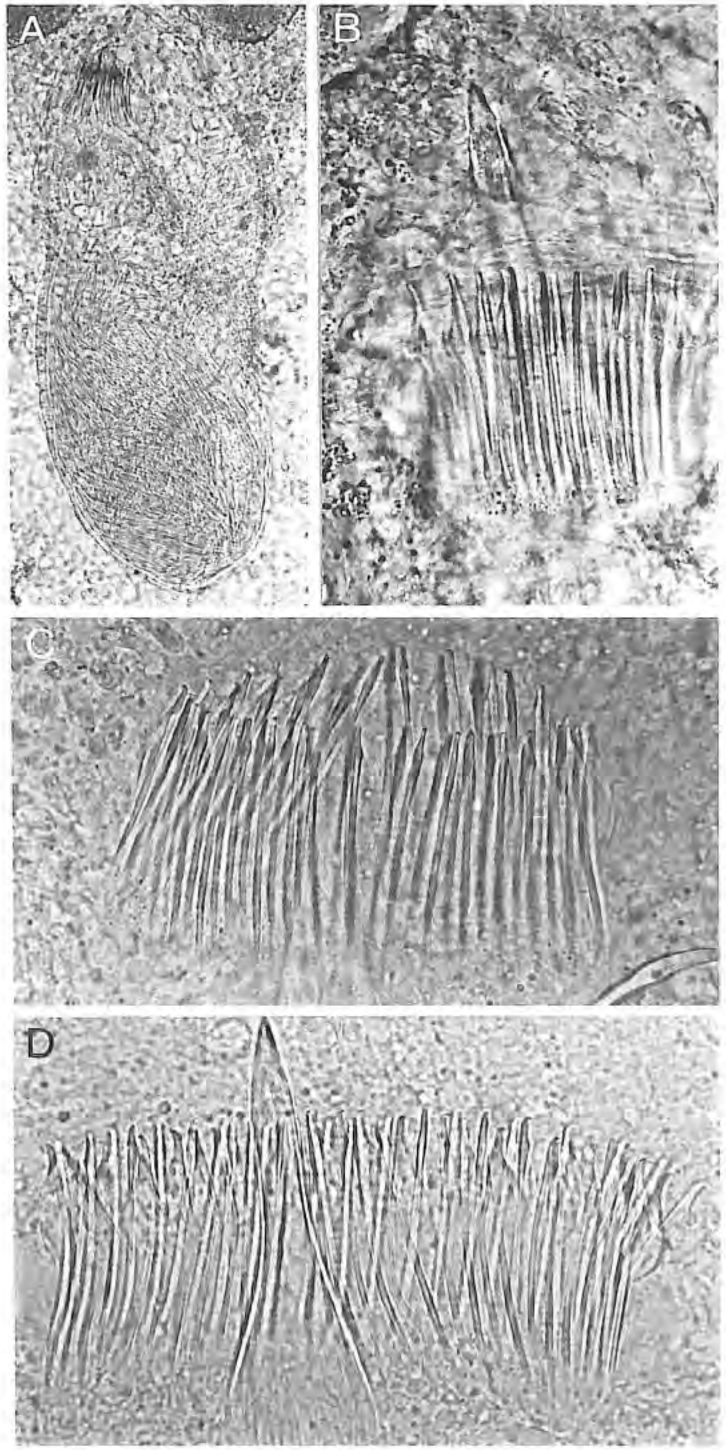

Fig. 17. *Archotoplana macrostylis*. A. Male organ. B–D. Sclerotic apparatus, different focus (Seward: Fourth of July Beach).

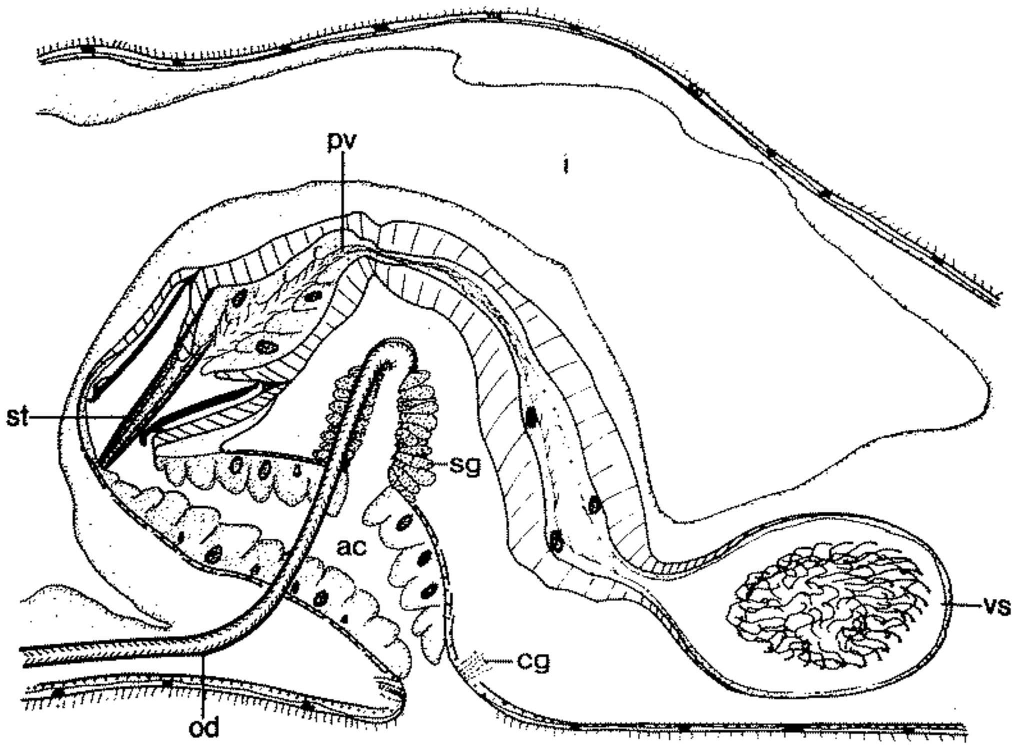

Fig. 18. *Archotoplana macrostylis*. Sagittal reconstruction of the atrial organs.

of the clasp is bifurcated into a minute outward pointation and a slender elongation which turns back to the spine.

The system of vasa deferentia may be quite complicated in *Archotoplana*-species (see Tajika 1983). Only two sections could be seen: (a) a piece of the paired caudal end of the vasa deferentia entering the copulatory organ, and (b) a single large median duct at the caudal end of the testis follicles leading to the andro-intestinal communication before the pharynx.

Discussion. With the description of *Archotoplana yamadai* and *A. abutaensis* by Tajika (1983) the now known species of the taxon "Archotoplaninae" Ax may be grouped under the following diagnosis (amended from Karling 1964): Epidermis entirely ciliated with intraepithelial nuclei. Anterior sensory bristles feebly differentiated, no sensory pits. Two pairs of dorsolateral adhesive discs in the pharynx region. Vitellaries laterally, interrupted beside the pharynx or restricted to the postpharyngeal region. Germaries in front of the pharynx,

Table 2. Differential characters of 5 *Archotoplana* species. + and – indicate presence and absence.

Character	*Archotoplana* *holotricha* Ax, 1956	*dillonbeachensis* Karling, 1964	*yamadai* Tajika, 1983	*abutaensis* Tajika, 1983	*macrostylis* n. sp.
Arrangement of testis follicles	2 lateral rows of aggregates	unpaired median row	unpaired median row	unpaired median row	unpaired median row
Position of vitellaries	before and behind pharynx	before and behind pharynx	only behind pharynx	only behind pharynx	before (?) and behind pharynx
Atrial uterus	+	–	–	–	–
Seminal receptacles	–	+	–	–	–
Andro-intestinal communication	+	–	+	+	+
Horizontal intestinal septum	–	–	+	–	–
Stylet, form	tube	?	tube	tube	groove
size µm	20 to 22	about 30	39	40	78 to 83
Spines, number	32 to 48	16 to 18	14 to 16	48 to 52	40 to 52
size µm	27 to 28	23 to 30	22	23	45 to 50
Body length mm	3	1.5 to 2	1.3	3	4

testicles in front of the germaries. Male sclerotic apparatus with a stylet and a group of bristles.

Taxon *Archotoplana* Ax, 1956, with the same attributes.

Historically, the taxon Archotoplaninae was introduced for those otoplanids which have an entirely ciliated epidermis. However, the holotrich ciliation is a plesiomorph character in the taxon Otoplanidae. Therefore there is currently no autapomorphy for the interpretation of the Archotoplaninae as a monophyletic taxon.

A. macrostylis differs from all other known species of *Archotoplana* by having a groove-shaped stylet. The stylet and the spines are longer than in any other known species of the taxon (Table 2).

Archotoplana macrostylis inhabits beaches which showed purely freshwater conditions at low tide (caused by melting water from adjacent glacier fields). Here they seem to be unrivaled by other species and often occurred very abundant. Similar beaches (with respect to granulometric composition and exposition to currents) with a higher salinity were not occupied. Specimens held in freshwater for three days retained full vitality.

Alaskaplana nov. tax.

Otoplanidae with entirely depressed epidermal nuclei. Seven to eight pairs of distinctly separated testis follicles in the forebody. Vitellaries in lateral rows of paired follicles reaching from the brain backwards to the copulatory organ. Germaries directly in front of the pharynx, forming a coherent mass of separated follicles. Male sclerotic apparatus with a stylet and 12 to 15 bristles. Stylet groove-shaped, partly closed to a tube. With ciliated ductus genito-intestinalis between the common atrium and the intestine. With an accessory female genital opening (vagina) between the pharynx and the common atrium. The accessory female opening is surrounded by numerous large glands, and it is connected with the germovitello-ducts.

Single species: *Alaskaplana velox* n. sp.

Alaskaplana velox n. sp.

(Fig. 19–22)

Locality: Seward. Lowell Point, high energy beach with gravel and boulders near the rocky shore (locus typicus); low tide level (2. 8. 1988, salinity at low tide 13 to 14 ‰; 5. 8. 1988, salinity at low tide 21 ‰).

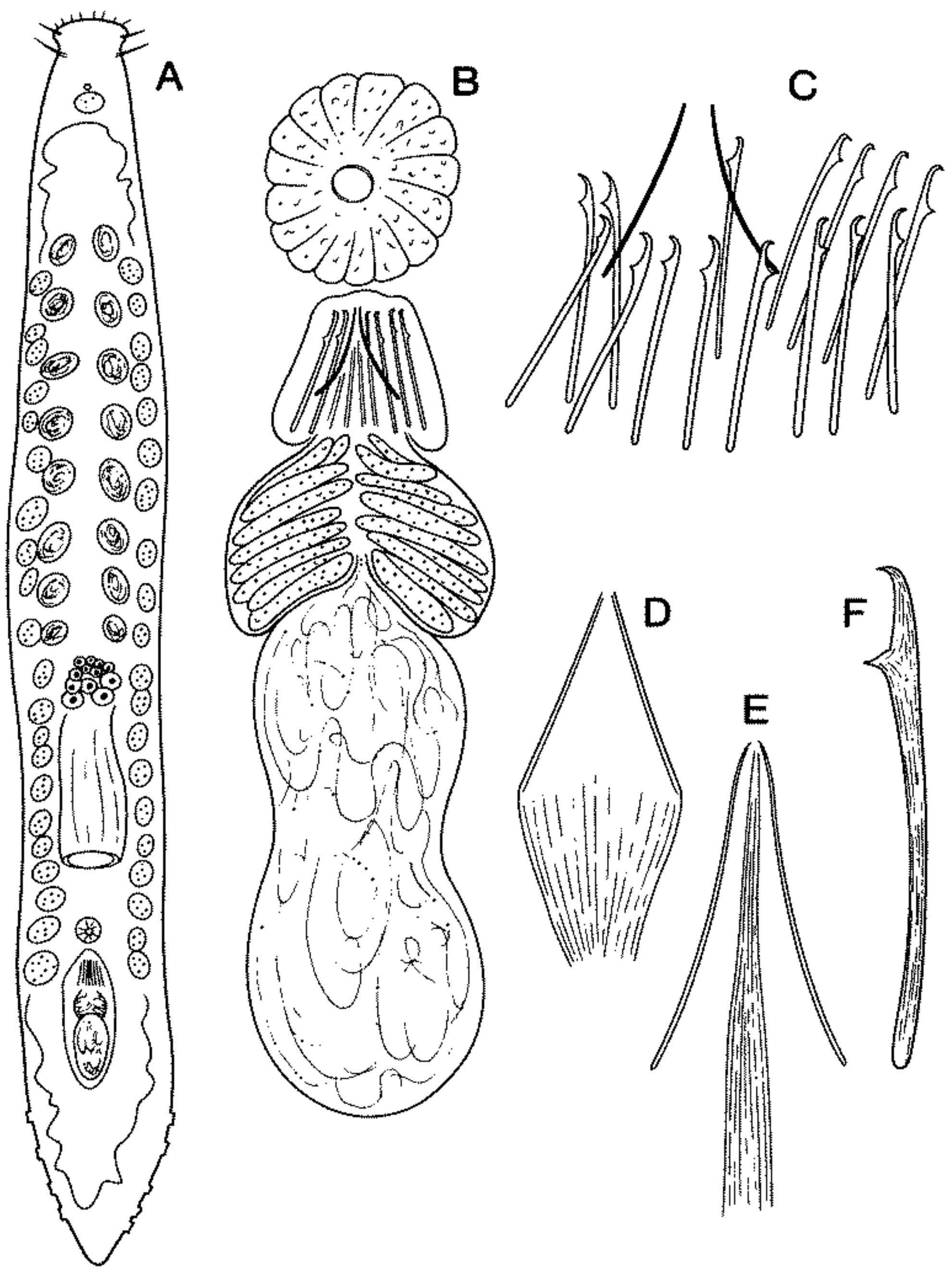

Fig. 19. *Alaskaplana velox*. A. Habitus and organisation. B. Female accessory pore with glands and male organ. C. Sclerotic apparatus. D, E. Median plate of the sclerotic apparatus. F. Spine (Seward: Lowell Point).

Material: Live observations on several specimens, including drawings and photographs. Seven individuals sectioned; one specimen sectioned sagittally = holotype No. P. 2151, 5 paratypes No. P. 2152–P 2156, Zoological Museum of the University of Göttingen.

Very lively specimens of 3 to 4 mm length. The frontal tip is slightly marked with two pairs of prominent lateral tactile bristles. Caudally the body tapers conically. Epidermal nuclei depressed throughout the body. The creeping-sole starts at the opening of the frontal organ and ends at the accessory female opening. It is interrupted below the caudal half of the pharynx. Height of the creeping sole 7 (6 to 8) µm. Frontally a lateral band of cilia stretches between the creeping sole and the region of the tactile hairs. In preserved material the caudal pair of tactile bristles is withdrawn in a small cavity. There are no cilia dorsally between the tactile bristles. In the subepidermal musculature the longitudinal muscles above the creeping sole are strengthened. Rhabdoids occur scattered all over the non-ciliated parts of the epidermis, mostly in groups. Two pairs of dorsolateral adhesive discs with 20 to 30 papilla each before and directly behind the pharynx. Adhesive papilla in the caudal region as usual in Otoplaninae. The cylindrical pharynx lies horizontally in the second half of the body. It is ciliated at both sides, with normal musculature. Circular nerve in the caudal third of the pharynx.

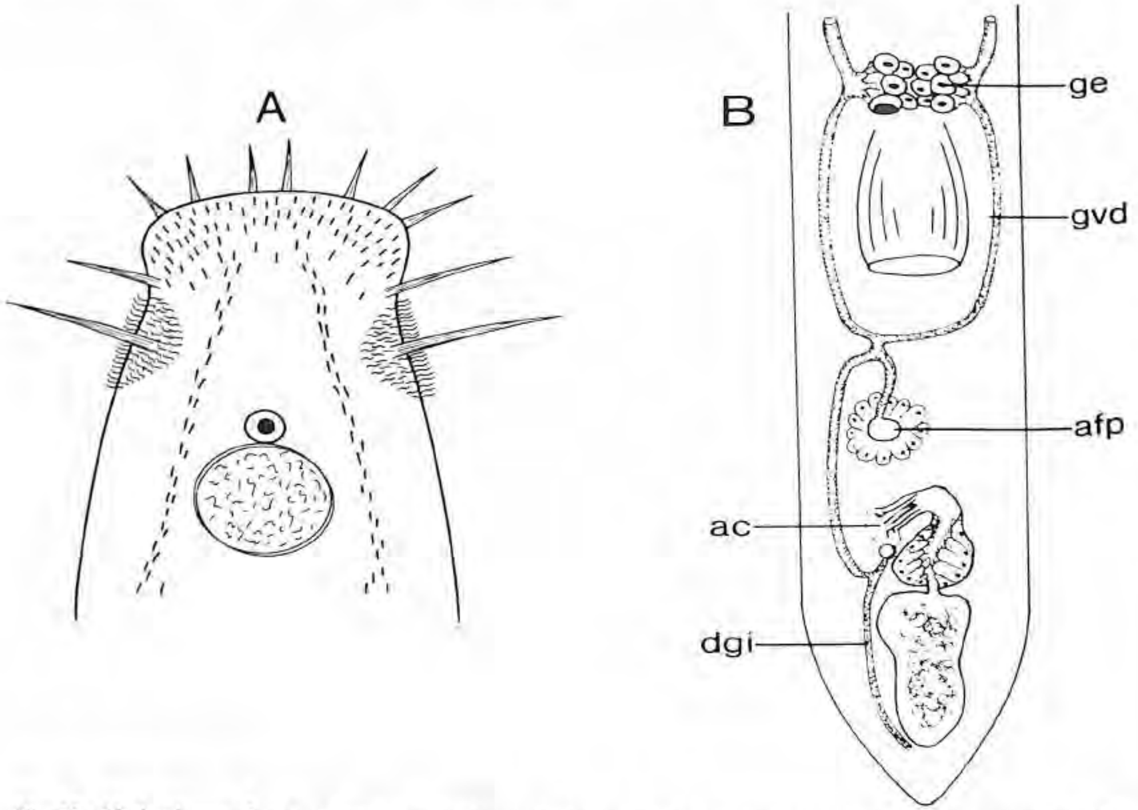

Fig. 20. *Alaskaplana velox.* A. Frontal tip with tactile bristles. B. Reconstruction of the germo-vitelloducts. (Seward: Lowell Point).

Male organs. 7 to 8 pairs of distinctly separated testis follicles median before the pharynx. The copulatory apparatus consists of a seminal vesicle, prostatic vesicle, and the sclerotic apparatus. The large seminal vesicle (preserved 80 µm long and 50 µm high) has a caudally thin, frontally increasingly higher inner

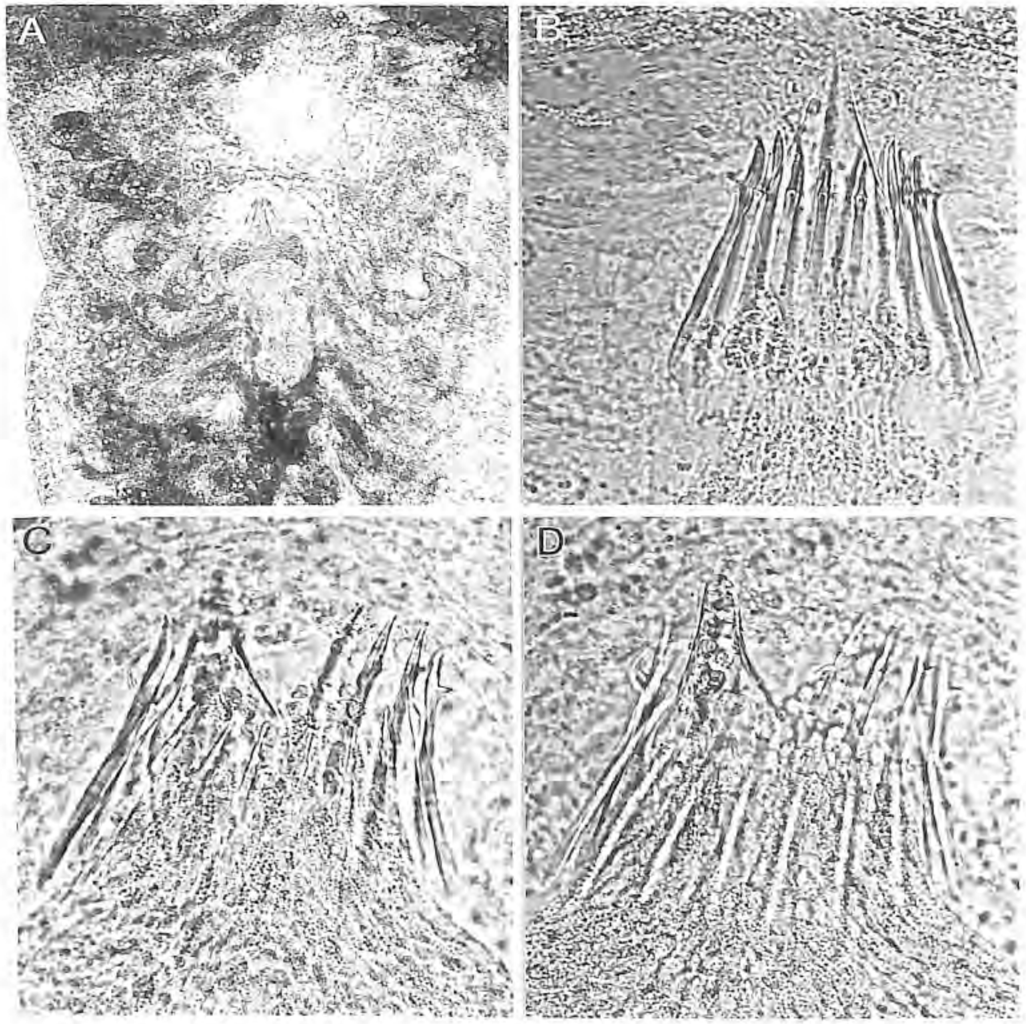

Fig. 21. *Alaskaplana velox.* A. Male organ. B–D. Sclerotic apparatus, different focus (Seward: Lowell Point).

epithelium with few nuclei. It opens through a narrow duct into the prostatic vesicle. The duct and the proximal part of the prostatic vesicle are covered by strong circular muscles. The prostatic vesicle is nearly completely filled with secretory glands. A cavity was only seen in the proximal part. Cilia of the peripheral cells enter the cavity.

The sclerotic apparatus consists of 12 to 14 spines and a median plate. The spines are 45 to 48 µm long and rather straight. The distal tip is pointed and bent outwards. About 8 µm from the tip there is a lateral pointed process. The median plate is 30 to 35 µm long and 10 to 20 µm wide (depending on the degree of coverslip compression). In the basal and the most proximal section the plate is groove-shaped while it seems to be tubiform in the middle part. The spines are surrounded by circular and longitudinal muscles. Distally the muscles insert at the outward directed processes of the spines. In sections the seminal vesicle and prostatic vesicle are oriented horizontally in the longitudinal axis while the sclerotic apparatus points to the ventral side. The stylet was always positioned frontally in the sclerotic apparatus.

Female organs. Germaries ventrally, directly in front of the pharynx, separated into single follicles. The right and left sided follicles join median and thus form a single mass. Vitellaries in paired lateral rows of follicles, beginning at the brain and stretching backwards to the copulatory organ. Ciliated germo-vitello-ducts positioned ventrally of the vitellaries. Beside the germaries the ducts ramify to the single follicles. Behind the pharynx the paired germo-vitello-ducts join and form a short unpaired part. Caudally the unpaired duct ramifies again. (1) One branch passes the sclerotic apparatus at the left side and opens from caudally into a funnel-shaped pocket of the common genital atrium. The mouth is surrounded by (?shell) glands. Shortly before the funnel-shaped pocket this part of the duct ramifies again to form a genito-intestinal duct which passes the seminal vesicle ventrally and then opens caudally into the intestine. (2) The second branch of the germo-vitello-duct opens into the female accessory atrium positioned between the pharynx and the copulatory organ. The accessory pore lies amidst a voluminous complex of glands. The walls of the accessory female atrium are conspicuously strengthened. Presumably the accessory duct acts as a vagina.

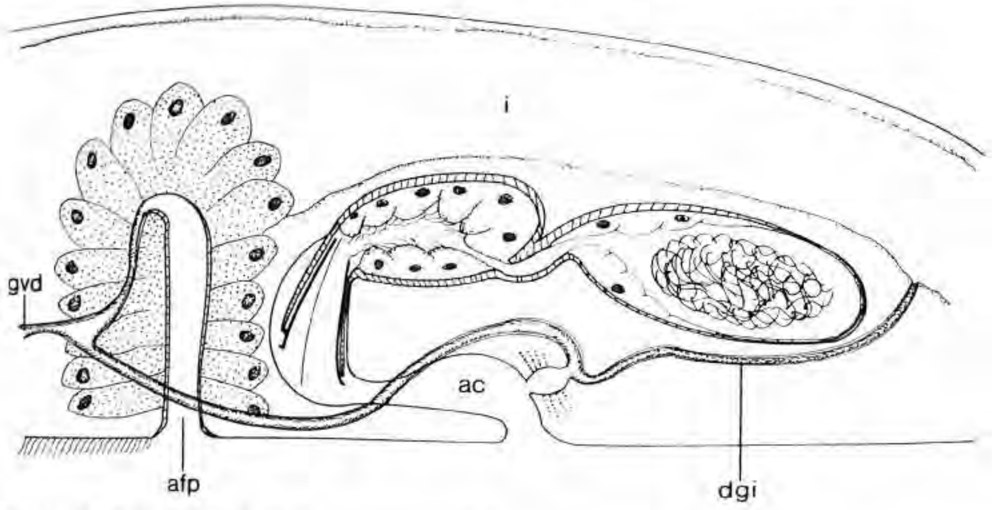

Fig. 22. *Alaskaplana velox.* Sagittal reconstruction of the atrial organs.

Discussion. Germaries separated into single follicles are also known from the otoplanid taxa *Itaspiella* Ax, 1956, *Itaspis* Marcus, 1952, and *Americanaplana* Ax & Ax, 1967 and may be interpreted as an autapomorphy of a group of these taxa and *Alaskaplana*. *Americanaplana* seems to be particularly similar to *Alaskaplana* in having an additional female duct presumably functioning as a vagina and seminal receptacle. As in *Alaskaplana* this duct is a postpharyngeal branch of the germo-vitello-duct. Further, both *Americanaplana* and *Alaskaplana* have a genito-intestinal duct. But unlike *Alaskaplana* the vagina does not open separately ventrally, but joins the common atrium from frontally. Thus, the situation in *Americanaplana* may be regarded as an evolutionary stage leading to the separated vaginal pore in *Alaskaplana*. *Americanaplana* and *Alaskaplana* may be adelphotaxa within the taxon Otoplanidae with the following synapomorphies: (1) the vagina is connected with the germo-vitello-duct; (2) the existence of a genito-intestinal duct. However, the latter duct is a minute structure which may have been overlooked in previous studies.

A vagina between the pharynx and the copulatory organ is also found in *Xenotoplana* Ax, Weidemann & Ehlers, 1978, but in this taxon the vagina has an independent connection with the germaries.

Orthoplana sewardensis n. sp.

(Fig. 23–25)

Locality: Seward. Lowell Point, high energy beach with boulders, gravel and coarse sand (locus typicus). High tide level (7. 7. 1988, 5. 8. 1988, 11. 8. 1988). Salinity varied strongly between 5 ‰ (low tide of Aug. 5th) and 26 ‰ (high tide of Aug. 4th).

Material: Live observations on several animals, including drawings and photographs. Three specimens sectioned; one animal sectioned sagittally = holotype No. P 2161, one paratype No. P 2162, Zoological Museum of the University of Göttingen.

Living specimens 1.5 to 3 mm long. The general organization and topography of the organs resemble *Itaspiella helgolandica*. Frontal end with one pair of larger

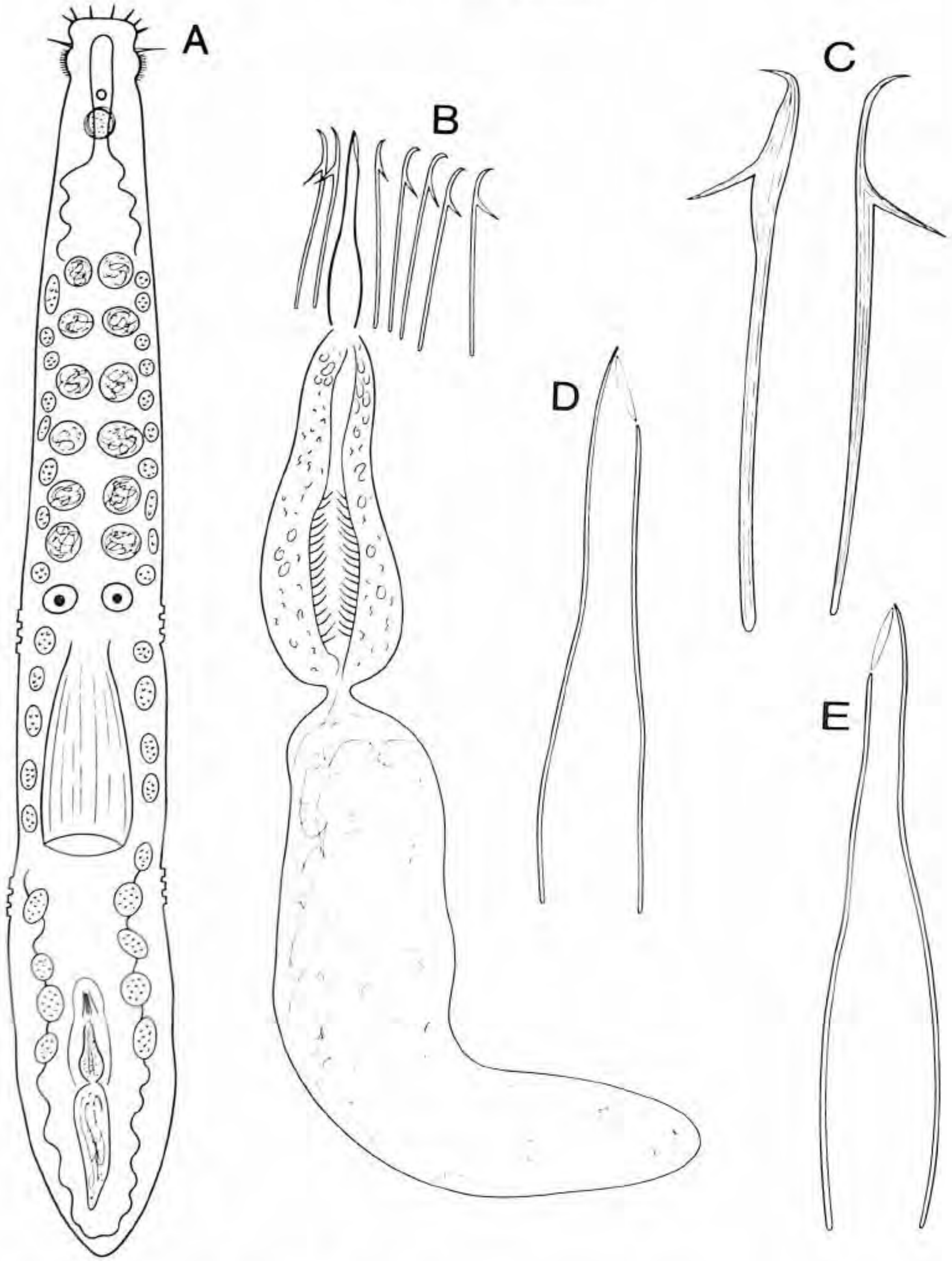

Fig. 23. *Orthoplana sewardensis.* A. Habitus and organisation. B. Male organ. C. Spines. D, E. Median stylet (Seward: Lowell Point).

tactile hairs and a row of fine hairs. With ciliated patches behind the larger tactile hairs which are a lateral prolongation of the ventral creeping sole. The ciliated patches are not dorsally fused. In free-swimming animals the region of the ciliated patches and large tactile hairs is projected like a hump. Pharynx in the posterior half of the body. Adhesive papilla cover the tail border, starting from about the common genital opening. Paired patches of about 10 adhesive papilla are seen dorsolaterally in front of the pharynx and between the pharynx and the copulatory organ.

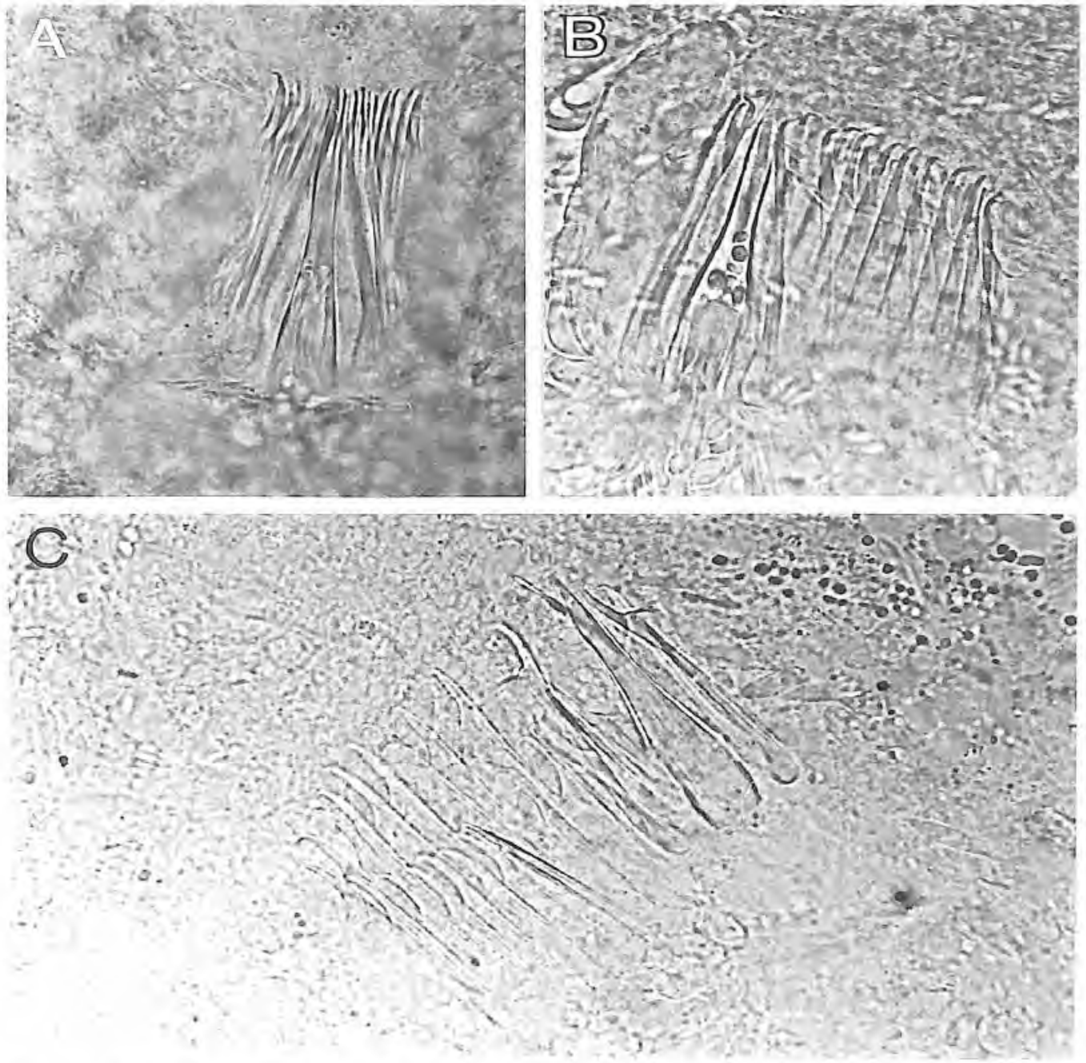

Fig. 24. *Orthoplana sewardensis.* A–C. Sclerotic apparatus, different focus (Seward: Lowell Point).

The nuclei of the epidermis are depressed all over the body. Epidermal ciliation absent except the ventral creeping sole between the frontal organ and the pharynx and between the mouth and shortly before the genital opening. Rhabdoids only occur in the non-ciliated area.

Pharynx tubiform, internally and externally ciliated. Cilia are only lacking at the distal border of the pharynx. Above the pharynx the intestine is restricted to a narrow tube while it forms lateral diverticles both anteriorly and posteriorly. A short gut diverticle extends rostrad above the brain.

The vitellaries stretch laterally alongside the testis follicles, germaries and pharynx and they end at the copulatory organ. Six pairs of testis follicles form two median rows in the forebody, caudally followed by the single pair of germaries. The germo-vitello-ducts lie below the vitellaries. They join in front of the copulatory organ to form the common oviduct which enters the genital atrium in common with shell glands. No vesicular bursa present. There is a genito-intestinal duct in the caudal prolongation of the common oviduct.

The general organization and topography of the atrial organs is the same as in *Orthoplana mediterranea* Ax, 1956 (with exception of the genito-intestinal duct). The cylindrical seminal vesicle is externally surrounded by strong circular muscles. It opens into the longish prostatic vesicle which is covered by strong circular muscles as well. The sclerotic apparatus of the penis consists of a median stylet surrounded by spines. The stylet is 37 to 41 µm long and distally cut-off oblique. Unlike in most other otoplanids the stylet is not tubiform but a dorsally open groove. The number of spines varied between 23 and 34 and their length between 27 and 38 µm. Possibly the smallest spines were not fully developed. The distal tip of the spines is curved and there is a lateral extension of about 5 µm length positioned 7 to 8 µm from the curved tip. All spines look the same.

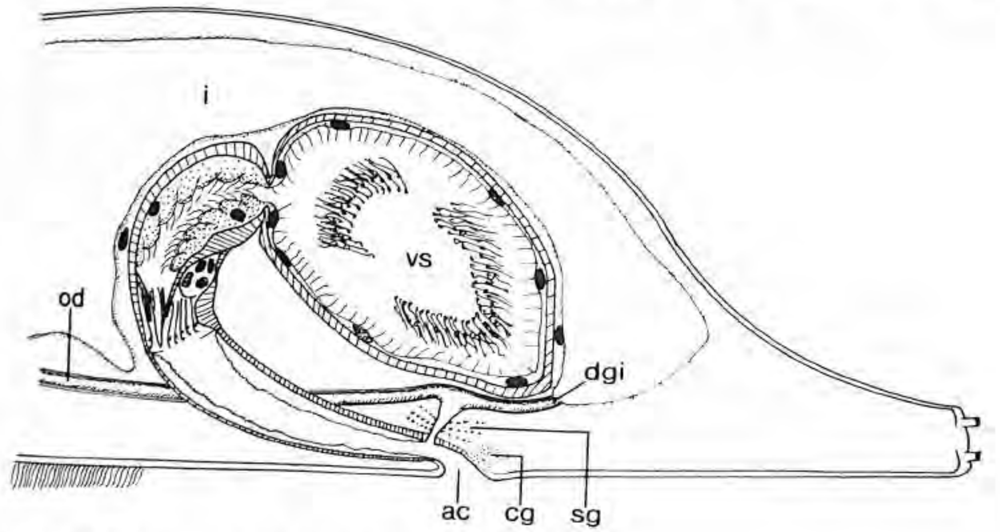

Fig. 25. *Orthoplana sewardensis.* Sagittal reconstruction of the atrial organs.

Discussion. In the taxon Otoplanidae the genus *Orthoplana* Steinböck unites species with a single genital pore, which lack a primary bursa and receptacula seminis, and which have an epidermis with depressed nuclei (Ax 1956 b, Ax & Ax 1967, Karling 1973). The delimitation of the taxon is rather provisionally, in particular with respect to *Itaspis* Marcus (with paired seminal receptacles and divided ovarial follicles) and *Itaspiella* Ax (with divided ovarial follicles and with primary bursa). There seems to be no clear autapomorphy of the taxon *Orthoplana.*

Valid species are *O. mediterranea* Ax, 1956, *O. kohni* Ax & Ax, 1967, *O. bregazzii* Karling, 1973, and the insufficiently known *O. borealis* (Steinböck, 1931). *O. sewardensis* is particular similar to *O. bregazzii.* Both species have (1) a groove-shaped stylet while the stylet is tubiform in *O. mediterranea* and *O. kohni.* (2) Both have a genito-intestinal duct which is a caudal prolongation of the common oviduct (overseen in other species?). Finally, (3) unlike all other species of *Orthoplana, O. sewardensis* and *O. bregazzii* have divided germaries. These characters may be used to substantiate an adelphotaxa-relationship between *O. bregazzii* and *O. sewardensis.* The stylet length and number and size of the spines are other features clearly separating the *Orthoplana* species known up to now (Table 3).

Table 3: Shape and size of the sclerotic apparatus in *Orthoplana* species.

	Stylet		Spines	
Species	Shape	Size µm	Number	Size µm
O. borealis	?	?	6,8 or more	?
O. bregazzii	groove	100–120	30–40	40–90
O. kohni	tube	30	9	25
O. sewardensis	groove	37–41	23–34	(27–)38
O. mediterranea	tube	70–85	17–22	55–65

***Itaspiella helgolandica* (Meixner, 1938)**

(Fig. 26, 27)

Localities: Kotzebue Sound, about 5 miles south of the village. (1) Medium to coarse sand with gravel from a freshwater outlet, salinity = 10 ‰. (2) Coarse sand, gravel and boulders of the beach exposed to Kotzebue Sound; salinity = 16 ‰ (8. 8. 1988).

Material: Live observations on several specimens, including drawings and photographs. Three specimens sectioned.

Distribution: Europe, North Sea, Baltic Sea, Atlantic coast of Norway. America, southern Canadian Atlantic coast, US Pacific coast (cf. AX & ARMONIES 1987).

The number of testis follicles varied between 6 and 9 pairs. The copulatory apparatus was in all studied specimens equipped with a median stylet of 38 to 39 µm and 8 spines of up to 36 µm. Examination of the sections stated the identity with *Itaspiella helgolandica*. The specimens have a body wall with depressed nuclei throughout the body, germaries divided into several follicles, and a primary bursal apparatus.

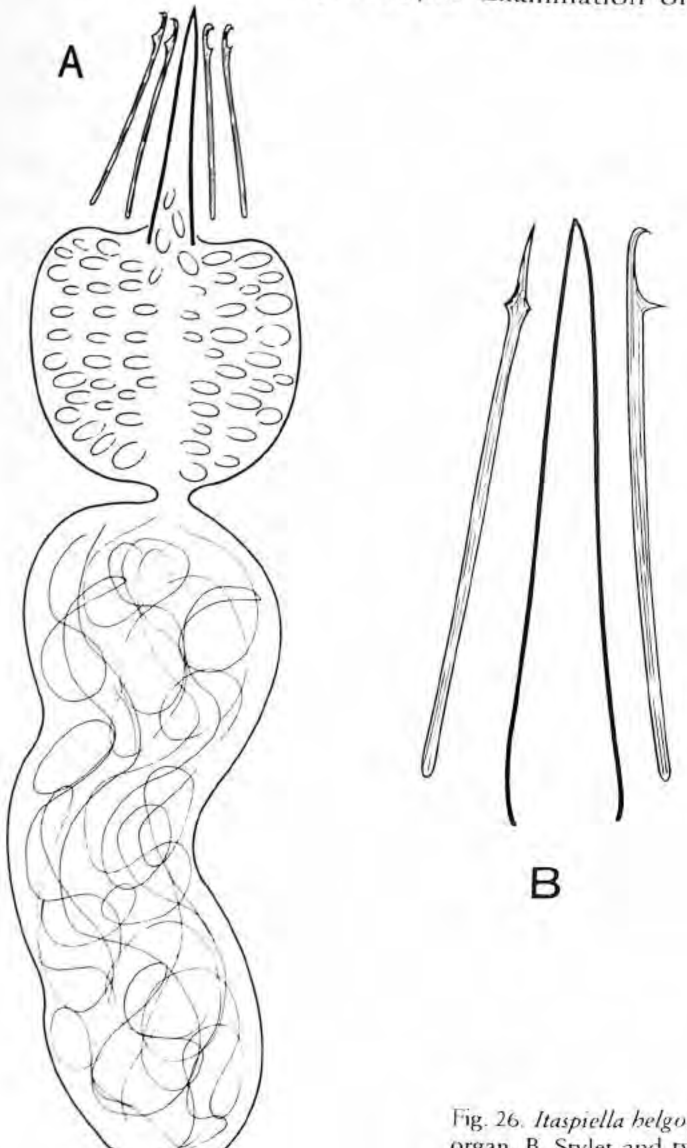

Fig. 26. *Itaspiella helgolandica.* A. Male copulatory organ. B. Stylet and two spines in top- and side-view, respectively (Kotzebue).

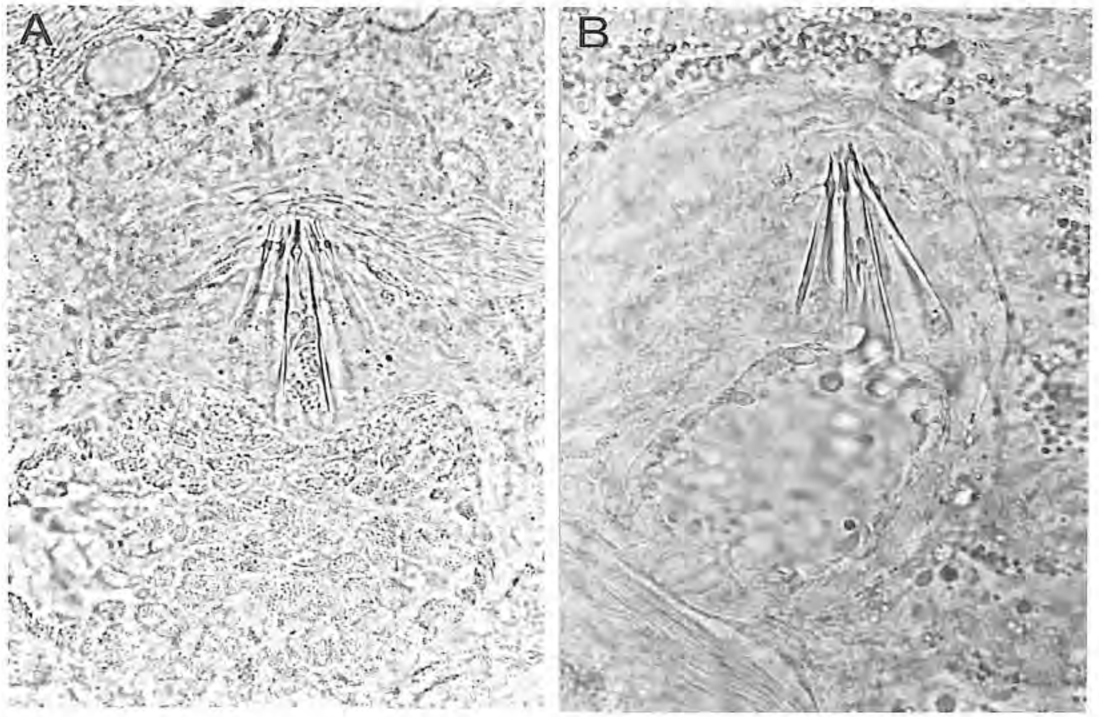

Fig. 27. *Itaspiella helgolandica.* A, B. Male copulatory organ (Kotzebue).

Archiloa tajikai **n. sp.**

(Fig. 28–30)

Localities: (1) Seward. Lowell Point (locus typicus). Lower beach slope with effluent freshwater. In fine sand (10. 7. 1988, salinity 0 ‰) and in medium sand (2. 8. 1988 and 4. 8. 1988, salinity 0 ‰). (2) Ninilchik. Sandy beach at the mouth of the Ninilchik River (21. 7. 1988, interstitial salinity 30 to 37 ‰). (3) Kotezbue Sound. Sandy beach close to the mouth of a small river about 5 miles south of the village. (a) medium to coarse sand with gravel of the river mouth (salinity 10 ‰), (b) coarse sand with gravel and boulders of the shore directly opposed to Kotzebue Sound (8. 8. 1988, salinity 16 ‰).

Material: Live observations on numerous specimens, including drawings and photographs. Twenty animals sectioned, one specimen sectioned horizontally = holotype No. P. 2171, Zoological Museum of the University of Göttingen.

Male mature specimens 1.5 mm long. Slender organisms, frontal tip of the body rounded, caudal end tapering. Pharynx in the second half of the body. Copulatory organ close to the tail end, female pore directly behind the copulatory organ.

Entire body ciliated, except the caudal end. Ventrally of the pharynx cilia are scarce. Epidermal nuclei depressed throughout the body. A few rhabdoids were seen caudally. Subepidermal musculature with fine circular and strong longitudi-

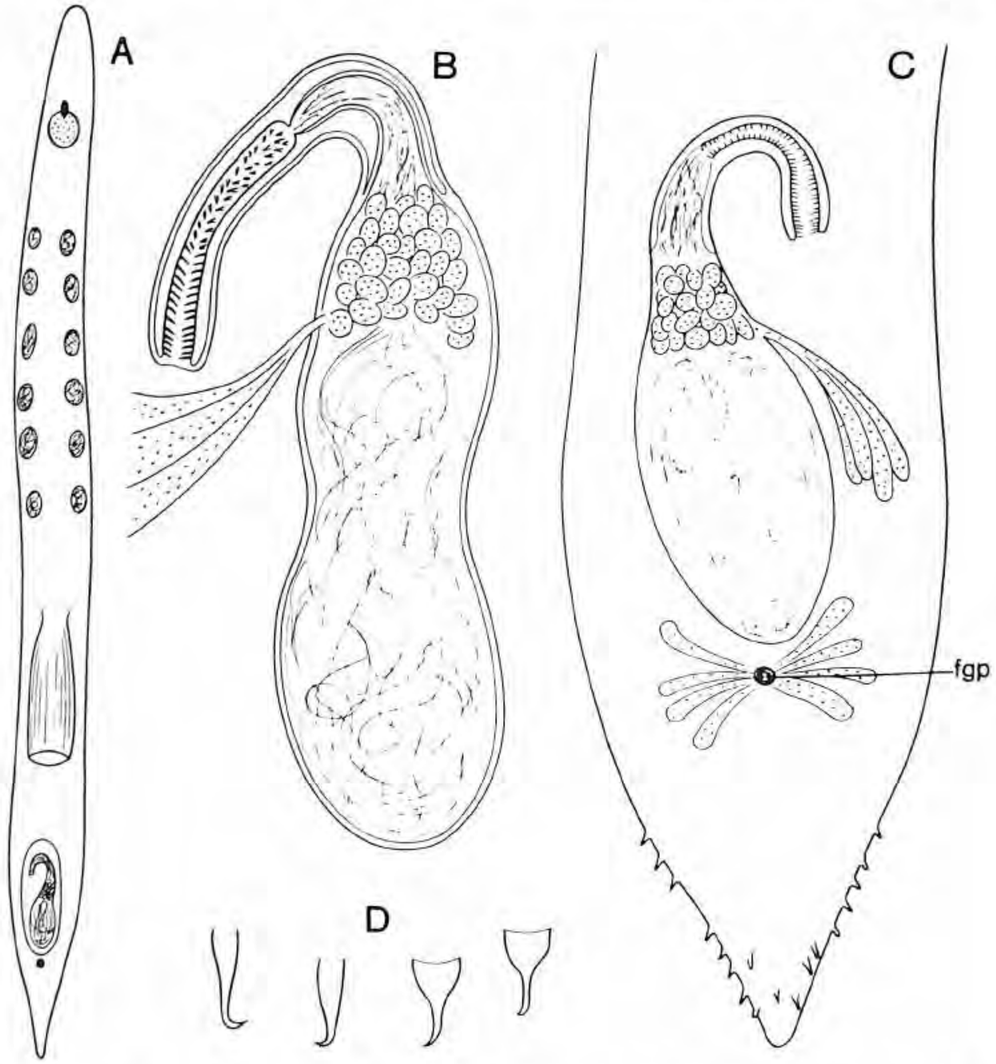

Fig. 28. *Archiloa tajikai.* A. Habitus (Seward: Lowell Point). B. Male copulatory organ (Kotzebue). C. Male copulatory organ. D. Single spines of the cirrus (Seward: Lowell Point).

nal muscles. Pharynx entirely ciliated except the distal border. It is distally inclined towards the ventral side.

Male organs. In younger specimens no more than 6 pairs of testis follicles were seen arranged in lateral rows. In older individuals the number of follicles

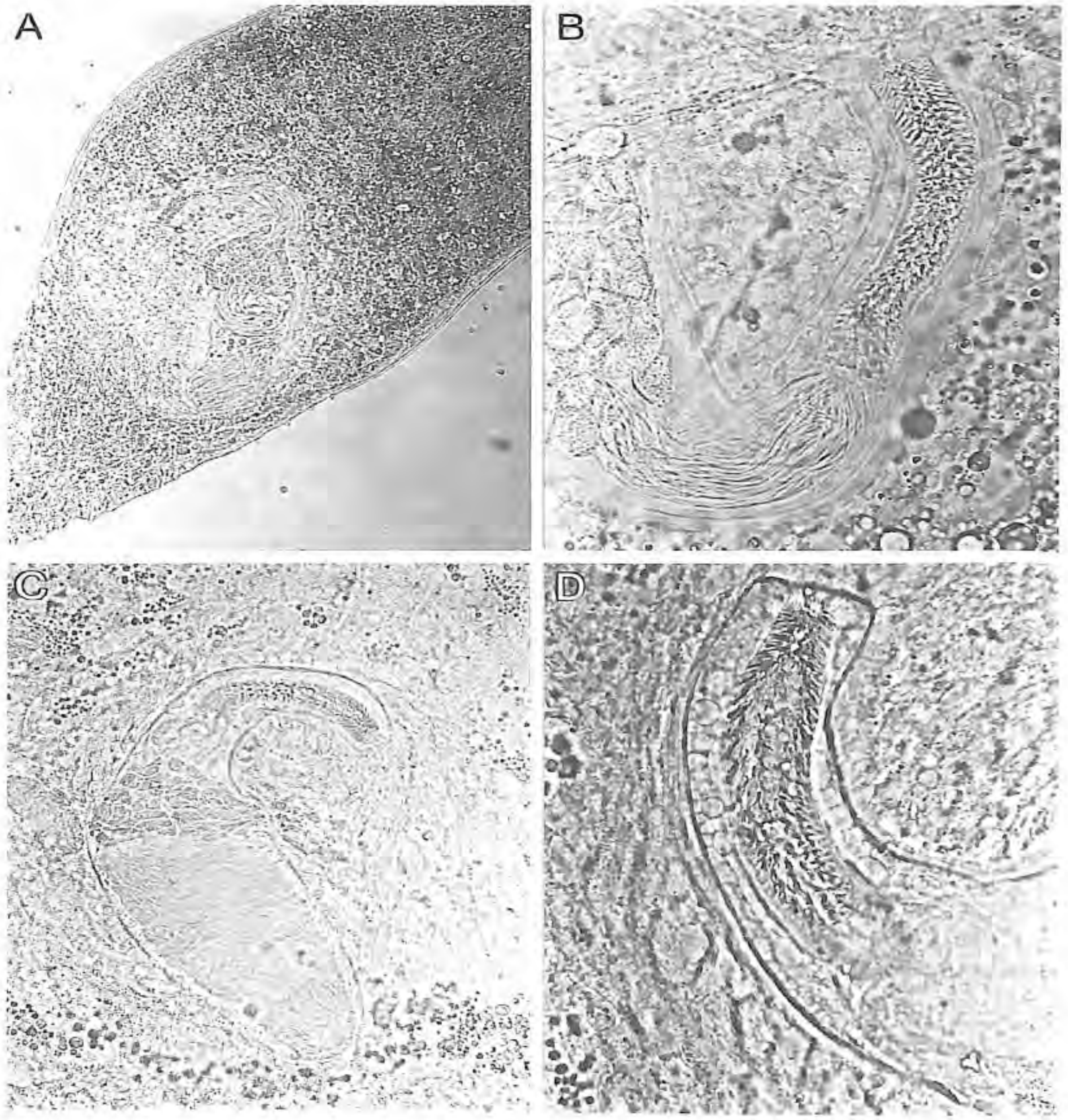

Fig. 29. *Archiloa tajikai.* A. Posterior tip with male copulatory organ. B. Male copulatory organ (Kotzebue). C. Male copulatory organ. D. Cirrus of the male organ (Seward: Lowell Point).

increases and their arrangement becomes less regular. In a fully mature specimen testis follicles inserted ventrally, laterally, and dorsally in the body cavity. The copulatory organ consists of a longish to ovoid seminal vesicle which continues into a section with peripheral glandular secretions and centrally sperms. The distal part of the copulatory organ is turned ventrally. Cirrus about 20 µm long with regularly arranged spines of about 5 µm in the distal half and less regular spines of 3 µm proximally. The spines are bottle-shaped with a curved tip and have a flattened basal plate. The copulatory apparatus has a strong muscular cover of outer longitudinal and inner circular muscles. Some prostatic glands enter the prostatic part of the organ from one side. The genital atrium is ciliated.

Female organs. Paired germaries in front of the pharynx. Vitellaries in lateral rows of tightly packed follicles, extending between the middle of the testis region and the copulatory organ. In front of the pharynx the vitellaries are more dorsolaterally and the testis follicles ventrally. The paired germo-vitello-ducts pass the pharynx ventrolaterally. Behind the pharynx they unite and continue dorsally to the middle of the body. Here the duct enters a strongly muscular part of the female apparatus. It consists of a frontal spherical and a caudal tubiform vesicle which are separated by strong circular muscles. Internally both vesicles have a cylindrical epithelium with intraepithelial nuclei. The tubular part is positioned above the copulatory organ. Further caudally it continues into a blistery tissue without visible musculature, presumably a postpenial bursa. Finally, the most distal part of the oviduct shows a muscular cover again. It is surrounded by shell glands (cement glands not seen).

The vagina is strongly muscular as well. Its opening into a ciliated frontal projection of the genital atrium is closed by circular muscles. Dorsally the vagina passes over into the spherical vesicle mentioned above. Some (alien) sperm were seen in the duct connecting both cavities. Some blistery tissue is seen above and in front of the spherical muscular bulb, possibly a prepenial bursa. Postpenial, some large cells with finely grained contents are countersunk from the intestinal epithelium and contact the non-muscular dorso-caudal part of the female duct. A direct connection between these large-sized cells and the female duct was not seen.

Discussion. An internal vagina connected with a prepenial bursa which furtheron joins the germo-vitelloduct, and a postpenial bursa (?of the resorbiens type) are also found in *Archiloa juliae* Tajika, 1982. These characters may substantiate an adelphotaxa-relationship of the two species in the taxon *Archiloa*. Specific differences between the two species are (1) the size of the penial spines (spines of 3 to 5 µm in *A. tajikai*, and spines of progressive size from 2 µm proximally to 11 µm distally in *A. juliae*), and (2) the strongly muscular female apparatus above the copulatory apparatus of *A. tajikai*.

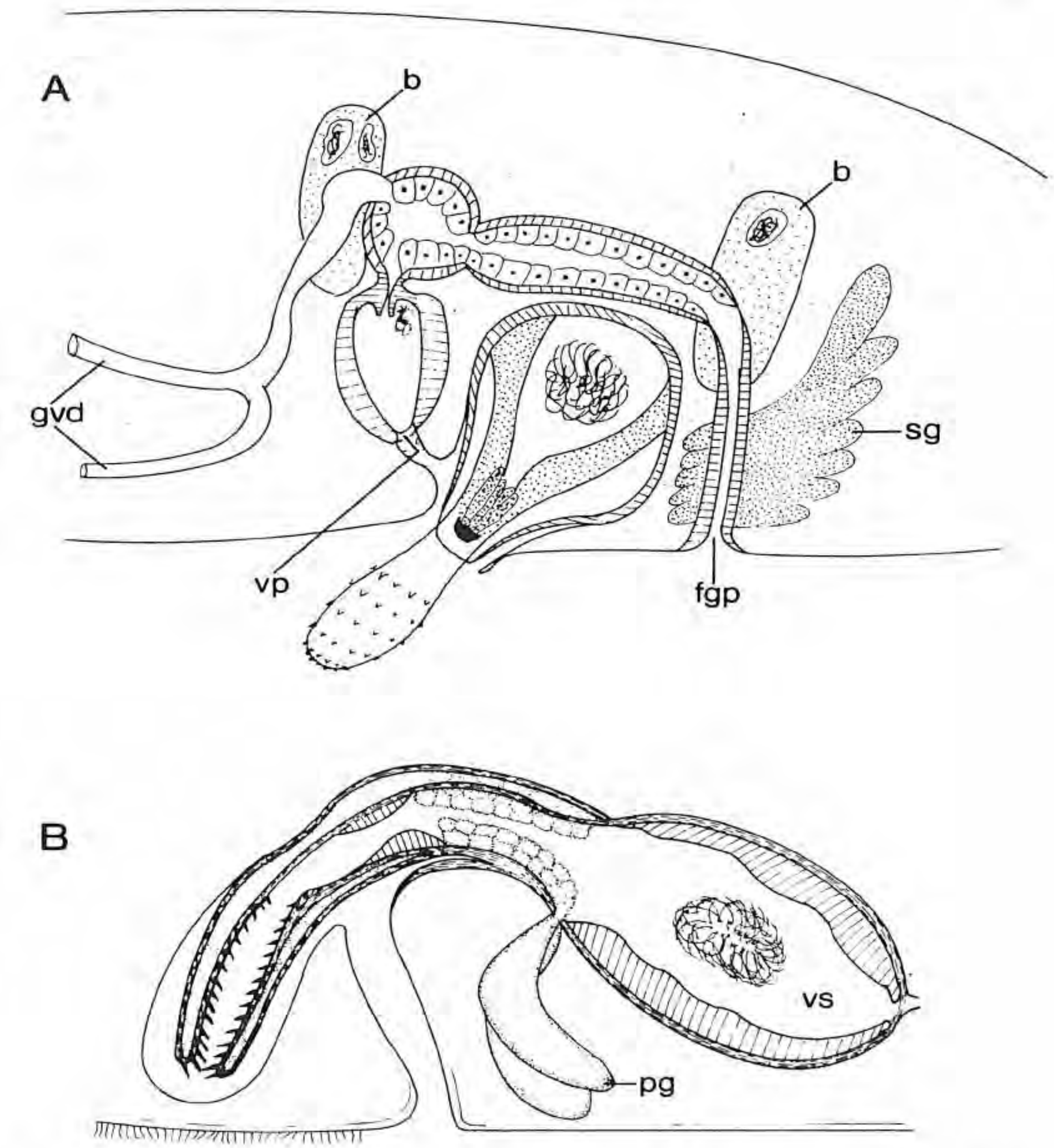

Fig. 30. *Archiloa tajikai*. A. Sagittal reconstruction of the atrial organs, cirrus everted. B. Sagittal reconstruction of the male copulatory organ.

However, these strongly muscular structures were only seen in a single fully mature specimen (the holotype). Nothing of it was seen in younger specimens which were already in male maturity. Arranging the sectioned material in a developmental series yields the following ordination: (a) the germaries, testis follicles, and the copulatory apparatus are first differentiated. (b) The germaries become larger, the vitellaries differentiate, and the female pore with some shell glands appears. (c) The vagina first appears as a non-muscular cavity (already filled with alien sperms, in one animal). (d) Non-differentiated tissue covers the copulatory organ dorsally, the vagina still appears as a blindly closed cavity; female pore with the shell glands clearly visible, as are the paired germovitelloducts. (e) The muscular part of the female duct, its connexion with the vagina, and the bursae appear last. These observations confirm the supposition of a late differentiation of the female pore (cf. Karling 1966) and the same applies to the distal muscular part of the female duct. Thus, there may be more species with a strongly muscular section of the female duct when in full female maturity.

Archiloa duplaculeata n. sp.

(Fig. 31, 32)

Locality: Seward. Lowell Point (locus typicus). Coarse sand and gravel with effluent freshwater of the lower beach slope (4. 8. 1988).

Material: Live observations on 2 specimens, including drawings and photographs. One specimen sectioned.

Animals in male maturity about 3 mm long. With an ovoid copulatory organ which contains proximally sperm. The cirrus is about 85 µm long with numerous spines of up to 8 µm. Prostatic glands enter the median part of the copulatory organ from both sides. Female pore closely behind the copulatory organ. An additional pore (?vagina) about 300 µm frontally of the copulatory organ. Most conspicuous is a second group of up to 35 µm long spines. They are slightly curved and have a pointed tip. In living animals at least 6 spines were seen on either side. In the only sectioned specimen the cirrus was everted. It is not clear if the giant spines belong to the genital atrium or an adjacent structure. However, they are not a part of the copulatory cirrus and were not everted in common with it.

Discussion. Although our knowledge of the general organization of *A. duplaculeata* is scarce, the existence of a cirrus plus a group of giant spines allows a proper identification. A copulatory organ of the duplex-type (i.e. composed of two cirrus-like structures) is also found in *Archiloa rivularis* de Beauchamp, 1910, *A. westbladi* Ax, 1954, and *A. petiti* Ax, 1956. But in none of these species are the additional spines as large as in *A. duplaculeata*. Strikingly large spines occur in *Promonotus wilsoni* (Stirewalt, Kepner & Ferguson, 1940) and in *P. villacae* Marcus, 1949 but these spines are part of the cirrus. In addition, there is no vaginal pore in *Promonotus*.

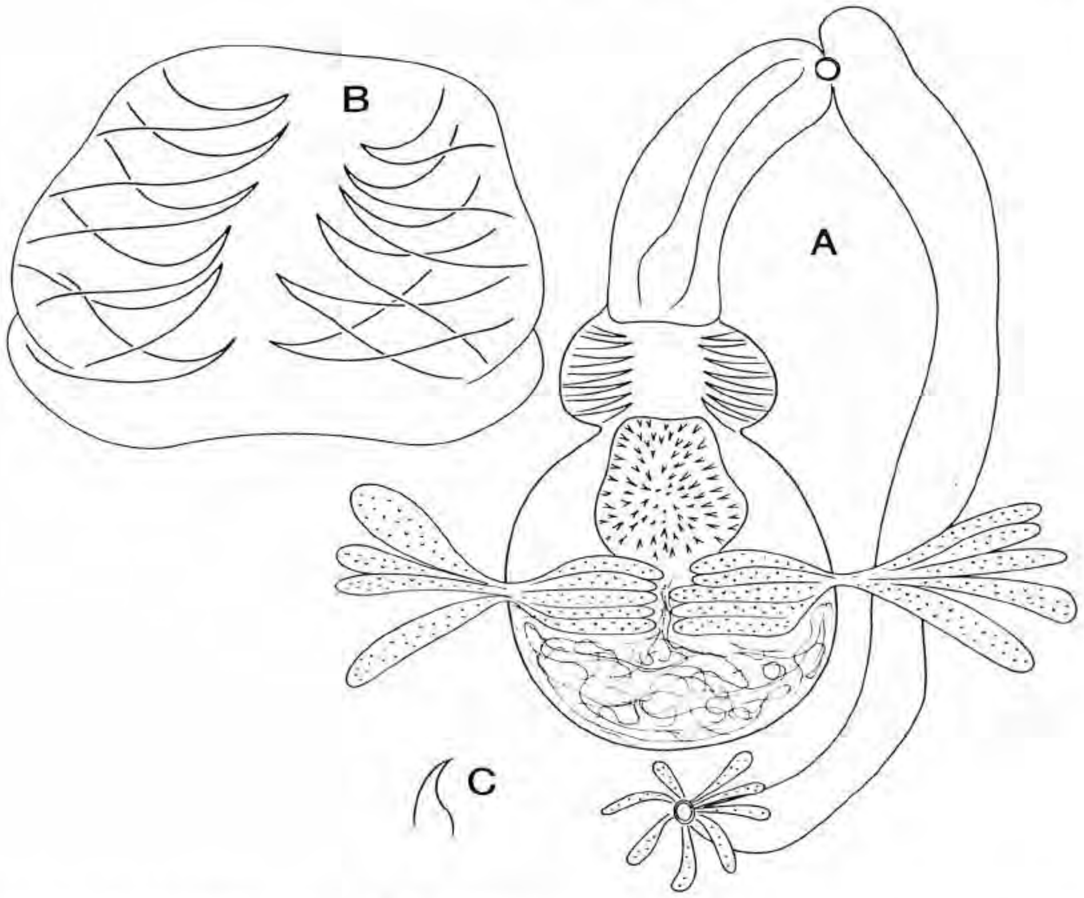

Fig. 31. *Archiloa duplaculeata*. A. Male copulatory organ. B. Second group of long spines, enlarged. C. Single spine of the cirrus (Seward: Lowell Point).

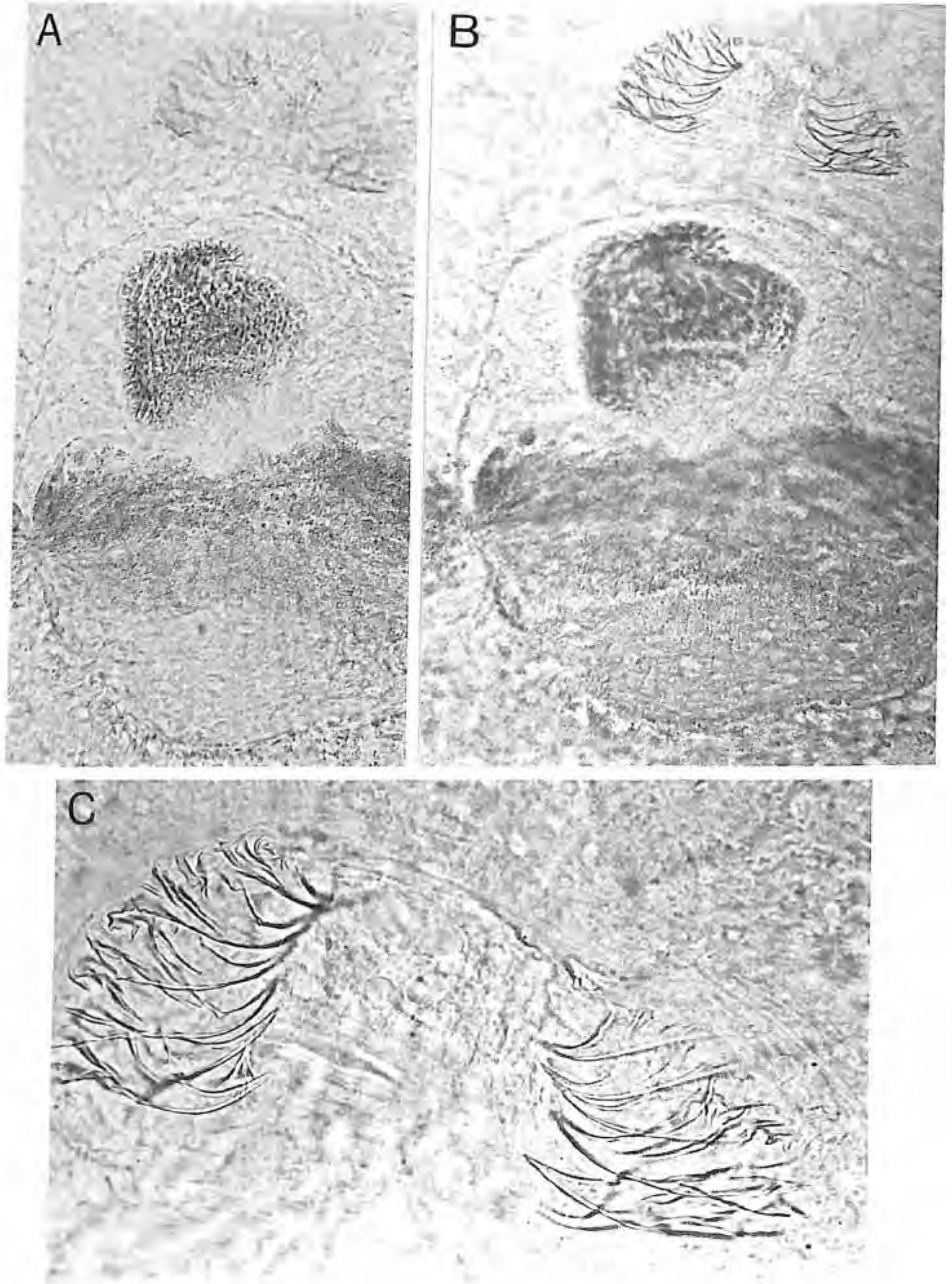

Fig. 32. *Archiloa duplaculeata*. A, B. Male copulatory organ, different focus. C. Second group of large spines in front of the cirrus (Seward: Lowell Point).

Minona gigantea n. sp.

(Fig. 33, 34)

Locality: Seward. Lowell Point (locus typicus). Coarse sand and gravel of the lower beach slope with effluent freshwater (4. 8. 1988).

Material: Live observations on several specimens, including drawings and photographs. 15 animals sectioned, one specimen sectioned sagittally = holotype No. P 2181, Zoological Museum of the University of Göttingen.

Animals 5 to 6 mm long with slender head end. Caudal end triangular with numerous conical adhesive papilla. Pharynx in the second half of the body, internally and externally ciliated. About 60 to 70 testis follicles in two praepharyngeal lateral rows. In a single cross-section 3 to 5 testis follicles positioned beside each other in each row. Copulatory organ, glandular organ and the female pore all very close to the caudal end. The copulatory organ is ovoid, 35 × 50 μm in one specimen and up to 120 × 170 μm in another. It is surrounded by a strong muscular cover, as is the glandular organ. The glandular stylet is strongly hardened only in the distal half (about 22 μm) while the proximal lobe

Table 4: Valid *Minona* species (cf. Sopott-Ehlers & Ax, 1985) and some of their morphological characters (No 1 to 6).

1 common opening for the copulatory organ and the male accessory organ
2 + the male openings distinctly separated
– opening of copulatory organ and male accessory organ close together
3 + with or – without paired eyes
4 + with or – without external vagina
5 + with or – without common pore for female opening and gladular organ
6 + with or – without accessory vaginal glands

Characters						
1	2	3	4	5	6	Species
–	+	+	+	–	–	*M. evelinae* Marcus, 1946
–	+	–	+	–	–	*M. divae* Marcus, 1951
–	+	–	–	–	–	*M. baltica* Karling & Kinnander, 1953
–	+	–	+	+	–	*M. trigonopora* Ax, 1956
–	–	+	+	–	–	*M. obscura* Karling, 1966
–	–	–	+	–	–	*M. cornupenis* Karling, 1966
+	–	–	–	–	–	*M. bistylifera* Karling, Mack-Fira & Dörjes, 1972
–	–	–	–	–	–	*M. fernandinensis* Ax & Ax, 1977
–	+	+	+	–	–	*M. peteraxi* Karling, 1978
–	–	–	+	–	–	*M. dolichovesicula* Tajika, 1982
–	–	–	+	–	–	*M. pelvivaginalis* Tajika, 1982
–	+	–	+	–	–	*M. degadti* Martens, 1983
+	–	–	+	–	–	*M. secta* Sopott-Ehlers & Ax, 1985
–	+	–	+	–	+	*M. gigantea* n. sp.

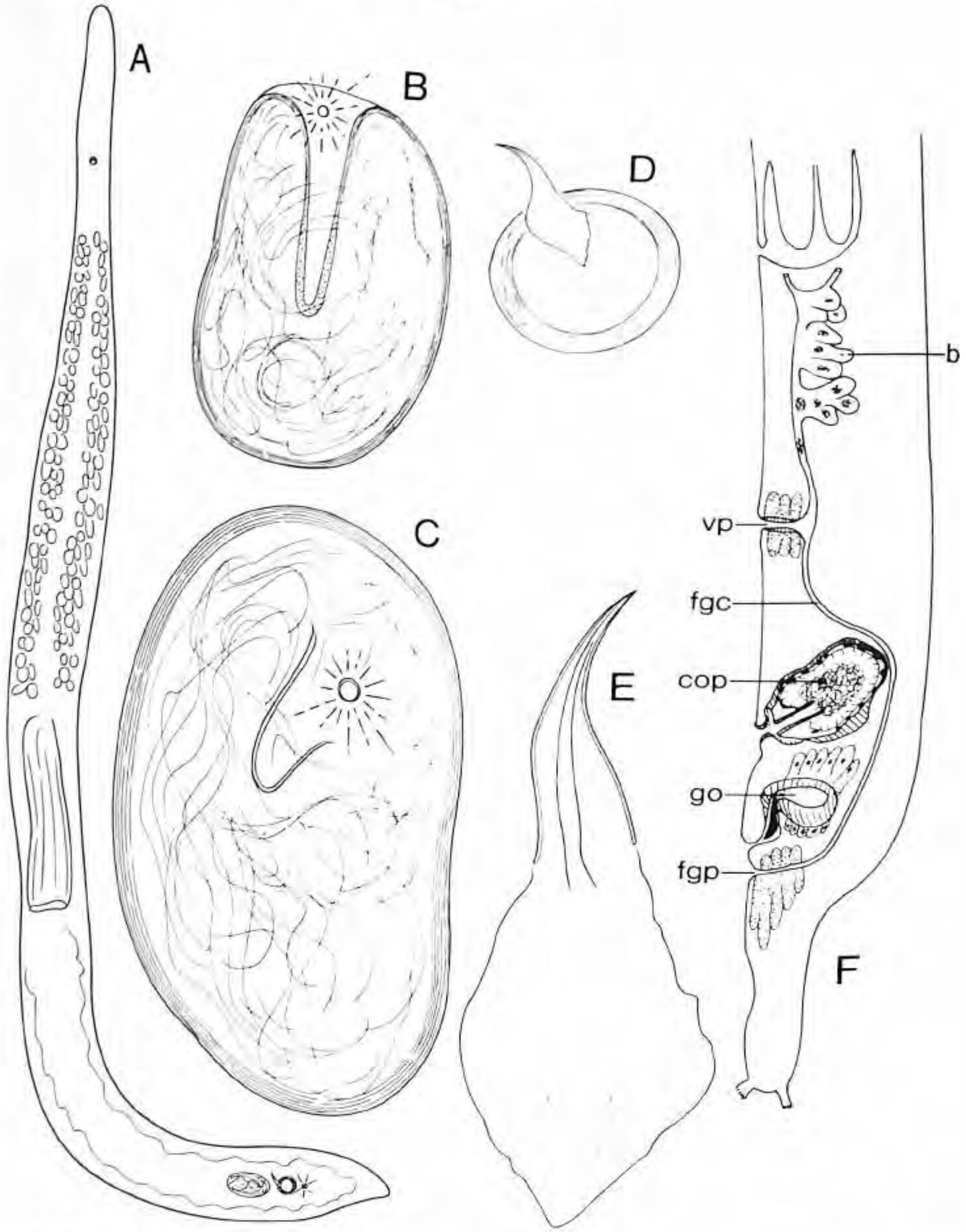

Fig. 33. *Minona gigantea*. A. Habitus and organisation. B, C. Male copulatory organ. D. Glandular organ with stylet. E. Stylet, enlarged. F. Sagittal reconstruction of the atrial organs (Seward: Lowell Point).

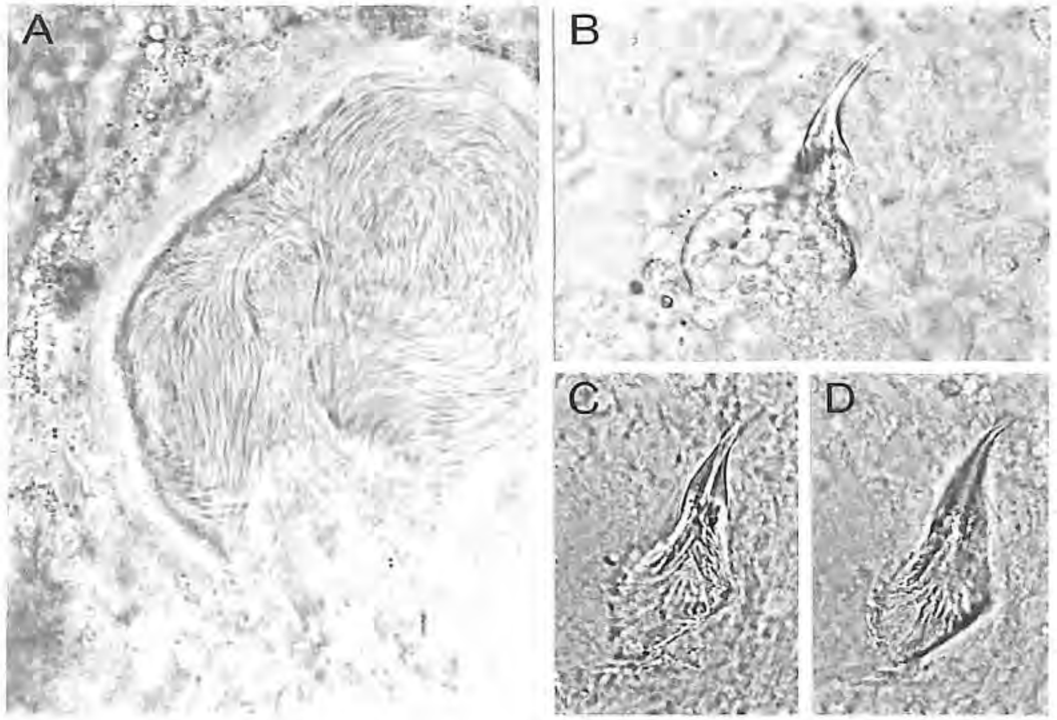

Fig. 34. *Minona gigantea*. A. Male copulatory organ. B. Glandular organ with stylet. C, D. Stylet enlarged, different focus (Seward: Lowell Point).

is only weakly sclerotic with a striped pattern. Total length of the glandular stylet 45 µm.

Vitellaries in lateral stripes starting already in front of the testis follicles and extending caudally to the copulatory organ. Paired germaries ventrally directly before pharynx. A tunica propria was only seen in the ventral part of the germaries. The paired germo-vitelloducts unite directly behind the pharynx amidst a blistery tissue. The cavities are partly filled with sperms. Dorsally this bursal tissue communicates with the intestine. Half the distance between the pharynx and the copulatory organ there is a vaginal pore. It is surrounded by voluminous accessory glands forming a thick layer reaching upwards to the middle of the body. The female duct continues dorsally of the copulatory and male glandular organ to the caudal female pore which lies amidst voluminous shell glands. The copulatory organ is surrounded by strong outer longitudinal and weakly differentiated inner circular muscles. The inner side is covered by a thin epithelium with flat nuclei and few cilia. The penis protrudes into a small atrium with a few cilia at the ventral side. The atrium is closed by circular muscles. Both male pores and the caudal female pore are clearly separated from each other.

Discussion. The existence of 4 separated genital pores in *M. gigantea* is presumably a plesiomorph character in the taxon *Minona* and there are several other species which still retain it (Table 4). *M. gigantea* differs from these and all other species of the taxon by having a voluminous glandular tissue around the vaginal pore (character 6 in Table 4). The glandular stylet of *M. gigantea* is most similar to *M. baltica* (see Ax & Armonies 1987, Fig. 8 A) and both species seem to replace each other in the same type of habitat. Possibly they are sister-species in the taxon *Minona*.

Minona dolichovesicula Tajika, 1982

(Fig. 35)

Localities: (1) Seward. Lowell Point, fine sand from the lower beach slope with effluent freshwater (10. 7. 1988). (2) Homer Spit. Sandy beach behind a dune wall, abundant (16. 7. 1988).

Material: Live observations including drawings and photographs.

Distribution: Hokkaido, Japan (Tajika 1982). San Juan Archipel, Washington, USA (Sopott-Ehlers & Ax 1985).

Specimens with a glandular stylet of 30 µm. Glandular vesicle spherical with a strong muscular cover. The seminal vesicle is conspicuously long (about 170 µm) and has a strong muscular cover as well. This is in agreement with *M. dolichovesicula* from Japan which has, however, a glandular stylet of 48 µm (Tajika 1982). In a population from San Juan Archipel, the copulatory organ is only 85 µm long and the glandular stylet 20 µm (Sopott-Ehlers & Ax 1985). Thus, with respect to the sizes of these organs the Alaskan population represents an intermediate state between those of the more southern US Pacific coast and the type locality in Hokkaido, Japan.

Rhabdocoela

Maehrenthalia americana n. sp.

(Fig. 36, 37, 38 A)

Byrsophlebidae spec. 1: Ax & Armonies 1987, p. 40

Localities: (1) Homer Spit (locus typicus). Eastern shore and wadden area (16. 7. 1988); (a) in the lower sandy shore; (b) abundant in intertidal mud with algal cover; (c) muddy sediment from a salt marsh pool (salinity 35 ‰). (2) Anchorage. Salt marsh at the northern shore next to the 5th Avenue; muddy sediment with algal cover (13. 7. 1988). (3) Hope. Muddy wadden area in front of the salt marsh edge of erosion (19. 7. 1988, salinity 12 to 15 ‰).

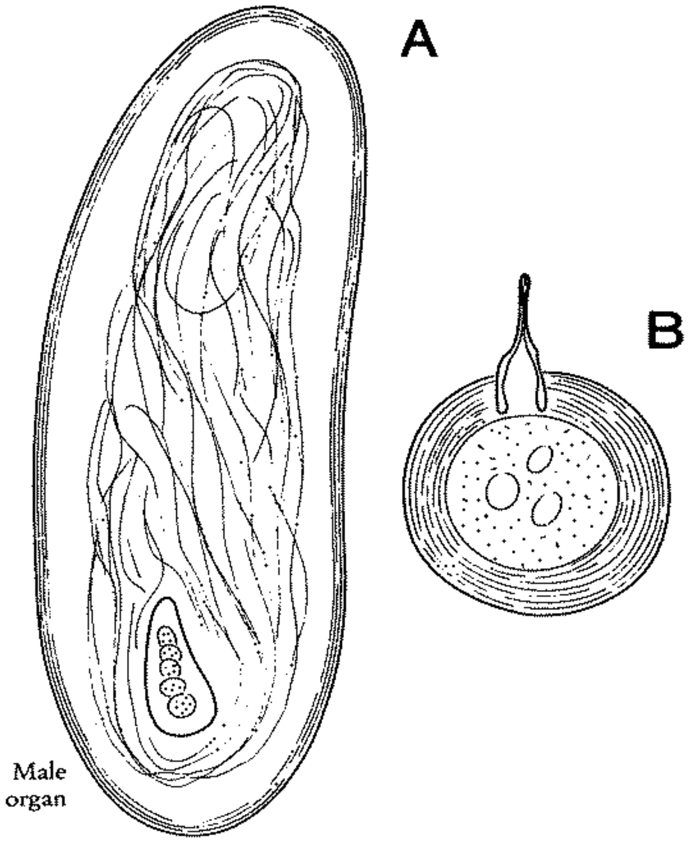

Fig. 35. *Minona dolichovesicula*. A. Male copulatory organ. B. Glandular organ with stylet (Seward: Lowell Point).

Material: Live observations on several specimens, including drawings and photographs. Two animals sectioned sagittally (holotype No. P 2191, paratype No. P 2192, Zoological Museum of the University of Göttingen).

Distribution: Canadian Atlantic coast, brackish water (Ax & Armonies 1987).

With paired eyes, pharynx closely behind the middle of the body. Anterior end rounded, caudal end tapering. Male genital pore directly behind the mouth, female pore subcaudally. Testes and yolk glands paired, unpaired germary in the caudal portion of the body. With a tubular stylet of 98 to 110 µm (Canada: 83 to 98 µm), proximal diameter 22 (Canada: 20) µm, distally cut-off oblique (diameter 6 µm; Canada: 3–4 µm). The walls of the stylet are slightly undulatory. Animals in full female maturity contained up to 8 egg capsules with embryos in various stages of development in the intestinal cavity.

The male copulatory bulb is covered by a single layer of strong muscular fibres. The prostatic glands enter the copulatory bulb from above. Inside the bulb they are turned in plaits leaving a median canal for sperm. The same arrangement of prostatic secretions and sperm is also seen in the stylet cavity. There is a thin epithelium in the male genital canal and a high epithelium of cylindrical cells in the male atrium.

The female atrium branches into the female genital canal and a bursal apparatus. The atrium and female genital canal have a high epithelium of cylindrical cells, surrounded by distinct longitudinal and circular muscles. Proximally the epithelium of the female genital canal becomes more diffuse without a distinct inner cavity. The bursal apparatus has a thin inner epithelium with a few nuclei. The walls are muscular only in the lower portion, then consisting of diffuse material structurally similar to the stylet wall, perhaps also sclerotic. At the female atrium the bursal apparatus has a wide diameter, then it tapers and streches dorsally. In the sections it is sharply flexed in the middle of the body and then turns back to the ventral side. The final part is club-shaped. Both parts of the bursal apparatus contained sperm and granular secretions.

There is only a single caudal germary. At one side of the body the thin epithelium around the germary and the intestinal epithelium were interrupted, thus forming a large connection between the germary and the intestine in both sectioned animals. Obviously this is the way the egg capsules enter the intestinal cavity. Functionally it seems, therefore, that the bursal apparatus stores alien sperm and the upper more glandular part of the female genital canal produces egg capsules. Presumably the egg capsules and/or young specimens will leave the intestine via the mouth.

Discussion. Based on the latest revision of Byrsophlebidae by Karling (1985) *Maehrenthalia* is the single taxon with a single layer of strong muscles around the male copulatory bulb. As in the up to now only species *M. agilis* (Levinsen) the bursal apparatus is bipartite. Both species clearly differ in the shape and size of the stylets. In *M. agilis* it is 55 to 65 µm long with a curved tip (cf. Karling 1985) while it is a rather straight tube of up to twice that size in *M. americana*.

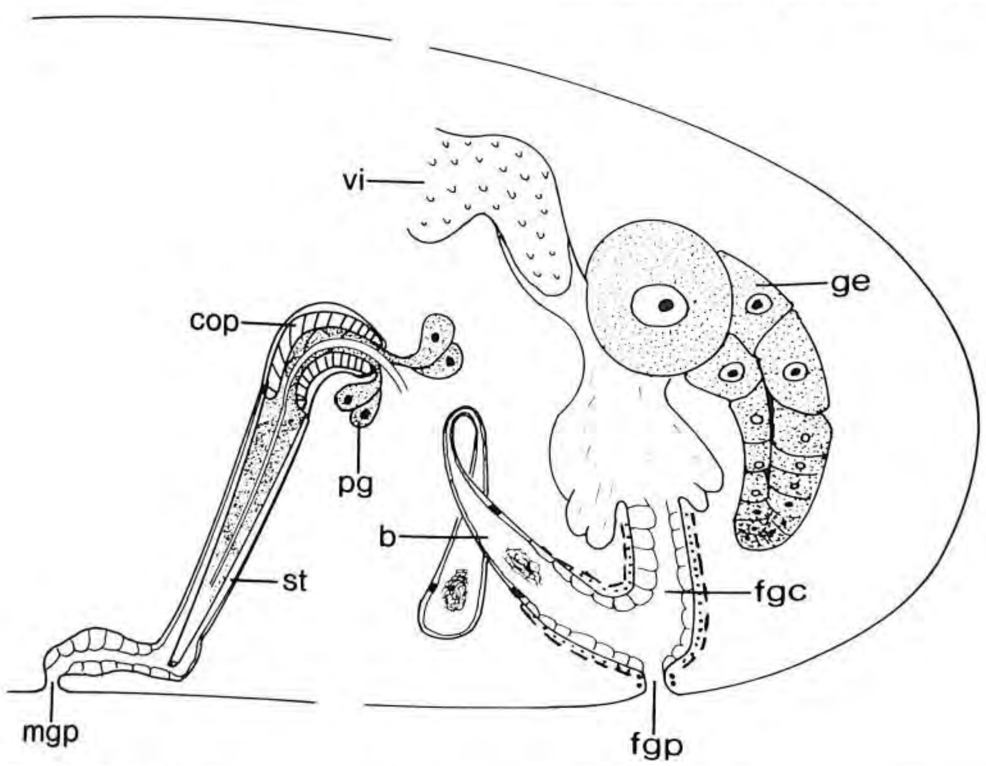

Fig. 36. *Maehrenthalia americana.* Sagittal reconstruction of the atrial organs. Male and female organs are positioned side by side. In the drawing the organs are put one after another.

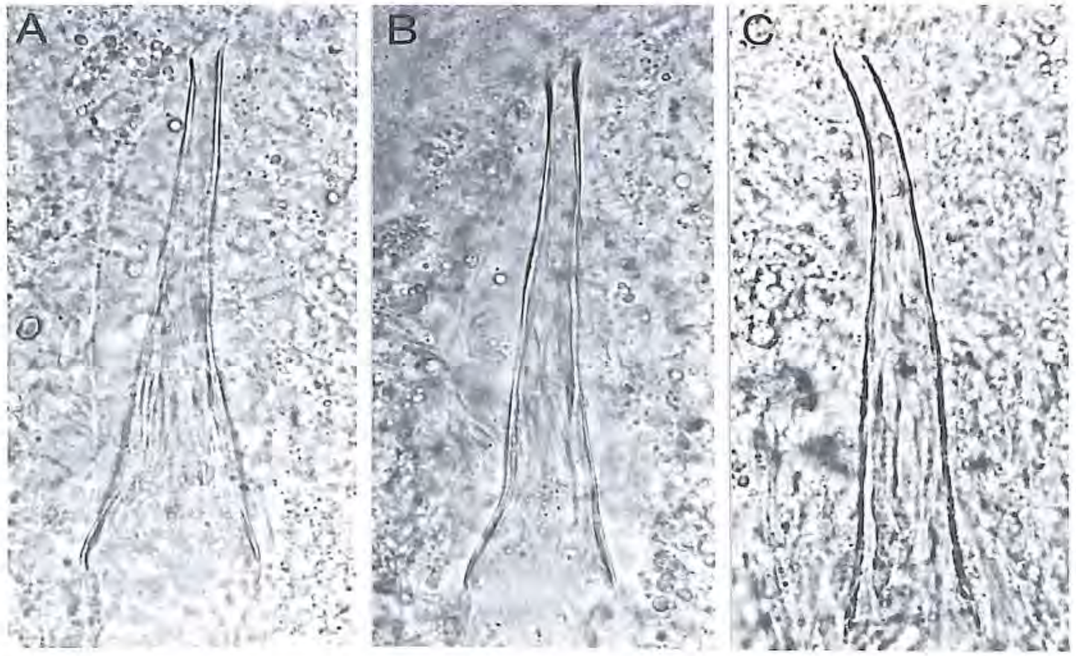

Fig. 37. *Maehrenthalia americana.* A, B. Stylet, different focus (Anchorage). C. Stylet (Kenai Peninsula: Homer Spit).

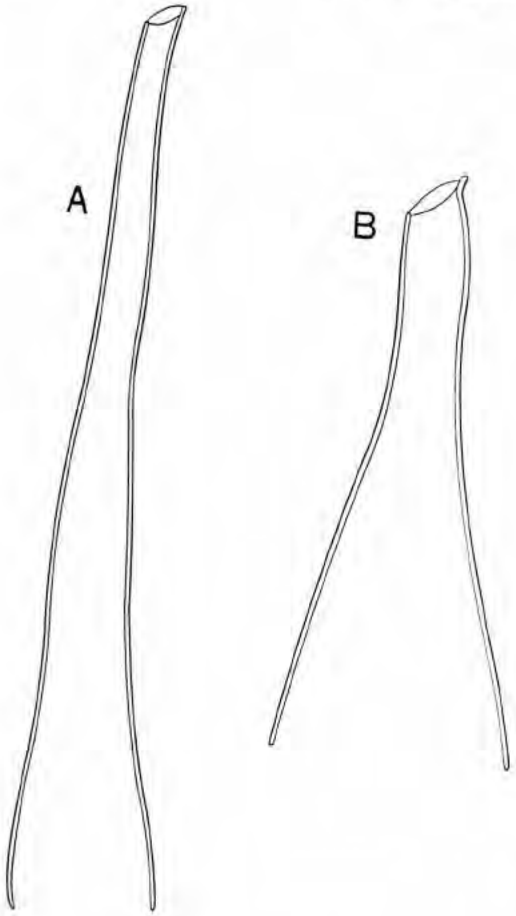

Fig. 38. A. *Maehrenthalia americana.* Stylet (Anchorage). B. *Byrsophlebs dubia.* Stylet (Seward: Airport).

Byrsophlebs dubia **(Ax, 1956)**

(Fig. 38 B, 39)

Locality: Seward. Airport, salt marsh beneath the air corridor; muddy sediment with algal cover (12. 8. 1988, salinity 7 to 8 ‰).

Material: Live observations, including drawings and photographs.

Distribution: Mediterranean (Ax 1956 a), Baltic Sea (Ax 1956 a, LUTHER 1962), North Sea (DEN HARTOG 1965, ARMONIES 1987, HELLWIG 1987).

Specimens with paired eyes, pharynx in the middle of the body. With paired vitellaries and an unpaired caudal germary. Copulatory bulb covered by spiral muscles. Prostatic glands enter the bulb from proximally. Inside the bulb the glandular secretions form a spiral pattern around the median spermatic duct.

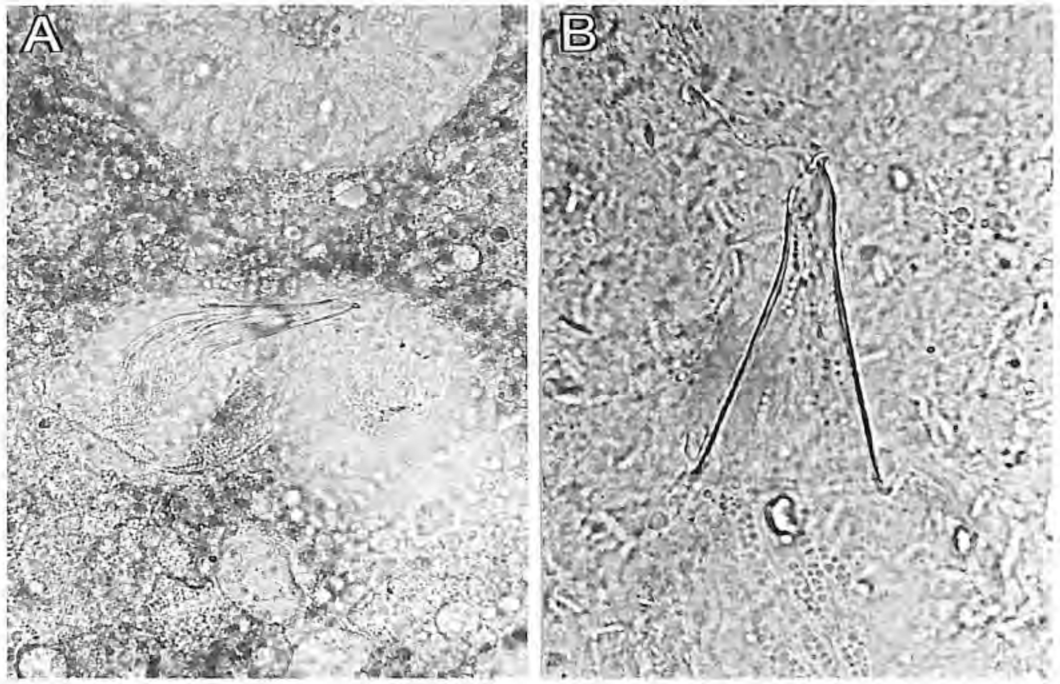

Fig. 39. *Byrsophlebs dubia.* A. Male copulatory organ behind the pharynx. B. Stylet (Seward: Airport).

The stylet is about 55 µm long with a proximal opening of 18 to 27 µm (depending on the degree of coverslip compression). Distally the tube is cut-off oblique, the longer side forming a small projection. The stylet enters the rather wide male genital atrium with the male pore positioned directly behind the pharynx. The shape and size of the stylet agrees well with European specimens (cf. KARLING 1985).

Haloplanella obtusituba **Luther, 1946**

(Fig. 40, 41)

Localities: (1) Seward. Fourth of July Beach, muddy sand of the upper intertidal zone (8. 7. and 13. 8. 1988); medium to fine intertidal sand (20. 7. 1988). (2) Seward. Airport, salt marsh beneath the air corridor; muddy sediment with algal cover (12. 8. 1988, salinity 7 to 8 ‰). (3) Anchorage. Salt marsh at the northern shore; muddy sediment with algal cover (13. 7. 1988, salinity 12 to 13 ‰).

Material: Live observations on several individuals, including drawings and photographs.

Distribution: North Sea, Baltic Sea; presumably a mesohaline brackish water species (ARMONIES 1987).

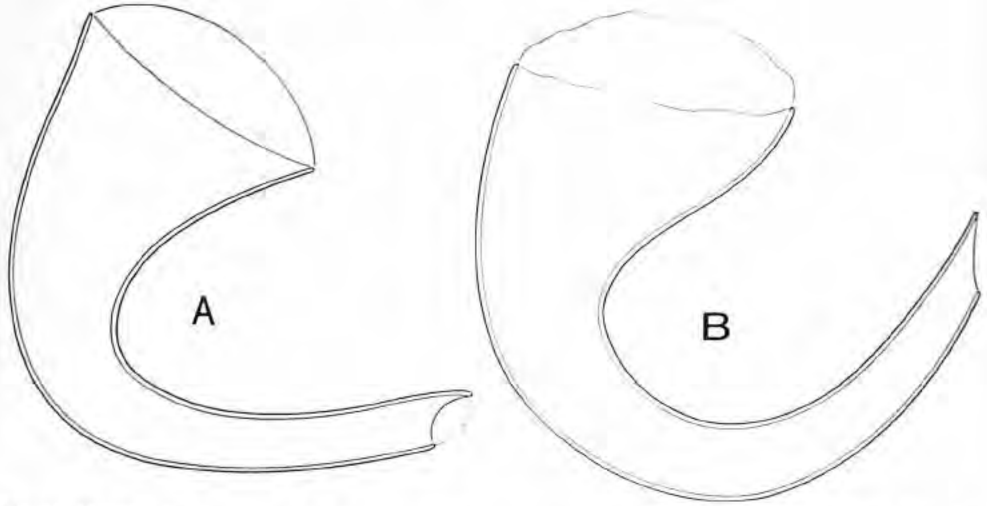

Fig. 40. *Haloplanella obtusituba*. A, B. Stylets of different animals (Seward: Fourth of July Beach).

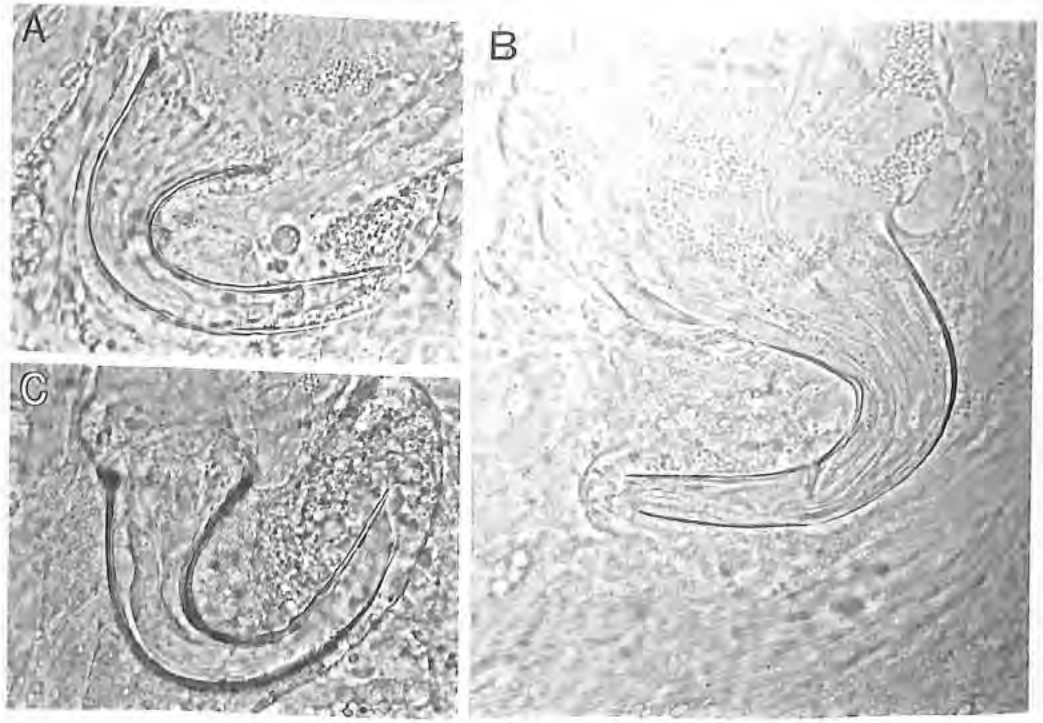

Fig. 41. *Haloplanella obtusituba*. A–C. Stylets (Seward: Fourth of July Beach).

The specimens have a semicircular curved stylet with a wide proximal opening (22 to 29 μm). Distally the stylet is cut-off oblique, diameter of the opening about 7 μm. Diagonally the stylet measures 62 μm (68 μm in a strongly squeezed specimen). Vertically it is 45 to 54 μm high and horizontally it is 55 to 60 μm wide.

There are no measures of European animals of *H. obtusituba*. In European specimens the distal opening may or may not be slightly widened and provided with a small lateral keel (LUTHER 1946); it is not clear, if these forms are varieties or represent different species. All Alaskan specimens have a narrow distal opening without a keel.

Coronhelmis lutheri Ax, 1951

Locality: Kotzebue. Mouth of a small river into the Kotzebue Sound, about 5 miles south of the village; medium to coarse sand with gravel (8. 8. 1988, salinity 10 ‰).

Material: Live observations on a few specimens, including photographs.

Distribution: North Sea, Baltic Sea (AX 1951, EHLERS 1974); S Canadian Atlantic coast (AX & ARMONIES 1987).

The shape and size (27 μm) of the stylet conforms well with specimens from the Canadian Atlantic coast and Europe (AX & ARMONIES 1987). *C. lutheri* is a brackish water species occurring in rather pure (medium to coarse) sand of supralittoral beaches. It tolerates wide ranges of temperature and salinity what seems to be a prerequisite for colonizers of supralittoral sites (JANSSON 1968).

Promesostoma alaskana n. sp.

(Fig. 42, 43)

Locality: Homer Spit (locus typicus). Beach slope of the eastern shore (16. 7. 1988).

Material: Live observations including drawings and photographs.

Unpigmented animals 0.6 to 0.7 mm long, tapering at both ends of the body. Pharynx shortly behind the middle of the body. With paired eyes. Paired testes in front of the pharynx, paired germaries behind the pharynx. The copulatory organ is oviform, about 50 μm long and up to 25 μm in diameter. It has a distinct muscular cover. A short duct connects it with the funnel-shaped (5 μm diameter) proximal opening of the stylet which is about 250 μm long. 15 μm from the proximal opening the tube is sharply flexed at an angle of about 135°. At the flexure the tube is triangularly enlarged thus having a maximum diameter of 7 to 8 μm. The diameter of the tube before and behind the flexure is 3 μm. From the flexure the stylet is turned in a circle and then continues laterally of the pharynx to the genital pore. Distally the stylet is cut-off oblique, without additional structures. The bursa is a longish bag of about 100 µm starting at the sharp flexure of the stylet and then turning laterally.

Discussion. The triangular excavation of the proximal part of the stylet is a common character of *P. alaskana* and *P. fibulata* Ax & Armonies, 1987 from the Canadian Atlantic coast. But the distal part of the stylet is distinctly different in the two species. In *P. alaskana* it is simply cut-off oblique while it is widened and bearing a lateral clasp in *P. fibulata.* In both species the bursa starts at the sharp flexure of the stylet. Both species live in sheltered sandy habitats of the upper intertidal in the boreal zone of N-America. They might be sister-species in the taxon *Promesostoma.*

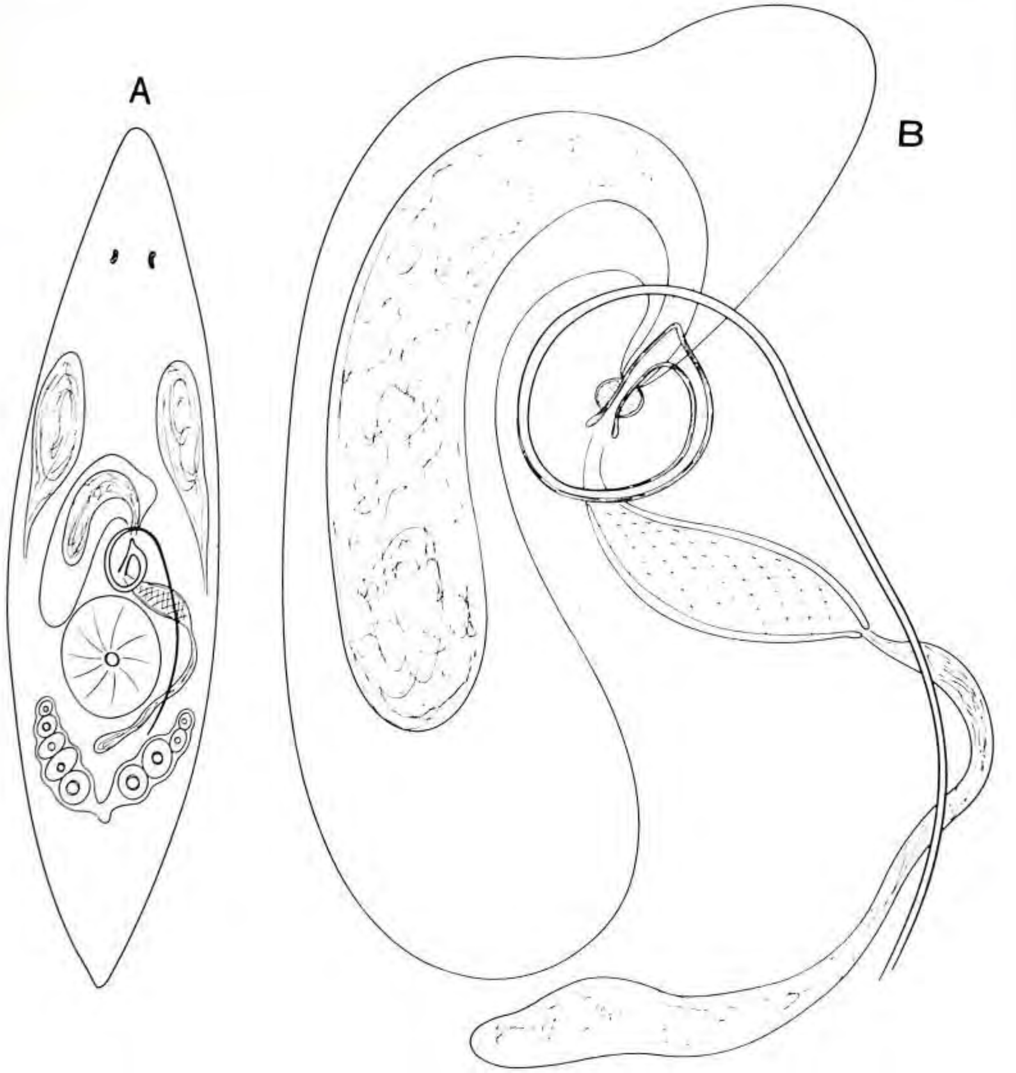

Fig. 42. *Promesostoma alaskana.* A. Organisation. B. Male copulatory organ and bursa (Kenai Peninsula: Homer Spit).

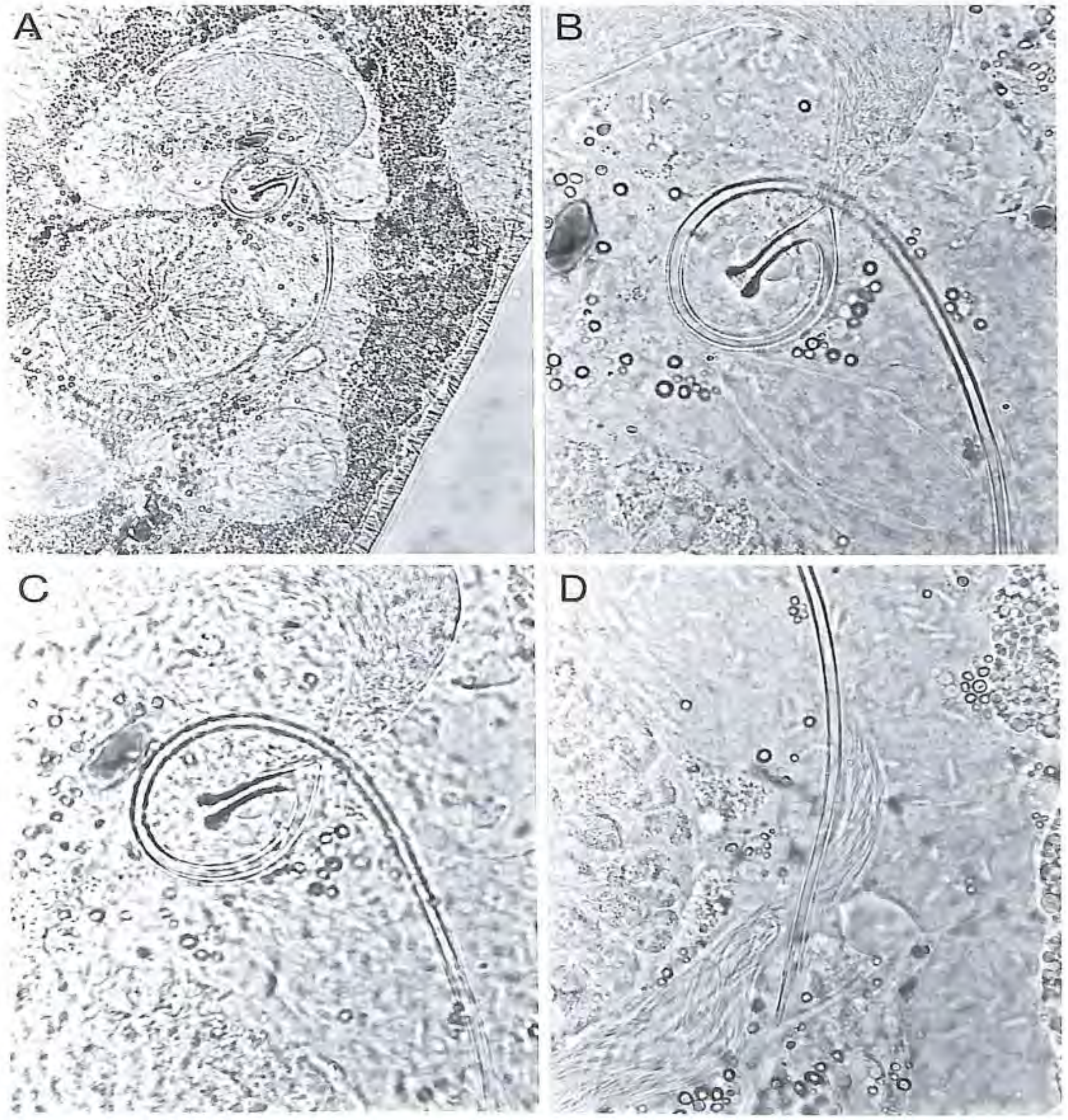

Fig. 43. *Promesostoma alaskana.* A. Male copulatory organ in front of the pharynx. B, C. Proximal part of the stylet, different focus. D. Distal part of the stylet (Kenai Peninsula: Homer Spit).

Proxenetes arctica n. sp.

(Fig. 44–47)

Localities: (1) Anchorage. Salt marsh of the northern shore (locus typicus). Muddy sediment with algal cover (13. 7. 1988, several). (2) Homer Spit. Eastern shore; intertidal mud with algal cover and muddy sediment from salt marsh pools (16. 7. 1988). (3) Kotzebue. Salt marsh east of the village (8. 8. 1988, salinity 7 to 11 ‰).

Fig. 44. *Proxenetes arctica*. Male copulatory organ and seminal receptacle (Anchorage).

Material: Live observations on numerous specimens, including drawings and photographs.

The stylet is triangular in shape, diagonally 65 to 75 µm long. It consists of a slightly curved 'main' tube which is proximally about 25 and distally about 3 µm wide, a pair of long spines which are proximally triangular, and a pair of shorter spines which are proximally concavely indented. The entire apparatus is surrounded by a delicate membrane which only leaves the proximal third and distal sixth of the stylet uncovered.

The sclerotic insemination apparatus ('Bursamundstück') consists of two completely separated tubes of 75 µm and a ring with a peripheral basal enlargement fixed on the seminal receptacle. The ring (diameter 15 µm) bears a triangular indentation pointing towards the inner side of the seminal receptacle. The tubes are slightly enlarged distally.

There is an additional hardened apparatus in the bursal wall. It consists of an irregularly shaped basal plate with a finely granulated structure of the wall and a dentiform projection. Both the basal plate and dentiform projection are hardened but not completely stiff. Mostly there was only one 'tooth', rarely two

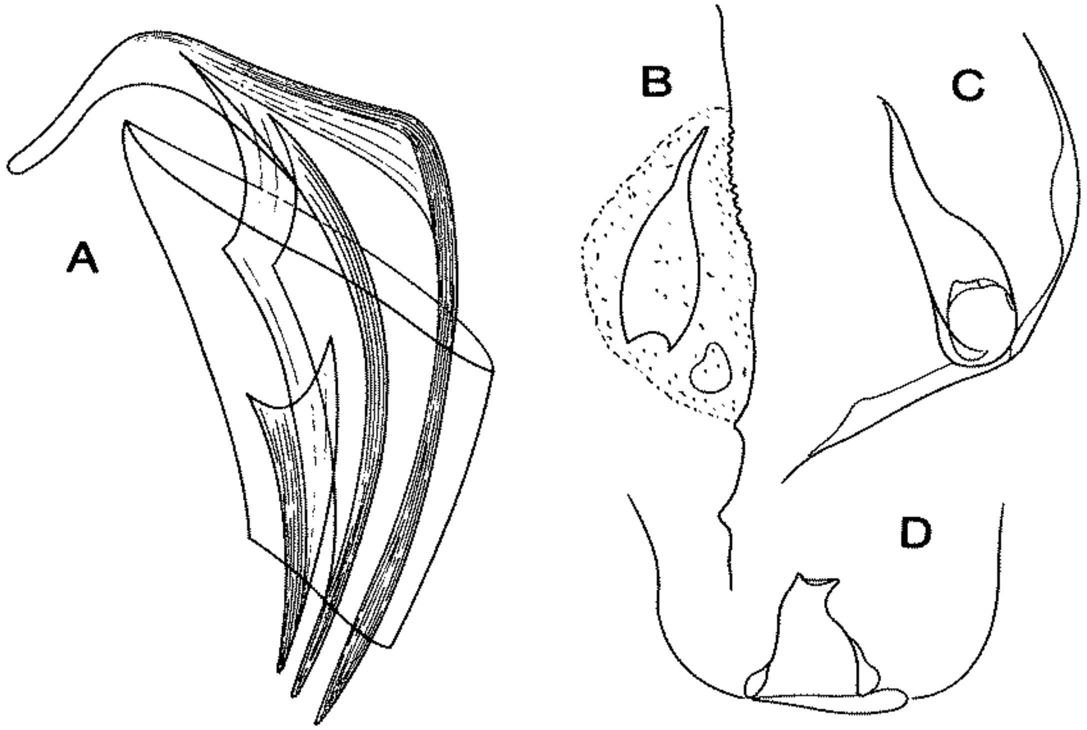

Fig. 45. *Proxenetes arctica*. A. Stylet (Anchorage). B–D. Hardened apparatus in the bursal wall (B Kotzebue, C Anchorage, D Kenai Peninsula: Homer Spit).

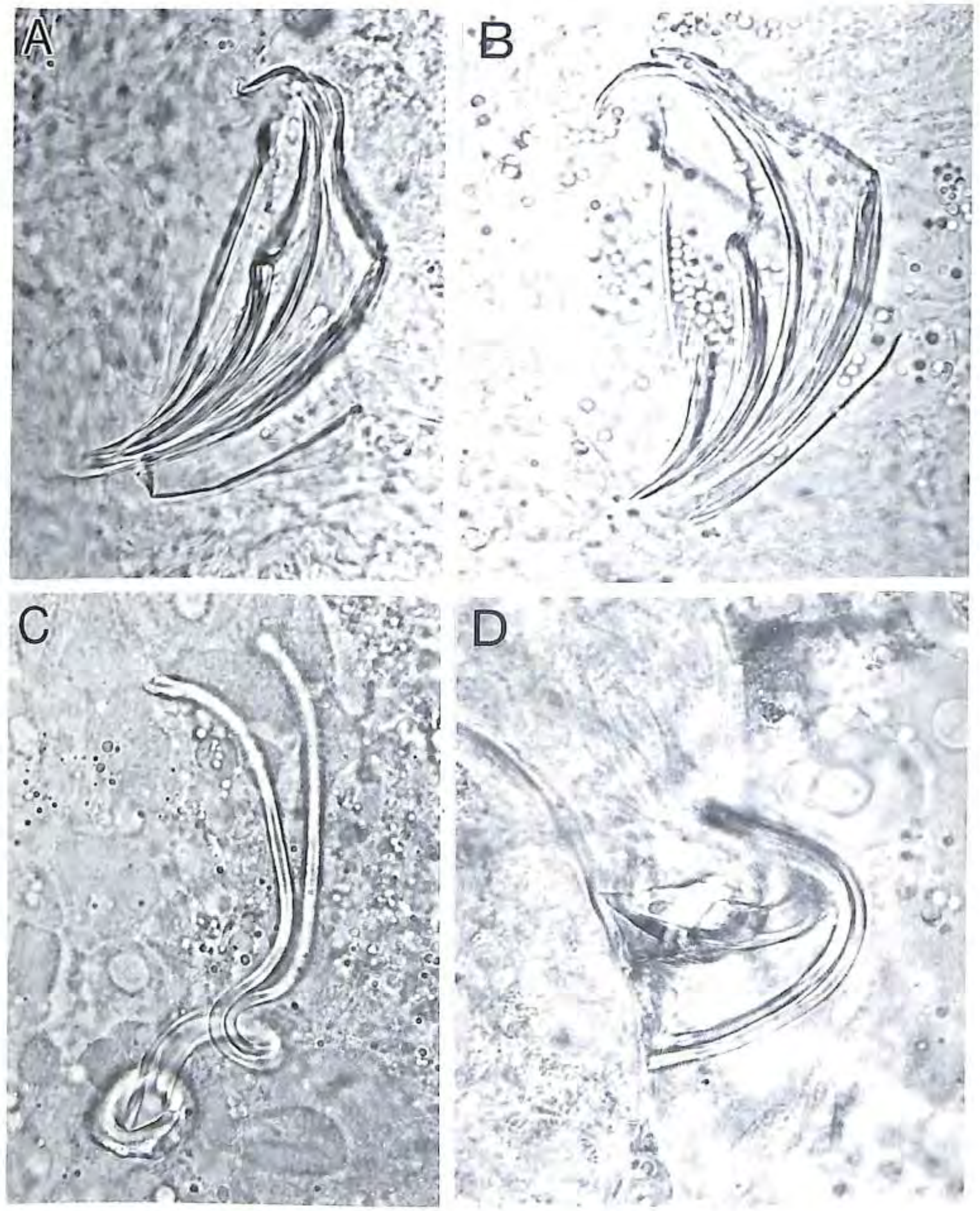

Fig. 46. *Proxenetes arctica.* A. Stylet (Anchorage). B. Stylet (Kotzebue). C. Sclerotic insemination apparatus (Kotzebue). D. Sclerotic insemination apparatus (Anchorage).

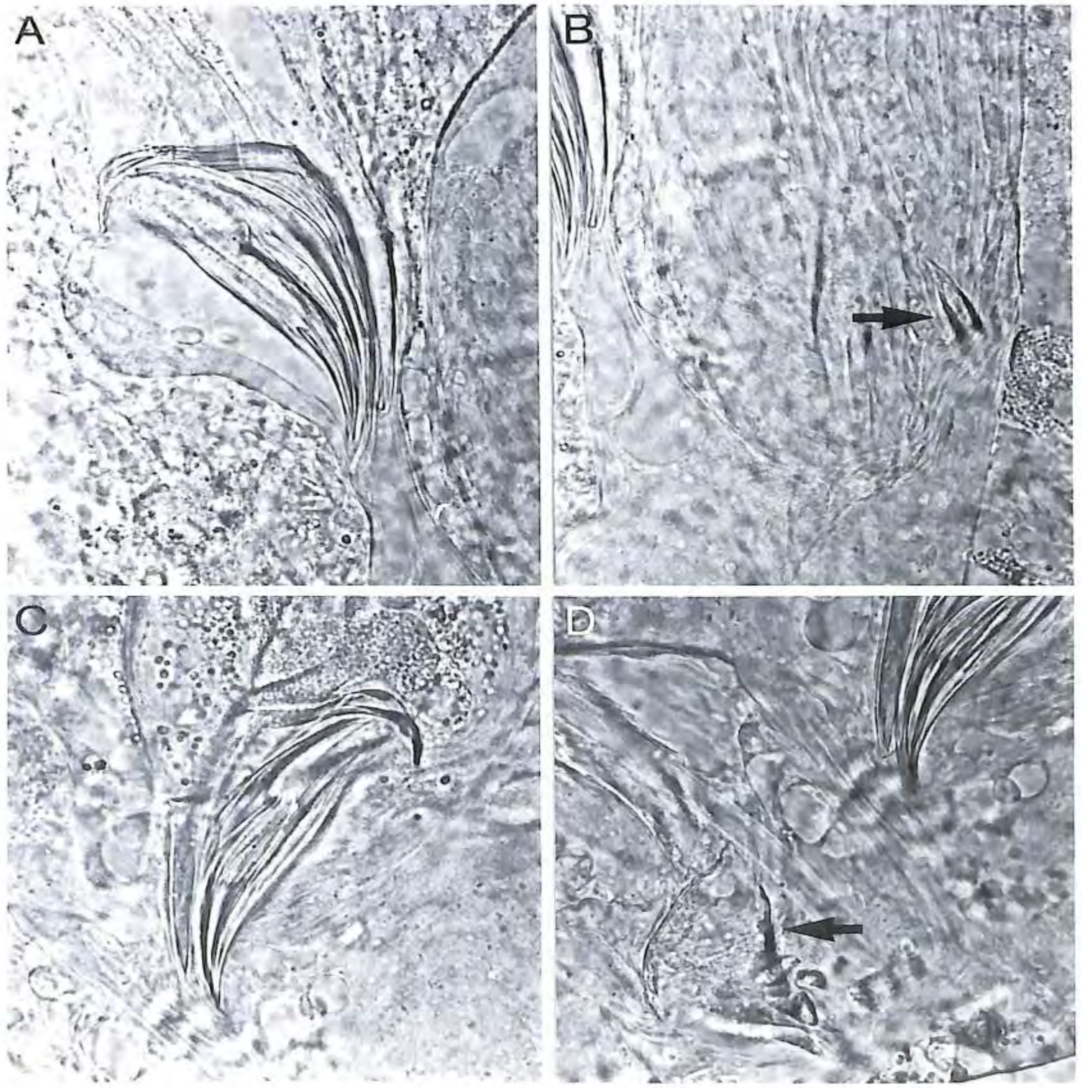

Fig. 47. *Proxenetes arctica.* A. Stylet. B. Tip of the stylet (left) and hardened apparatus of the bursa (arrow) (Anchorage). C. Stylet. D. Distal part of the stylet and hardened apparatus of the bursa (arrow); compare Fig. 45 D (Kenai Peninsula: Homer Spit).

teeth, and once a wider conical structure. The length of the teeth varied between 18 and 20 µm while a single individual had a projection of only 12 µm (not completely differentiated?).

Discussion. *Proxenetes* species with an additional sclerotic bursal apparatus are united in the taxon *Proxenetes Proxenetes* (Ax 1971). *P. arctica* belongs to this group. It is most similar to *Proxenetes unidentatus* Den Hartog, 1965. In *P. unidentatus* the basal plate in the bursal wall always bears a single dentiform projection of about 15 µm and the stylet is similar in shape but much smaller – 38 to 40 µm (DEN HARTOG 1965, AX 1971) versus 65 to 75 µm in *P. arctica*. *P. arctica* and *P. unidentatus* might be sister-species.

Ptychopera alaskana n. sp.

(Fig. 48, 49)

Localities: (1) Seward. Fourth of July Beach (locus typicus). Muddy (11. 7. and 13. 8. 1988) and medium – to fine intertidal sand (20. 7. 1988). (2) Anchorage. Salt marsh at the northern shore next to the 5th Avenue, mud (13. 7. 1988).

Material: Live observations on several specimens, including drawings and photographs.

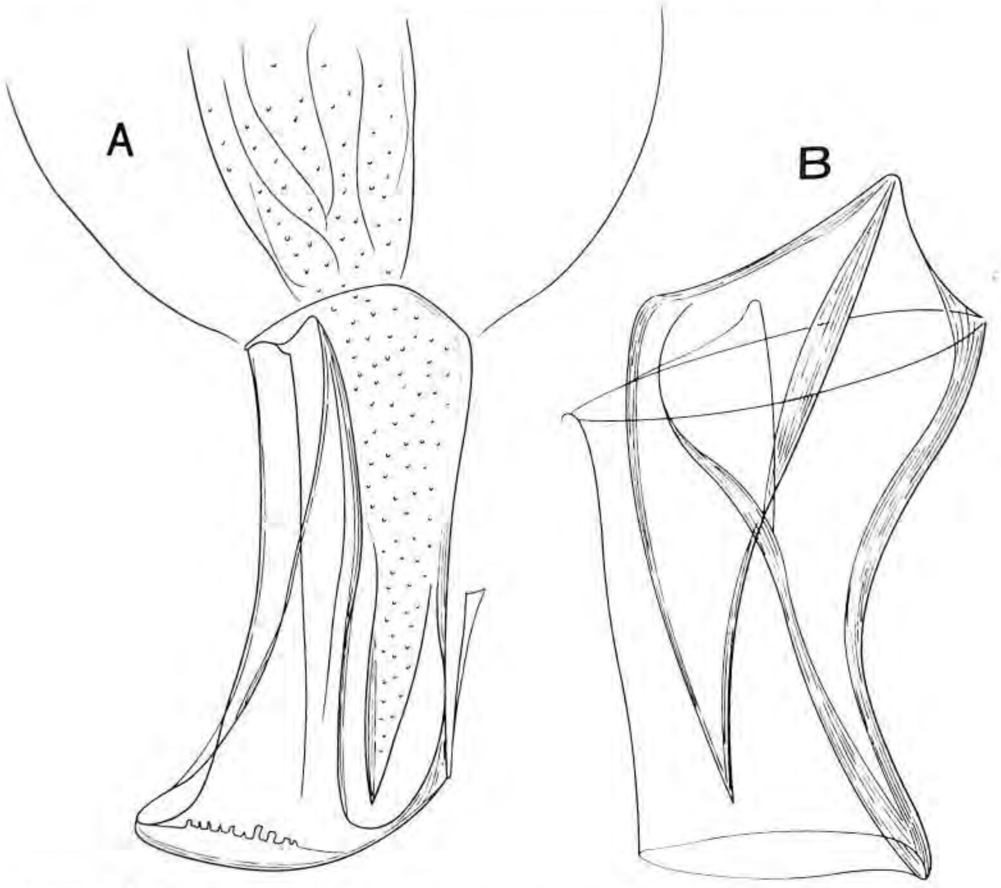

Fig. 48. *Ptychopera alaskana*. A. Stylet (Seward: Fourth of July Beach). B. Stylet (Anchorage).

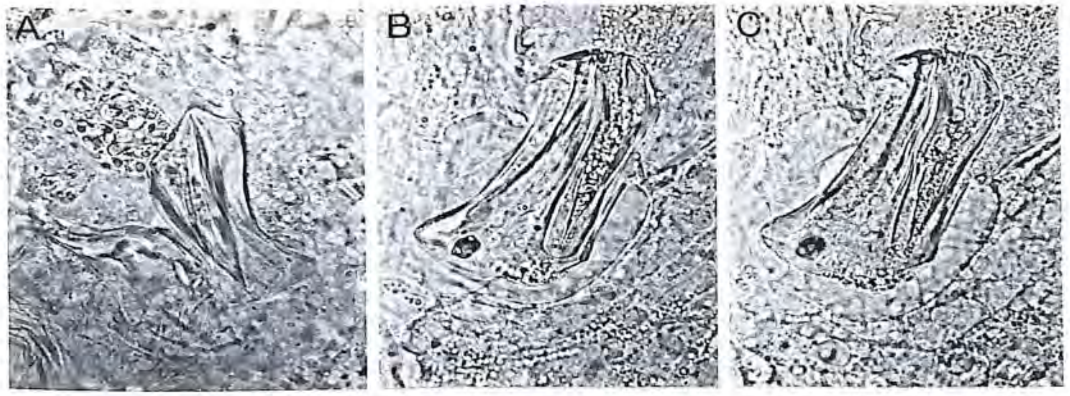

Fig. 49. *Ptychopera alaskana*. A. Stylet (Anchorage). B, C. Stylet, different focus (Seward: Fourth of July Beach).

The present data concerning the copulatory organ permit a positive identification. Despite of incomplete records we therefore characterize a new species of the taxon *Ptychopera*. The box-shaped stylet is 47 to 55 µm long. The distal border may be regularly indented. The granular secretions only pass one half of the stylet; here the secretions gather in a solid conical spine.

Discussion. The shape of the stylet is similar to *Ptychopera purasjokii* Ax (AX 1971, EHLERS 1980). The stylets have the same size and in both species a large spine passes through the stylet at one side. On the other hand, the stylet of *P. purasjokii* is proximally broadly rounded and there are 3 to 4 spines at the concave side. There are no comparable structures in *P. alaskana*.

Gyratrix hermaphroditus Ehrenberg, 1831

(Fig. 50 A)

Locality: Seward. Lowell Point, lower beach slope with effluent freshwater (4. 8. 1988).

Material: Live observations, photographs.

G. hermaphroditus is a holeuryhaline cosmopolitan and ubiquistic species (KARLING 1963, KARLING et al. 1972). In Alaskan specimens the stylet is 130 µm long, the stylet sheath 32 µm, and its stalk 75 µm. These measures are all in the known range (KARLING et al. 1972).

Phonorhynchus helgolandicus (Mecznikow, 1865)

Locality: Homer Spit. Intertidal mud with algal cover at the eastern shore (16. 7. 1988).

Material: Live observations on two specimens, including photographs.

Distribution: N-Atlantic Ocean (European and American side), Arctic Ocean, Bering Sea, US Pacific coast (KARLING 1982).

In the Alaskan material the stylet is 155 µm long and the prostatic stylet about 65 µm. The shape of the sclerotic apparatus is intermediate between the forms "winged" and "spatula" (cf. KARLING 1982).

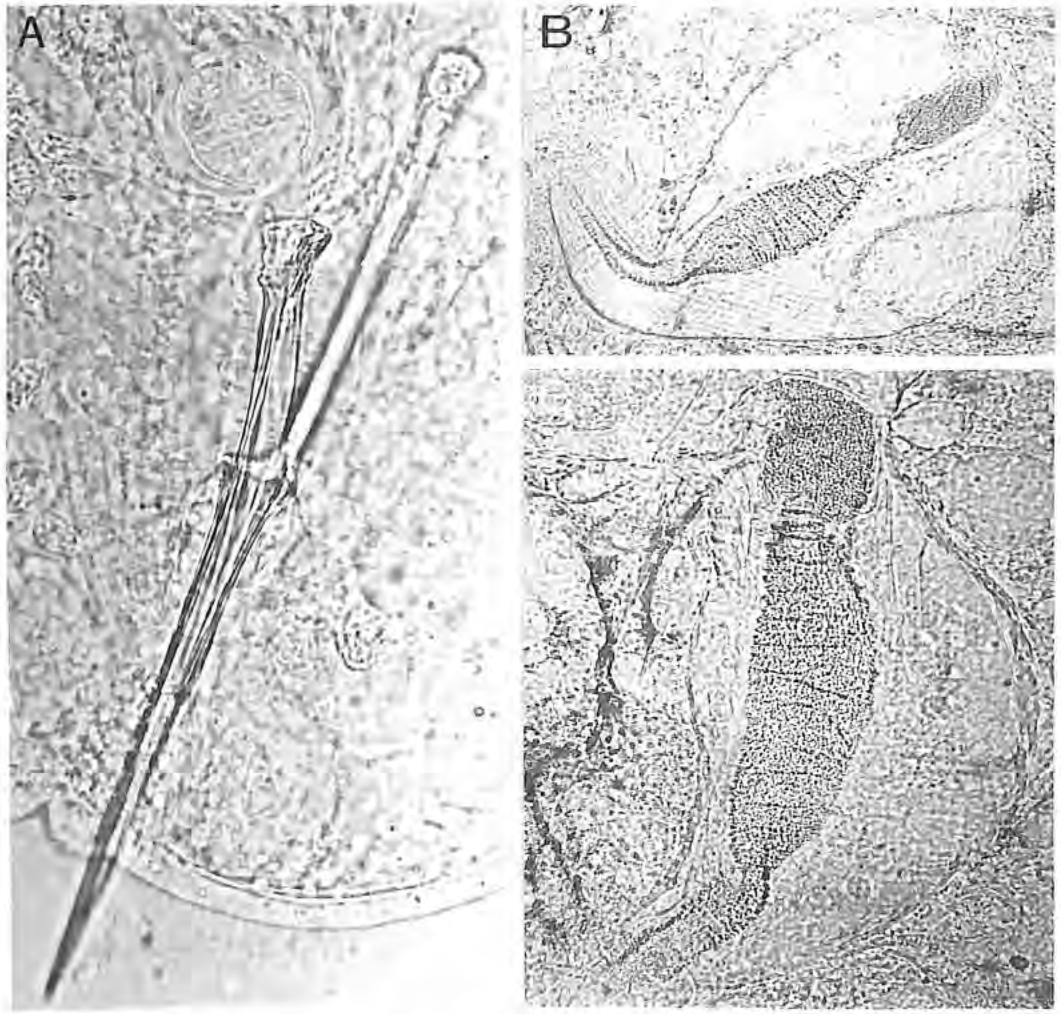

Fig. 50. A. *Gyratrix hermaphroditus*. Stylet (Seward: Lowell Point). B, C. *Duplacrorhynchus major*. Male copulatory organ, different individuals (Kotzebue).

Duplacrorhynchus major Schockaert & Karling, 1970

(Fig. 50 B, C)

Localities: (1) Seward. Fourth of July Beach, upper intertidal muddy sand (8.7. and 13. 8. 1988) and intertidal medium to fine sand (20. 7. 1988). (2) Anchorage. Salt marsh at the northern shore next to the 5th Avenue; mud with algal cover (13. 7. 1988, salinity 12 to 13 ‰). (3) Homer Spit. Intertidal mud with algal cover (16. 7. 1988) and mud from salt marsh pools (16. 7. 1988, salinity 35 ‰). (4) Hope. Intertidal mud in front of the salt marsh edge of erosion (19. 7. 1988). (5) Ninilchik. Mouth of the Ninilchik River; sand to muddy sand (21. 7. 1988, salinity 0 ‰). (6) Anchor Point. Mouth of the Anchor River into the sandy beach (24. 7. 1988, salinity 0 ‰). (7) Kotzebue. Salt marsh east of the village (8. 8. 1988, salinity 7 to 11 ‰).

Material: Live observations on numerous specimens, including drawings and photographs; 14 animals sectioned.

Distribution: US Pacific coast, Oregon, sandy mudflat (SCHOCKAERT & KARLING 1970).

One of the most widespread species in the area of investigation, occurring in sandy to muddy areas without strong currents. The salinities measured at the localities indicate that *D. major* is euryhaline. Examination of the sectioned material yielded entire conformity with the original description. The only difference was an age-dependent stronger development of the uterus which took about half of the body diameter in sagittal sections. As a consequence the uterine glands opened at the caudal side of the uterus. The section caudally of the glands thus functions as an uterus stalk (cf. SCHOCKAERT & KARLING 1970, Fig. 17). In Europe and SE Canada, *Acrorhynchides robustus* (Karling, 1931) occupies comparable habitats and seems to be ecologically equivalent to *D. major* (cf. AX & ARMONIES 1987).

Placorhynchus pacificus Karling, 1989

(Fig. 51 A, 52 A, B)

Localities: (1) Seward. Fourth of July Beach, muddy sand (11. 7. 1988). (2) Seward. Sandy beach north of the Industrial Camp; very fine sand (3. 8. 1988, salinity of tidal water 25 ‰). (3) Ninilchik. Sandy beach at the opening of the Ninilchik River; muddy sand, salinity 0 to 6 ‰ (21. 7. 1988). (4) Anchor Point. Sandy beach in the mouth of the Anchor River (24. 7. 1988, freshwater).

Material: Live observations on numerous specimens including drawings and photographs. Three animals sectioned.

Distribution: US Pacific coast, Oregon, Newport, Yaquina Bay (KARLING 1989).

Unpigmented slender organisms of 0.8 to 1 mm length, often swimming freely above the sediment in Petri dishes. Piriform copulatory organ with a tubiform stylet of 88 to 90 µm and numerous fine spines in the surrounding genital canal. The proximal part of the bursa is conspicuously striped (folds of the strengthened bursal wall).

Placorhynchus paratetraculeatus n. sp.

(Fig. 51 B-D, 52 C, D)

Locality: Anchorage. Salt marsh at the northern shore next to the 5th Avenue (locus typicus). Mud with algal cover (13. 7. 1988, salinity 12 to 13 ‰).

Material: Live observations on a few individuals, including drawings and photographs.

Animals 0.7 to 0.8 mm long, with a cirrus and additionally four larger robust spines. In the everted cirrus the proximal spines are small, less than 1 µm long. Their size increases distally to about 3 µm. The spines consist of a minute basal plate bearing a dentiform projection. The four additional spines are most proximal in the copulatory organ. They are 3.5 to 5 µm long with a strongly aberrant shape.

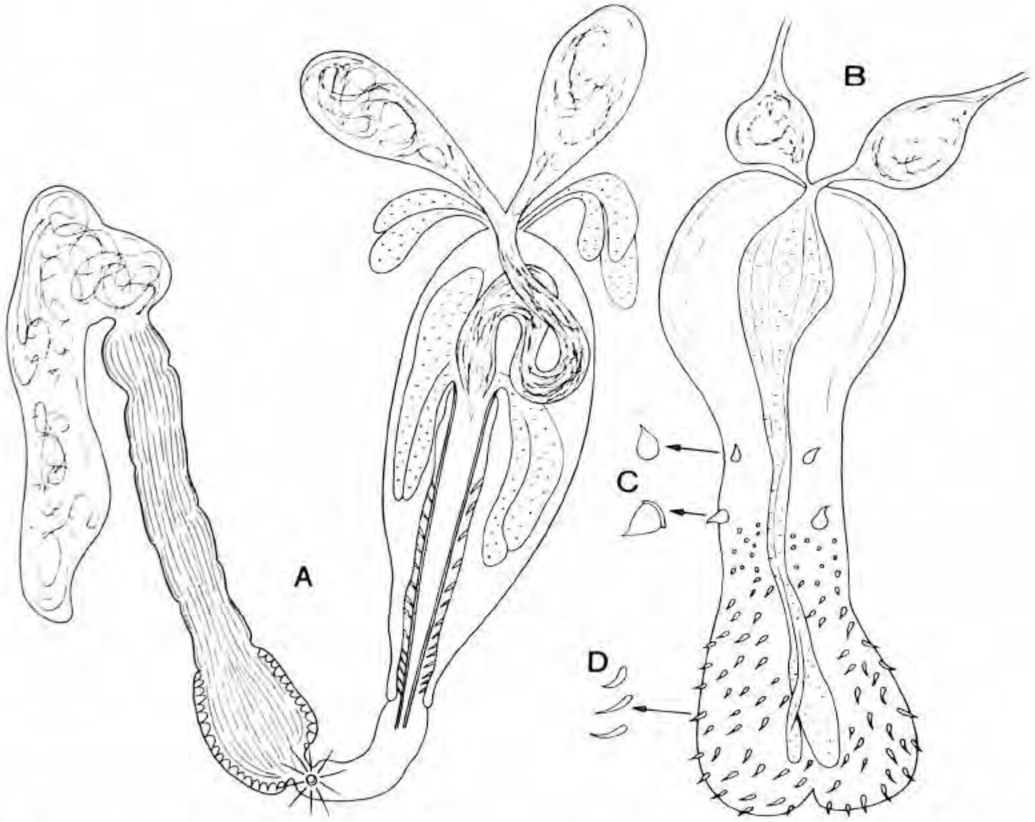

Fig. 51. A. *Placorhynchus pacificus*. Male copulatory organ and bursa (Kenai Peninsula: Ninilchik). B. *Placorhynchus paratetraculeatus*. Male copulatory organ. C. Larger spines of the cirrus. D. Smaller spines (Anchorage).

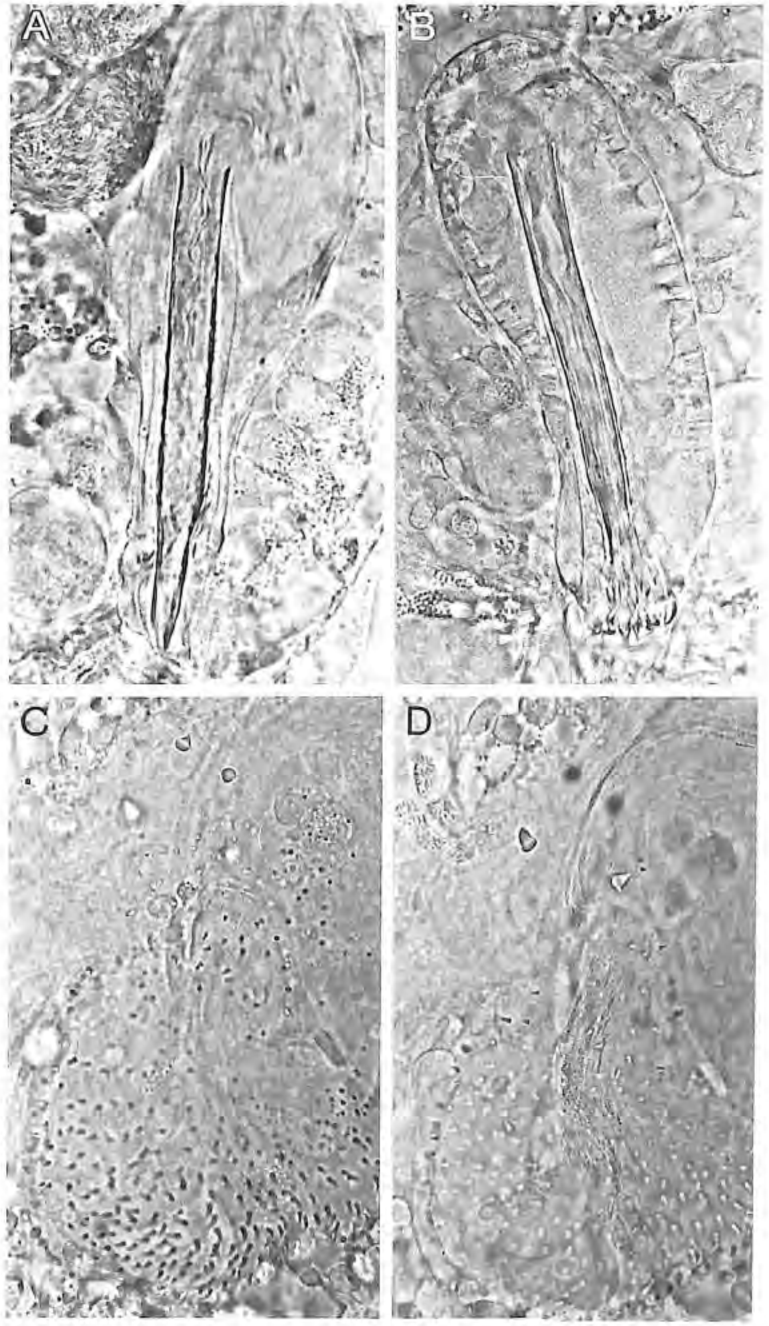

Fig. 52. A, B. *Placorhynchus pacificus*. Stylet (A Kenai Peninsula: Ninilchik, B Seward: Fourth of July Beach). C, D. *Placorhynchus paratetraculeatus*. Cirrus with 4 larger spines (above) and numerous smaller spines; different focus (Anchorage).

Discussion. The construction of a copulatory organ with numerous small spines and four larger spines is unique in the taxon *Placorhynchus*. A cirrus is also present in *P. echinulatus* Karling, 1947 and in *P. bidens* Brunet, 1973. *P. echinulatus* has one pair of larger spines among the smaller ones (Karling 1947; but see Ax & Armonies 1987 for specimens without larger spines). *P. bidens* has a pair of large bifurcated spines distally of the copulatory bulb. Finally, *P. tetraculeatus* Armonies & Hellwig, 1987 has four larger spines but lacks a cirrus.

Prognathorhynchus dividibulbosus n. sp.

(Fig. 53–55)

Locality: Seward. Lowell Point (locus typicus). Fine sand of the lower beach slope with effluent freshwater (10. 7. and 4. 8. 1988).

Material: Live observations on three specimens, including drawings and photographs. Five animals sectioned, one specimen sectioned sagittally = holotype No. P 2201. Zoological Museum of the University of Göttingen.

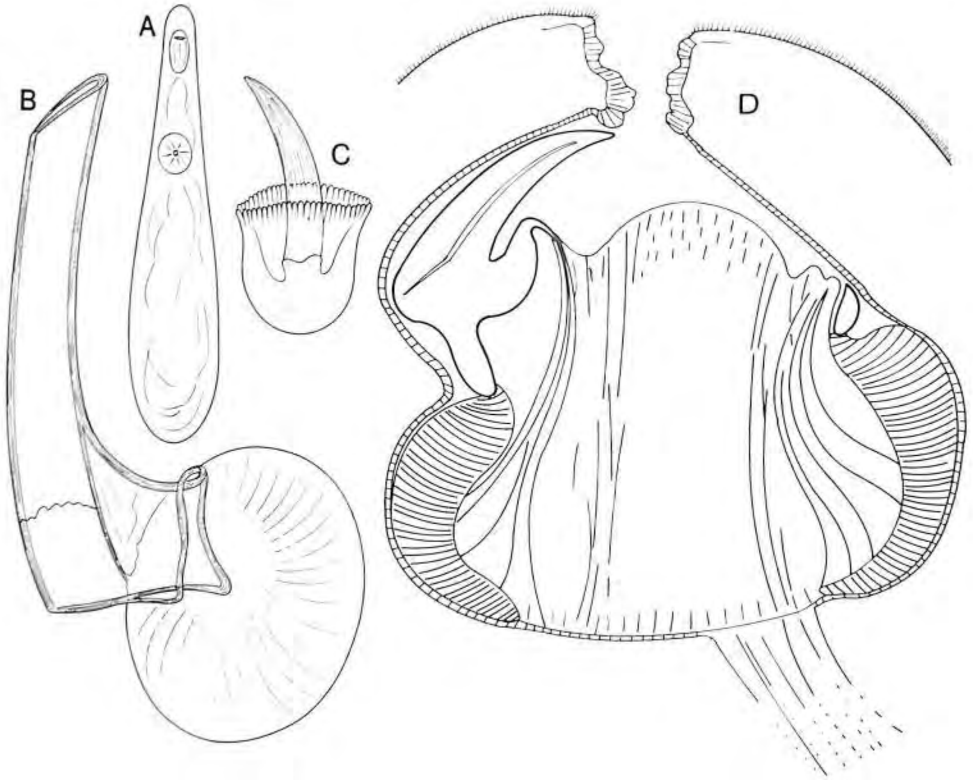

Fig. 53. *Prognathorhynchus dividibulbosus*. A. Habitus. B. Stylet and prostatic vesicle. C. Proboscis hook. D. Reconstruction of the proboscis, sagittal section (Seward: Lowell Point).

Robust animals up to 3 mm long, without eye pigmentations. Body club-shaped, both ends rounded. Widest diameter in the final third of the body, pharynx in the anterior half. Proboscis with a pair of hooks (about 38 μm long) inserted in a cup-shaped base. Germary, vitellary and testis unpaired, single genital opening terminally.

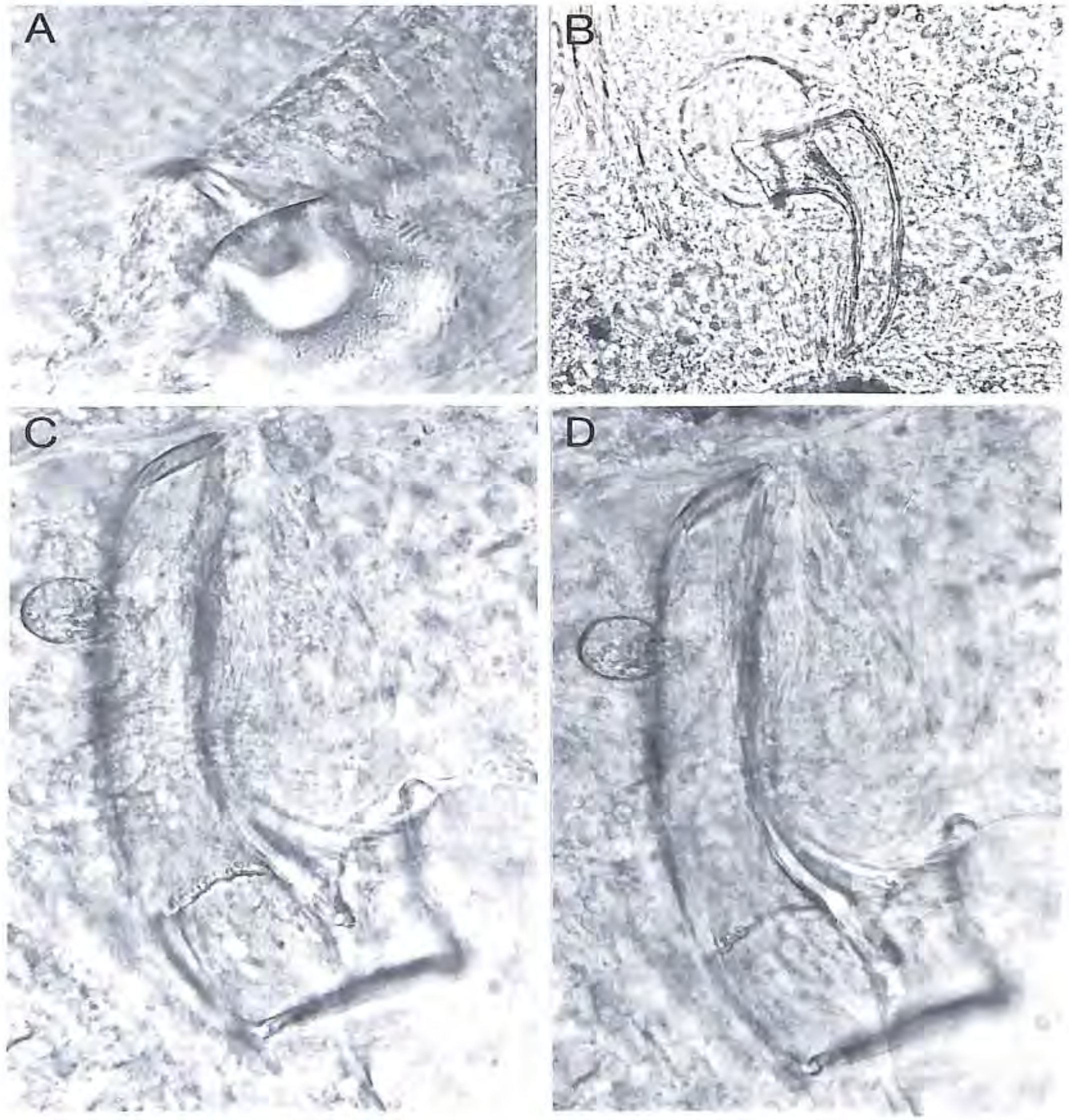

Fig. 54. *Prognathorhynchus dividibulbosus*. A. Proboscis hook. B. Stylet and prostatic vesicle. C, D. Stylet in different focus (Seward: Lowell Point).

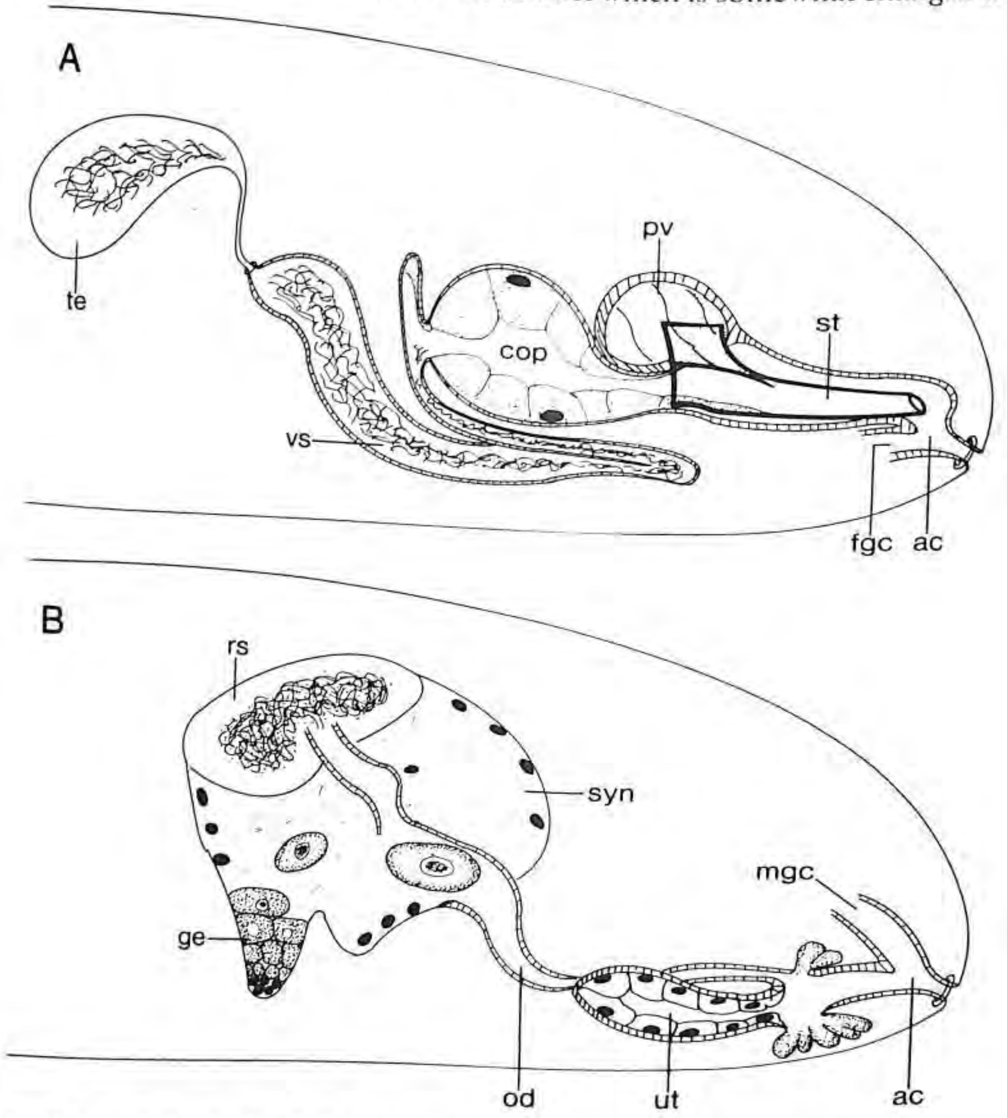

Fig. 55. *Prognathorhynchus dividibulbosus.* Sagittal reconstruction. A. Male organs. B. Female organs.

Common genital atrium small. Female genital canal short, then branching into the uterus bag and the long oviduct. Mouth of the uterus surrounded by glands, uterus with a high inner epithelium. The oviduct leads into a voluminous syncytial tissue with peripheral nuclei. Some sperms can be found all over the syncytium, but most of it is aggregated in a special dorsal section presumably serving as a seminal receptacle. A muscular duct connects these masses of sperm (mixed with granular secretions) with the oviduct which is somewhat enlarged at this site. The germary is ventrolaterally joint to the syncytial tissue. Mouth of the vitellary not seen.

Testis behind (in living specimens possibly beside) the pharynx, longish, without a visible outer epithelium. Spermatic duct short, leading into a long tubiform seminal vesicle. It enters the copulatory bulb from frontally. Most of the copulatory bulb is filled by a high epithelium with peripheral nuclei and coarsly grained contents. Projections of these cells enter the main tube of the stylet.

The prostatic vesicle is distinctly separated from the copulatory bulb, provided with an own muscular cover. It contains finely grained secretions. No nuclei were found inside the prostatic vesicle, and there were no prostatic glands outside the muscular bulb. In a lateral part of the copulatory bulb the inner epithelium contained grains of decreasing size, finally identical in shape and colour with the contents of the prostatic vesicle. However, a direct connection between these cells and the prostatic vesicle was not found. Presumably the prostatic vesicle is loaded with secretions of the copulatory bulb epithelium via a plasmatic connection in the proximal part of the stylet. Thus, the production and the release of the prostatic secretions are separated from each other.

The stylet is about 110 µm long and has the shape of an "r". The main tube is slightly curved with a proximal opening of about 20 µm. Distally the stylet is cut off oblique. Proximally there is a separate opening for the granular secretions, tightly covered by the lower part of the prostatic muscular bulb. All structures of the genital system except the testis, uterine glands and syncytial tissue are covered by a thin muscular layer. The muscles around the uterus bag and the prostatic bulb are distinctly stronger.

Discussion. Inside the taxon *Prognathorhynchus* the species *P. dividibulbosus* is characterized by the very large stylet, the seminal receptacle which is a specialized part of the syncytial tissue, and the muscular prostatic vesicle divided from the copulatory bulb. The lack of nuclei suggests that the prostatic vesicle is loaded with secretions produced by the inner epithelium of the copulatory bulb. Thus, the prostatic vesicle seems to be a lateral excavation of the copulatory bulb with a mere pumping function.

Coronopharynx pusillus **Luther, 1962**

(Fig. 56, 57)

Localities: (1) Seward. Fourth of July Beach; mud from the border of a salt marsh (8. 7. 1988, occurring regular); muddy sand (11. 7. and 13. 8. 1988, regular in low abundance); fine to medium intertidal sand (20. 7. 1988). (2) Seward. Lowell Point, lower beach slope (26. 7., 2. 8., and 4. 8. 1988,

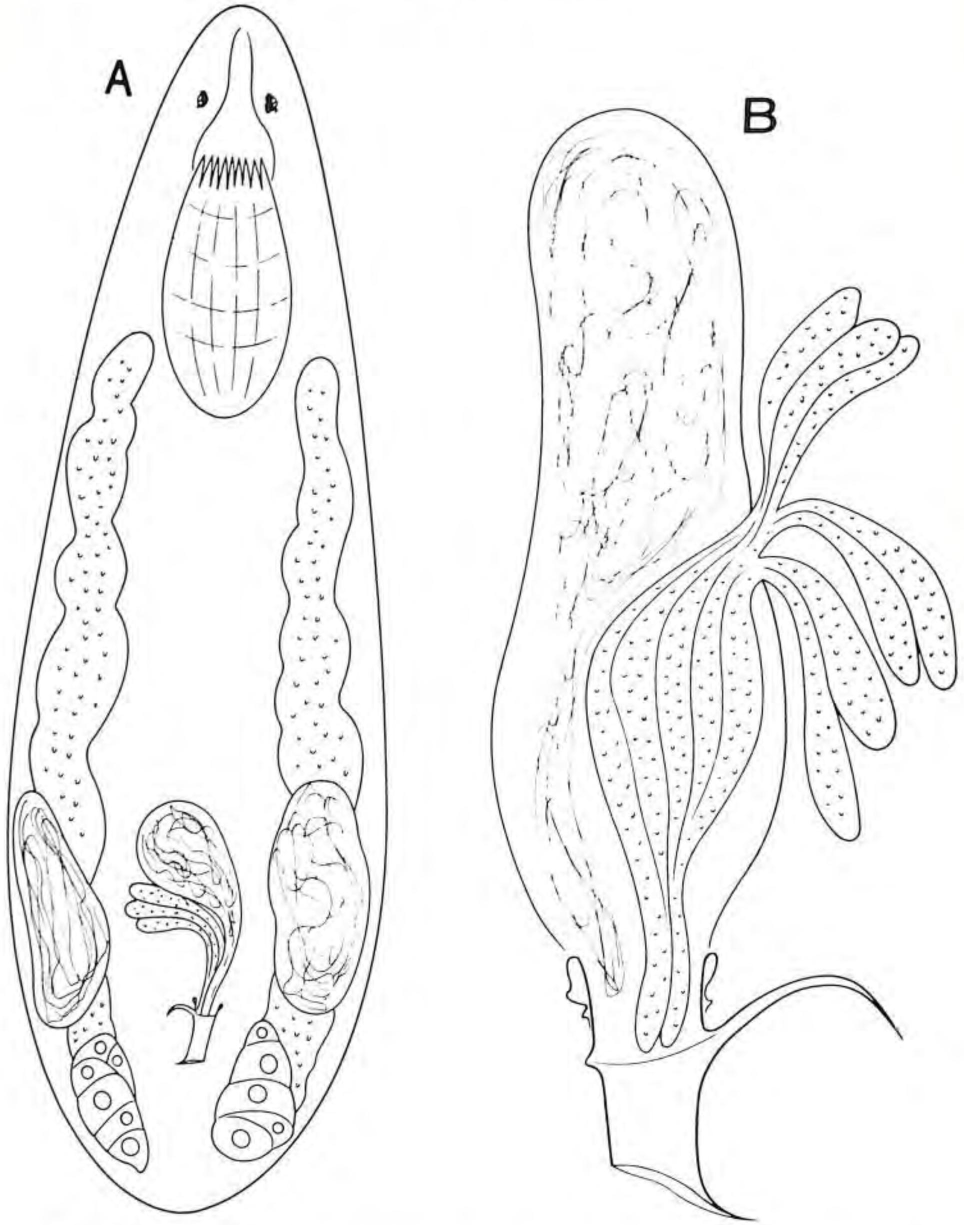

Fig. 56. *Coronopharynx pusillus.* A. Organisation. B. Male copulatory organ (A Seward: Fourth of July Beach, B Seward: Lowell Point).

always freshwater). (3) Ninilchik. Medium sand with moderate amounts of detritus from the shore close to the Cook Inlet River (16. 7. 1988).

Material: Live observations on numerous specimens, including drawings and photographs.

Distribution: Pacific coast of Oregon (KARLING 1986), North Sea (TULP 1974, ARMONIES 1987). Baltic Sea (LUTHER 1962, FENCHEL & JANSSON 1966), White Sea (KOTIKOVA & JOFFE 1988). As far as measurements are available, all localities have a salinity in the oligohaline (< 5 ‰ S) range.

Animals 0.5 to 0.6 mm long, with a ring of pointed tentacles around the pharynx mouth. Paired eye pigmentations in front of the pharynx. Paired vitellaries laterally with caudally joint germaries. Paired testes in the rear part of the body, above the caudal reaches of the vitellaries. Copulatory organ median of the testes. The copulatory bursa appears as a light area laterally of the stylet. Prostatic glands enter the seminal vesicle in the middle of the copulatory organ. Further distally, granular secretions and sperms remain clearly separated.

The stylet is a wide tube of 24 to 30 µm length, slightly narrowing distally

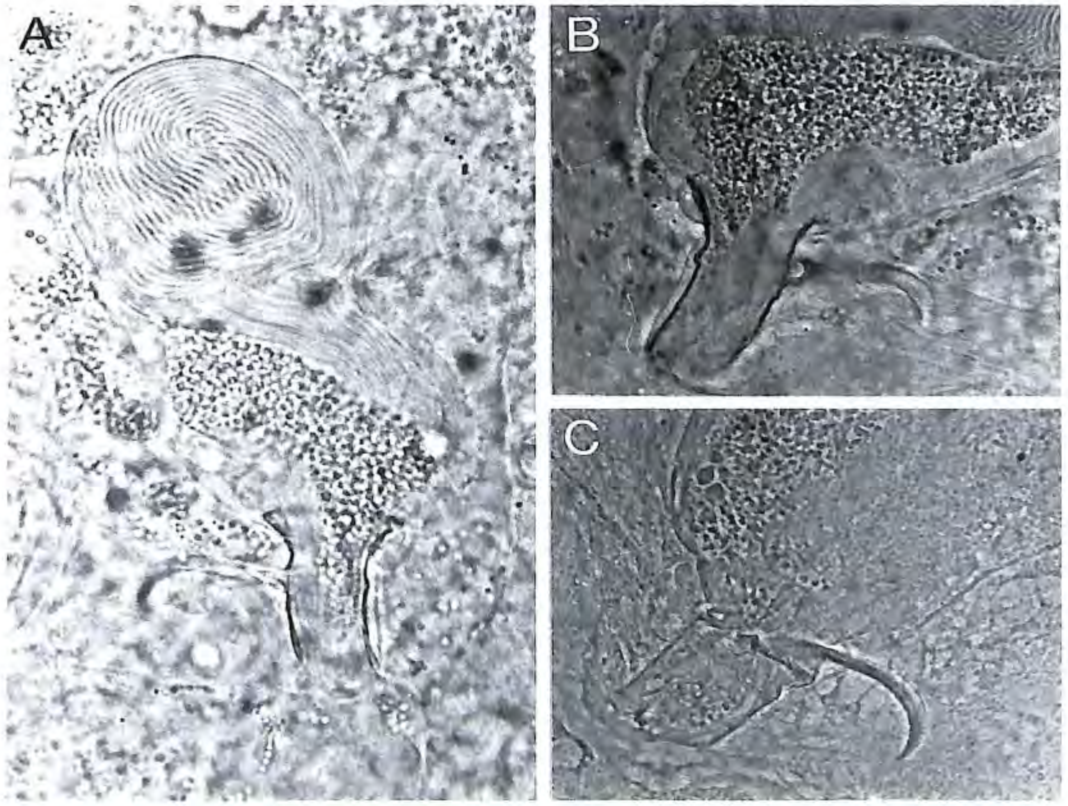

Fig. 57. *Coronopharynx pusillus.* A. Male copulatory organ. B, C. Stylets of different individuals (Seward: Fourth of July Beach).

(proximal diameter 17 to 19 µm, distal diameter 10 to 12 µm). Laterally the stylet bears a spur of 22 to 23 µm. It was curved in the Alaskan material but may be straight in European specimens (LUTHER 1962) and the Pacific population observed at the coast of Oregon (KARLING 1986).

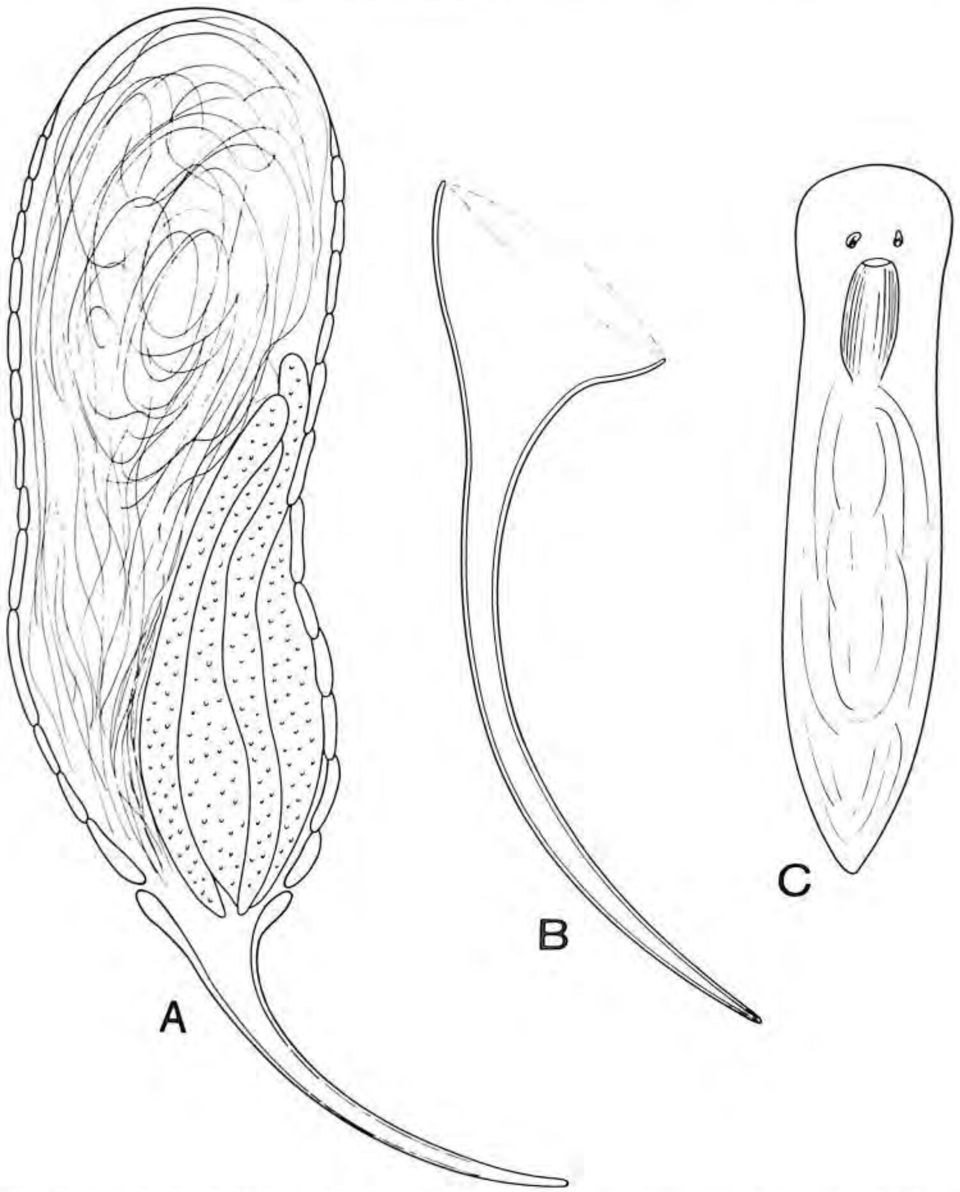

Fig. 58. *Pogaina alaskana*. A. Male copulatory organ. B. Stylet. C. Habitus (Seward: Fourth of July Beach).

***Pogaina alaskana* n. sp.**

(Fig. 58, 59)

Locality: Seward. Fourth of July Beach (locus typicus). Muddy sand of the upper intertidal (8. 7. and 11. 7. 1988).

Material: Live observations on several specimens, including drawings and photographs.

Animals 0.5 mm long, with broadly rounded frontal end and triangular caudal end. With brown pigmentation of longitudinal stripes and zooxanthellae. Pharynx doliiformis in the proximal third of the body. With paired eye pigmentations in front of the pharynx. Copulatory organ in the caudal third of the body, about 150 µm long and 45 to 50 µm wide. With a strong muscular cover. However, no distinct musculature was seen in the most proximal part of the copulatory organ. The stylet is a 68 to 75 µm long very slender tube with a proximal funnel of 23 to 28 µm (depending on the degree of coverslip compression).

Discussion. Valid species of the taxon *Pogaina* are *P. adriatica* (Dörler, 1900), *P. murmanicum* (Graff 1905; cf. LUTHER 1948), *P. ussuriensis* (Nasonov, 1932), *P. suecica* (Luther 1948), *P. natans* (Ax, 1951), *P. suslica* Marcus, 1951, *P. evelinae* (Marcus, 1954), *P. tifa* Marcus, 1954, *P. kinnei* Ax, 1970, *P. annulata* Ax, 1970, *P. bicornis* Karling, 1986, *P. paranygulgus* Karling, 1986, *P. oncostylis* Ax & Armonies, 1987, and *P. arcassonensis* recently described by EHLERS & SOPOTT-EHLERS (1989). With respect to the shape of the stylet, *P. alaskana* differs from them all.

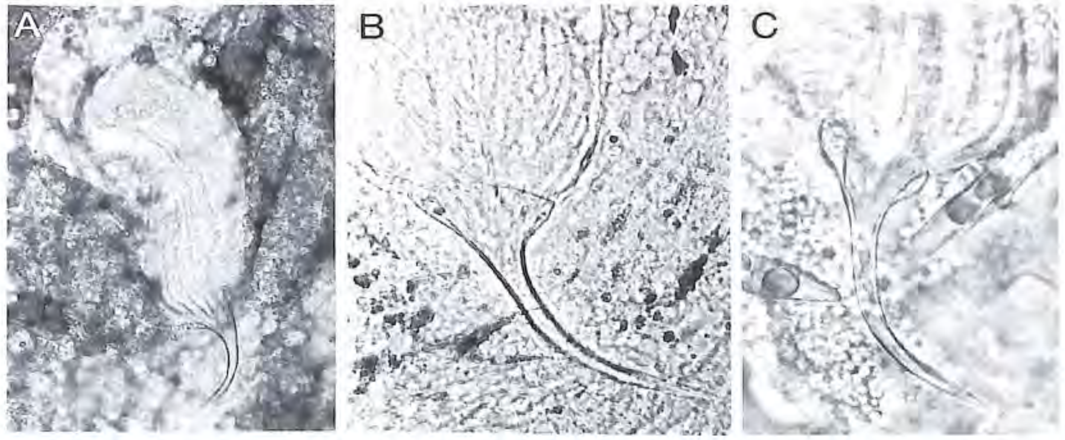

Fig. 59. *Pogaina alaskana*. A. Male copulatory organ. B, C. Stylets of different animals (Seward: Fourth of July Beach).

A curved stylet of similar size (60 µm or more) only occurs in *P. paranygulgus* from the Californian Pacific coast. In both species the stylet starts with a wide funnel about 20 µm in diameter. In *P. paranygulgus* the stylet narrows regularly to a diameter of about 7 to 8 µm at the tip (cf. KARLING 1986, Fig. 6). In *P. alaskana* the tube diameter narrows very rapidly already in the proximal fifth of the stylet and the diameter at the tip is only about 3 µm. Nevertheless, because of the size and the shape of the stylet and the absence of additional structures such as lateral or terminal clasps or laminae, *P. paranygulgus* and *P. alaskana* might be sister-species in the taxon *Pogaina*.

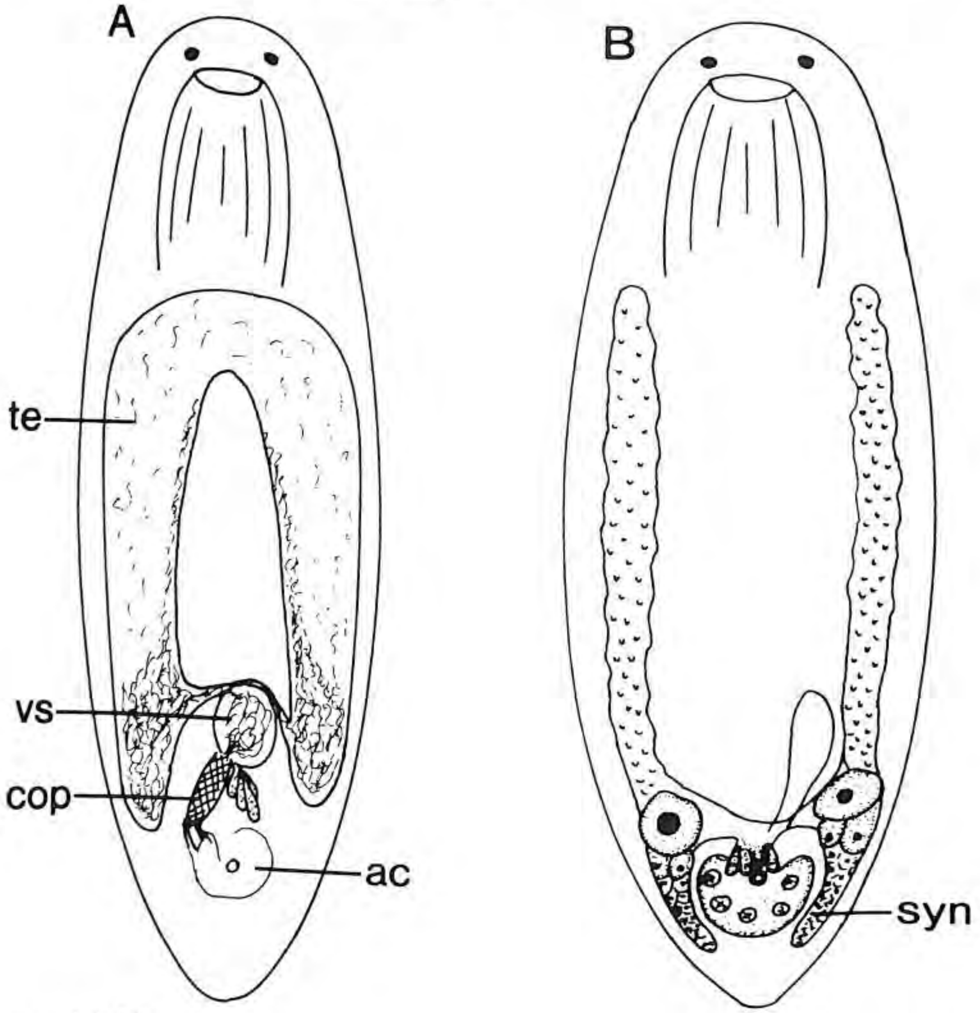

Fig. 60. *Baicalellia anchoragensis*. Reconstruction of the genital organs. A. Male organs. B. Female organs.

Baicalellia anchoragensis n. sp.

(Fig. 60–63)

Localities: (1) Anchorage. Salt marsh of the northern shore next to the 5th Avenue (locus typicus). Muddy sediment (13. 7. 1988, salinity 12 to 13 ‰). (2) Homer Spit. Upper intertidal mud with algal cover and salt marsh pools with muddy sediment (16. 7. 1988; low tide salinity in pools containing the species = 2–3, 8, and 35 ‰). (3) Ninilchik. Mouth of the Cook Inlet River; (a) upper intertidal medium sand with moderate amounts of detritus (16. 7. 1988, salinity 5 ‰); (b) muddy sand (21. 7. 1988, salinity 0 ‰). (4) Hope, near the Turnagain Arm. Muddy wadden area in front of the salt marsh edge of erosion (19. 7. 1988, salinity of adjacent tidal pools 12 to 15 ‰). (5) Seward. Airport, salt marsh below the air corridor next to the Resurrection River; mud with algal cover (12. 8. 1988, low tide salinity 7 to 8 ‰). (6) Kotzebue. Salt marsh east of the village (8. 8. 1988, salinity 7 to 11 ‰).

Material: Live observations on numerous specimens, including drawings and photographs. Twelve animals sectioned, one animal sectioned sagittally = holotype No. P 2211, two paratypes No. P 2212 and P 2213, Zoological Museum of the University of Göttingen.

Robust animals up to 2 mm long, habitually resembling *Pseudograffilla arenicola*. Paired testes ventrally, frontally horseshoe-like connected. Seminal vesicle

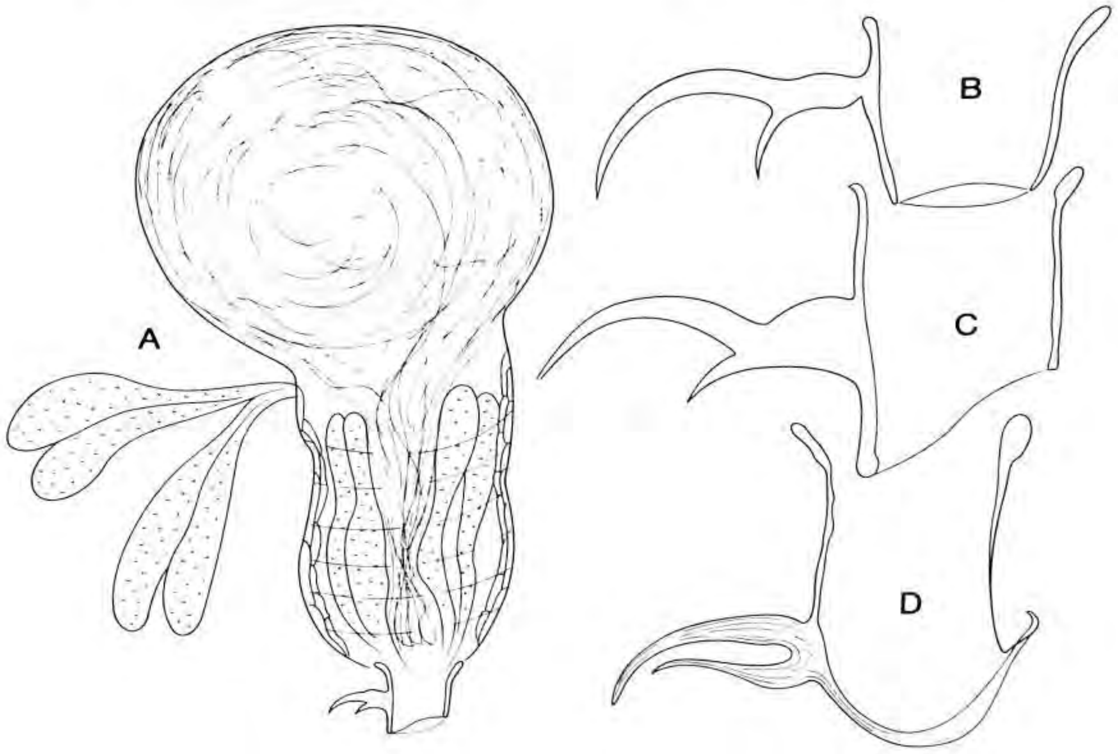

Fig. 61. *Baicalellia anchoragensis*. A. Male copulatory organ (Anchorage). B, C. Stylet (Kenai Peninsula: Ninilchik). D. Stylet (Anchorage).

spherical, distally joining the copulatory organ in common with prostatic glands. Copulatory organ covered by two layers of spiral muscles. The stylet is a wide tube about 35 µm long with a lateral appendage of up to 45 µm. The basal portion of the appendage is knob-shaped and bears a shorter distal spine and a larger curved spine.

Paired lateral vitellaries starting behind the pharynx, caudally tightly contacting the largest cells of the paired germaries. The single subcaudal genital opening is closed by circular muscles. It leads into a wide genital atrium. The copulatory organ enters a ventral excavation of the genital atrium. Further dorsally the atrial walls are enlarged forming a longish pocket which points frontally. Caudally the common oviduct enters the genital atrium. A syncytial tissue with numerous spherical cavities containing sperms branches caudally. Nuclei are only seen in the peripheral portion of the tissue. Dorsally of this appendage, glands empty into the common oviduct. The genital atrium including the male genital canal, the frontal elongation, and the lower part of the oviduct are all covered by muscles. Towards the germaries the musculature becomes continuously weaker. No musculature was seen around the syncytial tissue. In a few specimens the syncytial tissue was slightly bipartite by a median narrowing.

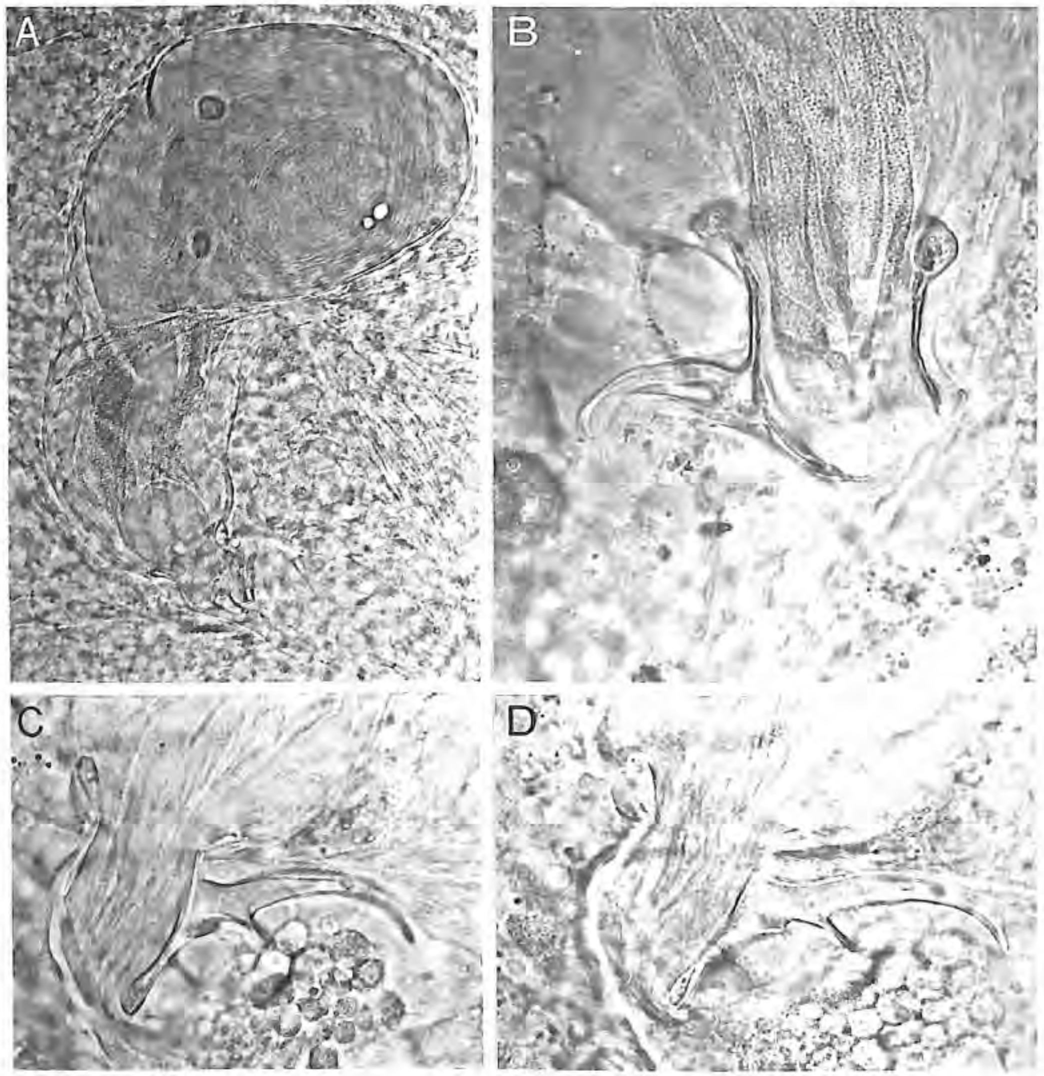

Fig. 62. *Baicalellia anchoragensis.* A. Male copulatory organ (Kenai Peninsula: Homer Spit). B. Stylet (Anchorage). C, D. Stylet, different focus (Kenai Peninsula: Ninilchik).

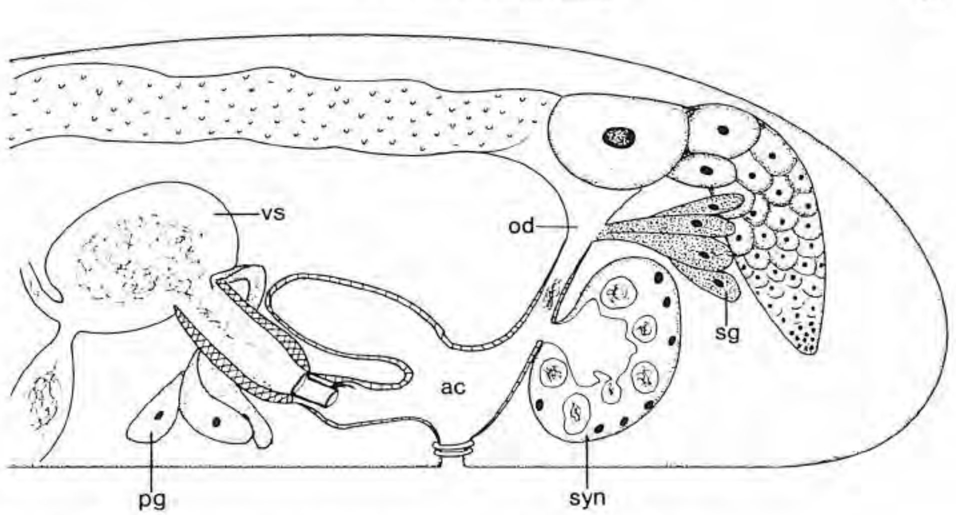

Fig. 63. *Baicalellia anchoragensis.* Sagittal reconstruction of the atrial organs.

Discussion. The general arrangement of the atrial organs and the existence of a frontal connection of the testes indicate that the species belongs to the taxon *Baicalellia.* Detailed morphological studies are available for *B. brevituba* (see Luther 1921) and *B. posieti* (see Nasonov 1932). There seems to be some variance in the location of the syncytial tissue. In *B. posieti* (and *B. sewardensis* n. sp., see below) it is a dorsal appendage of the common atrium (Nasonov 1932, Fig. 12) positioned between the vitellaries. In *B. brevituba* the syncytial tissue lies more caudally between or below the germaries (Luther 1921, Fig. 30 A). Finally, in *B. anchoragensis* the organ is rather a caudal appendage of the female genital canal than a dorsal one of the common atrium. In part, these differences may be due to a variable strength of the musculature around the respective ducts. The relatively short and wide stylet with a bipartite lateral appendage is a unique feature separating *B. anchoragensis* from all other species.

Baicalellia sewardensis n. sp.

(Fig. 64–67)

Locality: Seward. Fourth of July Beach (locus typicus). Muddy sand of the upper intertidal (8. 7., 11. 7., and 13. 8. 1988) and medium to fine intertidal sand (20. 7. 1988, abundant).

Material: Live observations on several specimens, including drawings and photographs. Ten specimens sectioned, one animal sectioned sagittally = holotype No. P 2221, three paratypes No. P 2222–P 2224, Zoological Museum of the University of Göttingen.

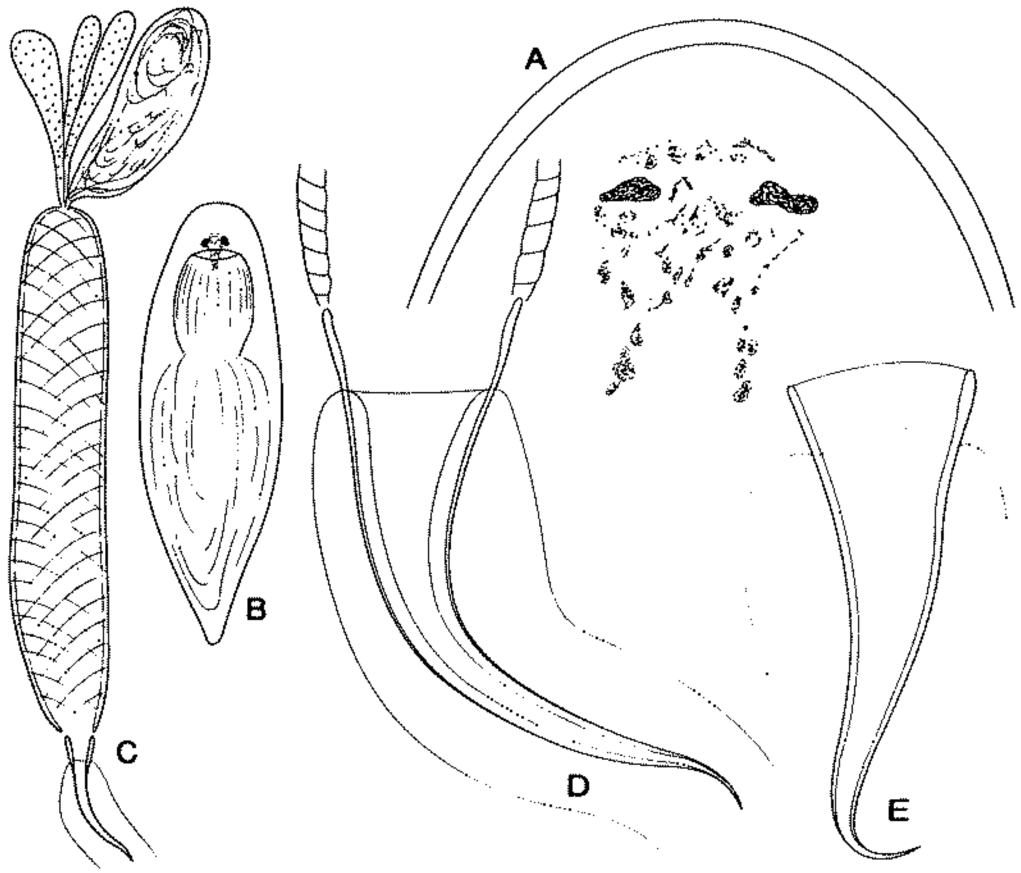

Fig. 64. *Baicalellia sewardensis.* A. Anterior end with eyes and groups of fine pigment granules. B. Habitus. C. Male copulatory organ. D, E. Stylets of different individuals (Seward: Fourth of July Beach).

Animals 2 to 3 mm long, stout with tapering tail end, habitually resembling *Halammovortex nigrifrons.* Paired eyes in front of the pharynx, with groups of fine pigment granules between the eyes and further caudally above the pharynx. Paired lateral vitellaries, caudally joining the paired germaries. Testes horseshoe-shaped. Copulatory organ with a proximal seminal vesicle. A single genital opening in the caudal half of the body.

Male organs. Horseshoe-shaped testes ventrally of the pharynx, in stretched organisms behind it. The caudal parts of the testes directly enter the seminal

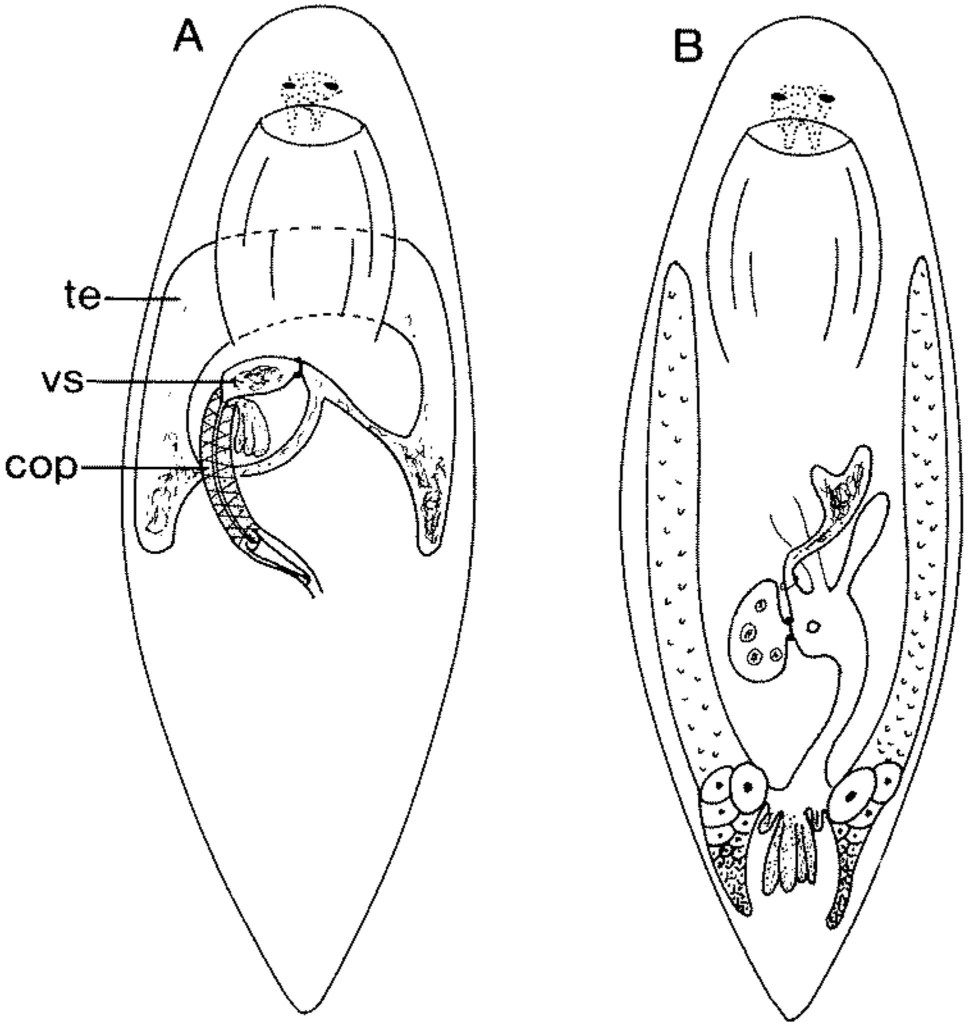

Fig. 65. *Baicalellia sewardensis.* Reconstruction of the genital organs. A. Male organs. B. Female organs.

vesicle and there is no structurally different spermatic duct. Circular muscles separate the testes from the ovoid seminal vesicle which is surrounded by several layers of very fine muscle fibres. Distally the seminal vesicle enters the tubiform copulatory organ, together with prostatic glands. The copulatory organ (in living specimens about 250 µm long) is covered by two layers of spiral muscles. Inside there is a median duct for sperm, surrounded by granular secretions. The stylet is a tapering curved tube of 70 µm. Presumably it is only tubiform in the proximal part and groove-shaped distally. The stylet opens into a pocket-like excavation of the frontal side of the genital atrium, close to the ventral side.

Female organs. The paired vitellaries are in tight contact with the largest cells in the germaries. A common oviduct with weak musculature and an inner epithelium of cylindrical cells connects the germaries with the genital atrium. Caudally in the oviduct there are (?shell) glands. Laterally at both sides of these glands the oviduct has spherical excavations filled with sperm.

Beside the oviduct and the male genital canal three further structures start from the genital atrium. Two dead-ended pockets stretch frontally, the first one close to the ventral side and the second one further dorsally. Strong circular muscles separate the latter bag from the genital atrium and its muscle cover is stronger than in the other structures of the genital atrium. Like all other cavities of the genital atrium this bag contained sperms in most specimens. Dorsally the genital atrium opens into a small muscular pocket which proceeds in a syncytial tissue further dorsally. Circular muscles separate the intermediate pocket from both the genital atrium and syncytial tissue. Most of the pocket is filled by a cylindrical epithelium and the small cavity is filled with sperms. Histologically the dorsal syncytium resembles the intestinal epithelium and at its lateral borders it is barely discernible from the surrounding intestine. The syncytium has several cavities which contain sperms in various degrees of destruction. Thus it seems the syncytial tissue functions as a resorbient bursa (see Nasonov 1932). It is the only appendage of the genital atrium without a visible muscular cover. A package of glands stretches frontally of the genital atrium at the right side of the specimens. Their function is unknown and it could not be seen where the glands empty. But from their arrangement they are likely to open somewhere in the genital atrium.

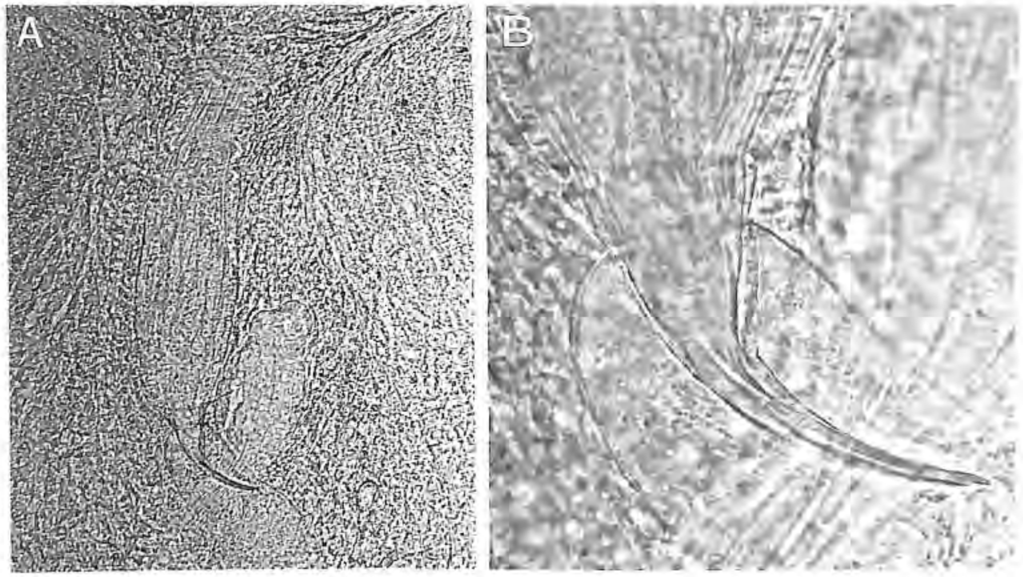

Fig. 66. *Baicalellia sewardensis.* A. Male copulatory organ. B. Stylet (Seward: Fourth of July Beach).

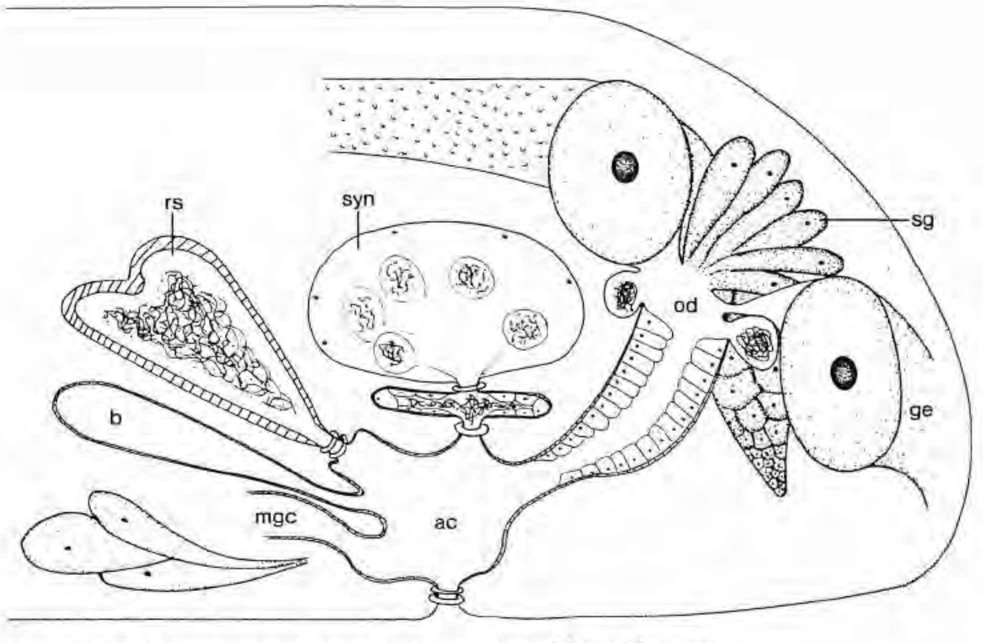

Fig. 67. *Baicalellia sewardensis.* Sagittal reconstruction of the atrial organs.

Discussion. Having a common genital pore in the caudal half of the body, paired germo-vitellaries, horseshoe-shaped fused testes, and a copulatory organ with a proximal seminal vesicle, the species fits the diagnosis of the taxon *Baicalellia* Nasonov, 1930. However, there are differences in the appendages of the genital atrium. Besides the male genital canal, the common oviduct, the bursa resorbiens ("phagocytäres Organ" in Nasonov 1932), and a more or less distinctly separated copulatory bursa, *B. sewardensis* has an additional muscular bag which is separated from the genital atrium by circular muscles. Presumably this bag has a storing function for sperms. The pocket-shaped lateral dilatations of the dorsal part of the common oviduct are another character hitherto unknown in *Baicalellia.* Apart from this, the very long copulatory organ and the shape of the stylet are characters separating *B. sewardensis* from all other species of the taxon *Baicalellia.*

Halammovortex nigrifrons (Karling, 1935)

(Fig. 68)

Localities: Seward. (1) Fourth of July Beach; muddy sand of the upper intertidal (8. 7. 1988); medium to fine intertidal sand (20. 7. 1988). (2) Lowell Point, fine sand from the lower beach slope with effluent freshwater (10. 7. 1988).

Material: Live observations on several specimens, including photographs.

Distribution: North Sea, Baltic Sea (KARLING 1943, 1974; LUTHER 1955; ARMONIES 1987; HELLWIG 1987), Barents Sea (KOTIKOVA & JOFFE 1988), SE Canadian Atlantic coast (AX & ARMONIES 1987).

Specimens with 4 pigmented eye spots. The stylet has the same shape as in European (cf. KARLING 1974) and Canadian (cf. AX & ARMONIES 1987) specimens. However, it is considerably larger. Alaskan stylets are 100 to 110 µm long (including the distal spines) while European and Canadian stylets are only 56 to 72 µm. The distal spines are 17 to 30 µm long while European animals have spines of 12 to 18 µm (KARLING 1943).

Jensenia parangulata n. sp.

(Fig. 69, 70)

Locality: Ninilchik. Medium sand with moderate amounts of detritus from a brackish water (5 ‰ S) lagoon (locus typicus, 16. 7. 1988).

Material: Live observations on three specimens, including drawings and photographs.

Specimens with a very characteristic body shape. The frontal end is conspicuously broadened, with ear-shaped rounded lateral sides. The rear end tapers conically. The stylet consists of two long stalks of 60 µm and two distal branches which are connected to each other at their bases. Each of the distal branches bears about 15 pointed spines. Both distal branches are 35 to 38 µm long; total length of the stylet 95 to 98 µm.

A comparison of *J. parangulata* with the description of *J. angulata* (Jensen, 1878) given by EHLERS (1990) yielded the following differences between the two species. (1) The stylet is smaller in *J. parangulata* – total length 95 to 98 µm versus

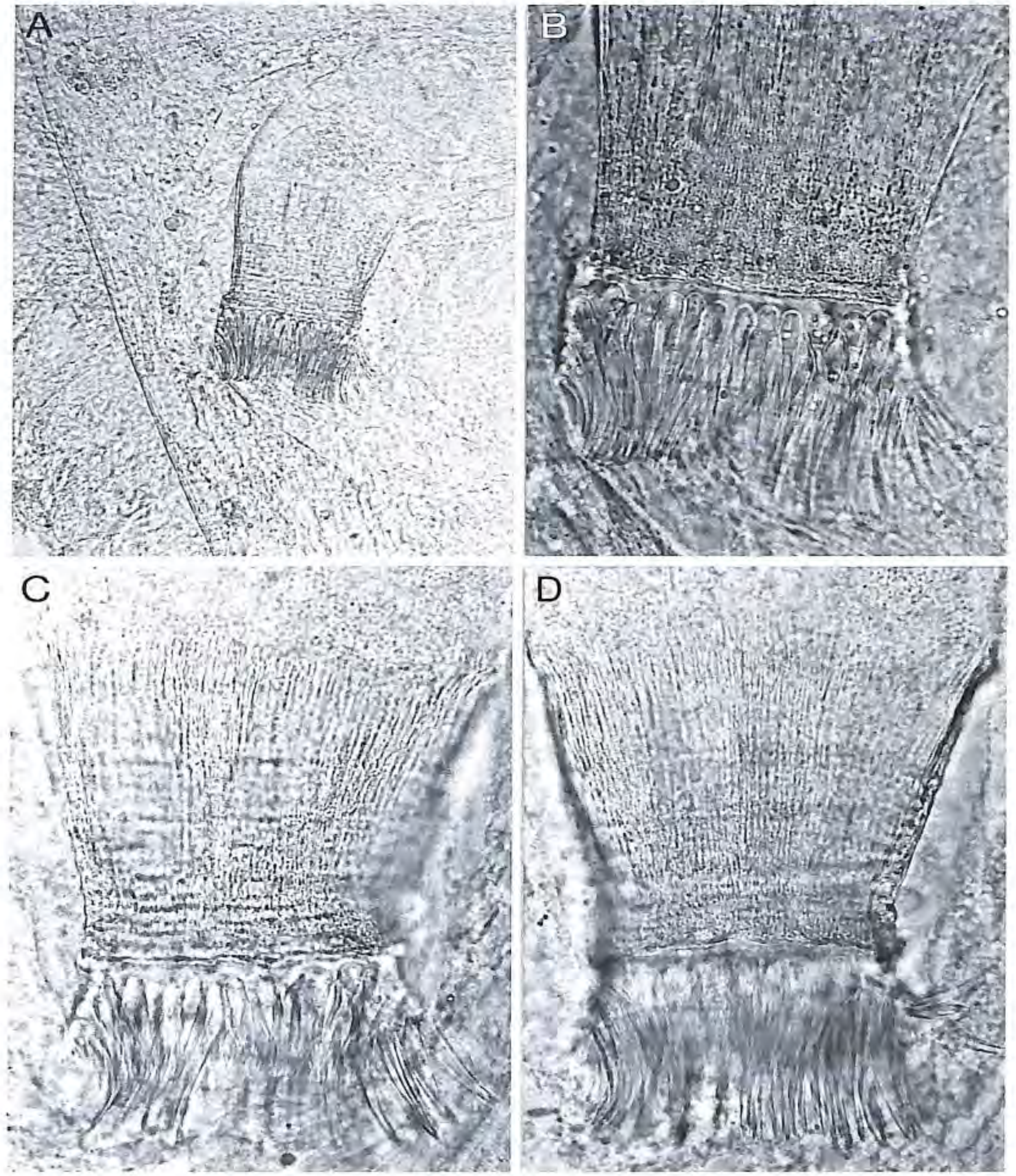

Fig. 68. *Halammovortex nigrifrons.* A. Male copulatory organ. B. Distal part of the stylet (Seward: Fourth of July Beach). C, D. Stylet, different focus (Seward: Lowell Point).

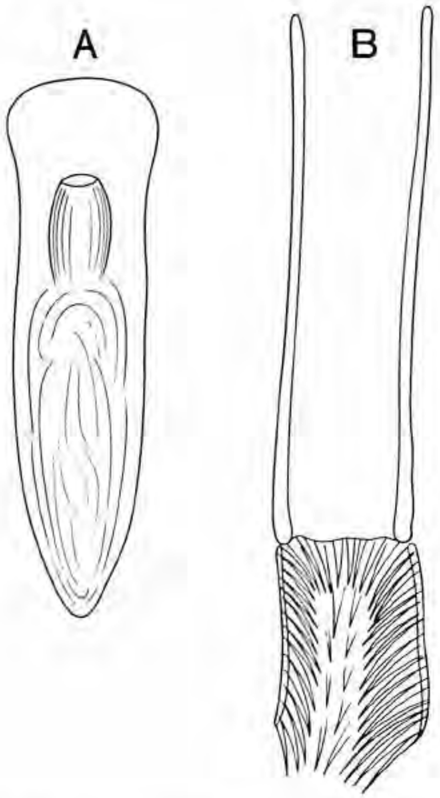

Fig. 69. *Jensenia parangulata*. A. Habitus. B. Stylet (Kenai Peninsula: Ninilchik).

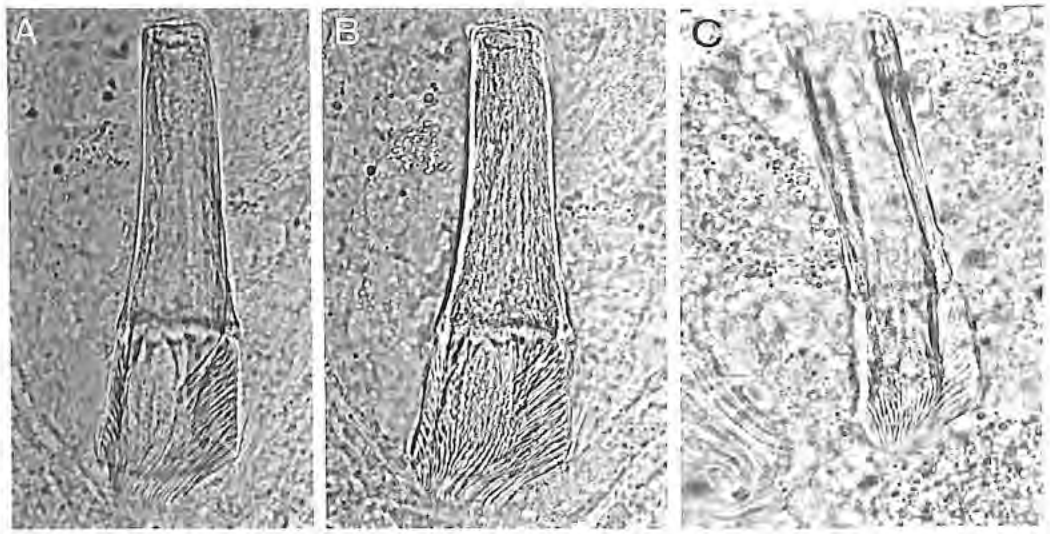

Fig. 70. *Jensenia parangulata*. A, B. Stylet, different focus. C. Stylet of another animal (Kenai Peninsula: Ninilchik).

117 to 120 µm in *J. angulata*. (2) *J. parangulata* lacks the "prominent distally oriented spine" present in the distal part of the stylet of *J. angulata*. (3) In *J. parangulata* the two branches in the distal part of the stylet are equal in length but they are strongly asymmetric in *J. angulata* (cf. EHLERS 1990, fig. 2). In addition, *J. angulata* seems to be a marine species while *J. parangulata* was found in oligohaline brackish water. Nevertheless, despite of these differences the general organisation agrees well in the two species. They might be sister-species in the taxon *Jensenia*.

D. Discussion

At the North American Pacific coast, plathelminth research has just begun. Until 1960, only 4 species were known (excluding polyclads, KARLING 1962 a). Including this study the number of species descriptions has increased to 131 since then (Table 5). This number is still small when compared with more intensively studied areas such as the North Sea. Around the small Island of Sylt in the European Wadden Sea, a total of 435 species is recorded (REISE 1988). Therefore, we expect that only a small portion of the Pacific plathelminth fauna is known by now.

From the material found during a 5 weeks stay in Seward, Alaska a total of 37 species of free living Plathelminthes is recorded. Five species could be identified with species known from the southern US Pacific coast and 13 with species also occurring in European coastal waters. Of these, at least 9 are brackish water species.

We are aware that species identifications based on morphological studies may be misleading, in one of two ways. Morphological differences may be overemphasized with the result that a new species is described although the members of distant populations may actually be able to interbreed. On the other hand, two populations may be morphologically identical but nevertheless represent different species. However, in the present biogeographical context both types of error do not generally call the results in question. In the first case, actual species identity is not recognized, we get a conservative decision to retain our null-hypothesis of different species in different geographical areas. The second case, species identity is falsely assumed, increases the probability to reject the null hypothesis. But this is only partly erroneous. Morphologically identical species are most likely to be closely related, probably sister-species in the phylogenetic system. This is just another way to state a connection between two geographically separated areas.

Of the 131 plathelminth species so far recorded from the North American

Table 5: Plathelminth species of the N American Pacific coast and their further distribution, as compiled from Karling (1962 a, b, 1964, 1966, 1967, 1977, 1980, 1982, 1983, 1985, 1986, 1989), Ax & Ax (1967), Schockaert & Karling (1970), Holmquist & Karling (1972), Karling & Schockaert (1977), Ax et al. (1979), Ax & Sopott-Ehlers (1979), Sopott-Ehlers & Ax (1985), and Kozloff (1987). References of localities only given if not part of the species description, for species found in this study (marked by *) see results. References of the above list abbreviated by the first two letters of the authors name + final two digits of the year of publication (thus, Karling 1966 = Ka66). In addition, Lu62 = Luther 1962, Dö68 = Dörjes 1968. Pacific distribution: C = California, O = Oregon, W = Washington, A = Alaska; further distribution: At = Atlantic (with suffix N North, S South, E European, A American), Arc = Arctic Sea (incl. Barents Sea), Be = Bering Sea, Jap = Sea of Japan, Med = Mediterranean including the adjoining seas (Sea of Marmara, Black Sea), No = North Sea (including the Baltic Sea), Ga = Galapagos Islands, So = the coast of Somalia.

	Distribution		
Species	Pacific	Other and	References
Acoela			
Otocelis luteola (Kozloff, 1965)	W		
Conaperta actuosa (Kozloff, 1965)	W		
Diatomovora amoena Kozloff, 1965	OW		
Paratomella unichaeta Dörjes, 1966	?	No	Dö68 Ko87
Polychoerus carmelensis Costello & Costello, 1938	C		Ka62a
Childia groenlandica (Levinsen, 1879)	C	AtN	Lu62 Ka62a
Macrostomida			
* *Macrostomum bicurvistyla* Armonies & Hellwig, 1987	A	No	
* *Macrostomum curvituba* Luther, 1947	A	No	
* *Macrostomum extraculum* n. sp.	A		
* *Macrostomum pusillum* Ax, 1951	A	AtN	
* *Macrostomum spirale* Ax, 1956	A	No Med	
* *Macrostomum tenuicauda* Luther, 1947	A	No	
Prolecithophora			
Plagiostomum abbotti Karling, 1962	C		
Plagiostomum hartmanae Karling, 1962	C		
Plagiostomum hedgpethi Karling, 1962	C		
Plagiostomum hymanae Karling, 1962	C		
Plagiostomum langi Karling, 1962	C		
Pseudostomum californicum Karling, 1962	C		
Cylindrostoma monotrochum (Graff, 1882)	C	AtE Med	Ka62b
Cylindrostoma triangulum Karling, 1962	C		
Allostoma amoenum Karling, 1962	C		
Tricladida			
Procerodes pacifica Hyman, 1954	C		Ka62a
Nesion arcticum Hyman, 1956	A		Ka62a
Nexilis epichitonius Holleman & Hand, 1962	CO		Ho&Ka72
Oregoniplana opisthopora Holmquist & Karling 1972	O		
Pacificides psammophilus Holmquist & Karling 1972	C		

Table 5 continued

	Distribution		
Species	Pacific	Other and	References
Proseriata			
Monocelis cincta Karling, 1966	C		
Monocelis hopkinsi Karling, 1966	C		
Monocelis spectator Sopott-Ehlers & Ax, 1985	C		
Monocelis tenella Karling, 1966	C		
* *Minona dolichovesicula* Tajika, 1982	W	Jap	So&Ax85
Minona cornupenis Karling, 1966	C		
Minona obscura Karling, 1966	C		
Minona secta Sopott-Ehlers & Ax, 1985	W		
* *Minona gigantea* n. sp.	A		
Duplominona stilifera Sopott-Ehlers & Ax, 1985	W		
Promonotus orthocirrus Karling, 1966	C		
Asilomaria ampullata Karling, 1966	C		
* *Archiloa tajikai* n. sp.	A		
* *Archiloa duplaculeata* n. sp.	A		
Archimonocelis coronata Karling, 1966	C		
Archimonocelis semicircularis Karling, 1966	C		
Coelogynopora brachystyla Karling, 1966	C		
Coelogynopora cochleare Ax & Sopott-Ehlers, 1979	W		
* *Coelogynopora falcaria* Ax & Sopott-Ehlers, 1979	WA		
Coelogynopora frondifera Ax & Sopott-Ehlers, 1979	W		
Coelogynopora nodosa Ax & Sopott-Ehlers, 1979	W		
* *Coelogynopora scalpri* Ax & Sopott-Ehlers, 1979	WA		
* *Coelogynopora sewardensis* n. sp.	A		
Coelogynopora tenuiformis Karling, 1966	C		
Vannuccia rotundouncinata Ax & Sopott-Ehlers, 1979	W		
Vannuccia tripapillosa Tajika, 1977 ssp. *americana* Ax & Sopott-Ehlers, 1979	W		
* *Invenusta paracnida* (Karling, 1966)	CWA		Ax&So79
Nematoplana nigrocapitula Ax, 1966	W		
Archotoplana dillonbeachensis Karling, 1964	C		
* *Archotoplana macrostylis* n. sp.	A		
Americanaplana fernaldi Ax & Ax, 1967	W		
* *Alaskaplana velox* n. sp.	A		
Pluribursaeplana illgi Ax & Ax, 1967	W		

Table 5 continued

	Distribution		
Species	Pacific	Other and	References
Orthoplana kohni Ax & Ax, 1967	W		
* *Orthoplana sewardensis* n. sp.	A		
Itaspiella bodegae Karling, 1964	C		
Itaspiella bursituba Karling, 1964	C		
* *Itaspiella helgolandica* (Meixner, 1938)	A	No AtN	
ssp. *magna* Ax & Ax, 1967	W		
Notocaryoplanella glandulosa (Ax, 1951)	W	No Arc	Ax&Ax67
Serpentiplana doughertyi Karling, 1964	C		
Polyrhabdoplana posttestis Ax & Ax, 1967	W		
Parotoplana pacifica Ax & Ax, 1967	W		
Philosyrtis sanjuanensis Ax & Ax, 1967	W		
Rhabdocoela			
* *Haloplanella obtusituba* Luther, 1946	A	No	
Maehrenthalia agilis (Levinsen, 1879)	C	AtN Arc	Ka85
* *Maehrenthalia americana* n. sp.	A	AtE	
* *Byrsophlebs dubia* (Ax, 1956)	A	No Med	
Brinkmanniella palmata Karling, 1986	CO		
* *Promesostoma alaskana* n. sp.	A		
* *Promesostoma dipterostylum* Karling, 1967	C		
Promesostoma hymanae Ax, 1968	W		
Promesostoma infundibulum Ax, 1968	W		
Tvaerminnea karlingi Luther, 1943			
ssp. *pacifica* Karling, 1986	C		
* *Coronhelmis lutheri* Ax, 1951	A	At	
Trigonostomum setigerum O. Schmidt, 1852	C	world-wide	Ka78
Messoplana pacifica Karling, 1986	C		
Ceratopera axi (Riedl, 1954)	CO	Med Ga AtS	Ka86
Ceratopera ehlersi Karling, 1986	C		
Ceratopera pilifera Karling, 1986	O		
* *Proxenetes arctica* n. sp.	A		
* *Ptychopera alaskana* n. sp.	A		
Cicerina bicirrata Karling, 1989	CO		
Cicerina triangularis Karling, 1989	O		
* *Placorhynchus pacificus* Karling, 1989	OA		
* *Placorhynchus paratetraculeatus* n. sp.	A		
Uncinorhynchus pacificus Karling, 1989	O		
* *Prognathorhynchus dividibulbosus* n. sp.	A		
Groveia unicornis Karling, 1980	C		
Itaipusa bispina Karling, 1980	CO		
Itaipusa curvicirra Karling, 1980	CO		
Neoutelga inermis Karling, 1980	C		
Rhinolasius dillonicus Karling, 1980	C		
Utelga montereyensis Karling, 1980	C		
Utelga pseudoheinckei Karling, 1980	C	Atl: Med	
Polycystis ali Schockaert, 1982	C	So Ga	Ka86
Polycystis hamata Karling, 1986	CO		

Table 5 continued

	Distribution		
Species	Pacific	Other and	References
* *Gyratrix hermaphroditus* Ehrenberg, 1831	COA	world-wide	Ka&Sc77
Gyratrix proaviformis Karling & Schockaert, 1977	C		
Scanorhyncus forcipatus Karling, 1955	C	AtE	Ka&Sc77
Paraustrorhynchus pacificus Karling & Schockaert, 1977	C		
Austrorhynchus pacificus Karling, 1977	CO		
Austrorhynchus californicus Karling, 1977	CO		
Alcha evelinae Marcus, 1949	C	AtS	Ka&Sc77
Duplacrorhynchus minor Schockaert & Karling, 1970	C		
* *Duplacrorhynchus major* Schockaert & Karling, 1970	OA		
Yaquinaia microrhynchus Schockaert & Karling, 1970	O		
* *Phonorhynchus helgolandicus* (Mecznikow, 1865)	COA	AtN Arc Be	Ka82
Proschizorhynchella lingulata Karling, 1989	C		
Proschizorhynchella inflata Karling, 1989	C		
Proschizorhynchella schilkei Karling, 1989	C		
Schizochilus hoxholdi Karling, 1989	C		
Paraschizorhynchoides glandulis Schilke, 1970		No Arc	
ssp. *hopkinsi* Karling, 1989	C		
Cheliplana californica Karling, 1989	C		
Cheliplana elkhornica Karling, 1989	C		
Cheliplana setosa Evdonin, 1971	C	Jap	Ka83
Balgetia pacifica Ax, Ax & Ehlers, 1979	W		
* *Coronopharynx pusillus* Luther, 1962	OA	No	Ka86
* *Pogaina alaskana* n. sp.	A		
Pogaina bicornis Karling, 1986	C		
Pogaina paranygulgus Karling, 1986	C		
* *Baicalellia anchoragensis* n. sp.	A		
* *Baicalellia sewardensis* n. sp.	A		
* *Halammovortex nigrifrons* (Karling, 1935)	A	AtN	
* *Jensenia parangulata* n. sp.	A		
Bresslauilla relicta Reisinger, 1929	?	AtN Med	Ko87

Pacific coast, 102 have not been found outside this region (see Table 5). Nineteen species are suspected to have a circumpolar subarctic to boreal distribution since they also occur in the Northern Atlantic or the Arctic Sea (Table 6). However, because of our limited knowledge of the plathelminth fauna (outside northern Europe, above all) the categories 'Pacific' and 'circumpolar boreal' are rather provisionally. Nevertheless, applying these categories shows significant differences between the plathelminth taxa. Although our knowledge on Pacific Proseriata is relatively high, only two species occur also outside the Pacific (Table 6). On the other hand, the number of Pacific macrostomid 'endemics' is significantly lower than the average. Five of the six recorded species are also found in European coastal waters, mainly in salt marshes. Four of them are truely brackish water inhabitants which favour low salinities, in contrast to marine species which merely tolerate low salinities (Table 6).

Table 6: Plathelminth species suspected to have a circumpolar boreal to subarctic distribution.

<table>
<tr><th>Marine species</th><th>Brackish water species</th></tr>
<tr><td>Childia groenlandica</td><td>Macrostomum bicurvistyla</td></tr>
<tr><td>Paratomella unichaeta</td><td>Macrostomum curvituba</td></tr>
<tr><td>Macrostomum pusillum</td><td>Macrostomum spirale</td></tr>
<tr><td>Notocaryoplanella glandulosa</td><td>Macrostomum tenuicauda</td></tr>
<tr><td>Itaspiella helgolandica</td><td>Haloplanella obtusituba</td></tr>
<tr><td>Scanorhynchus forcipatus</td><td>Byrsophlebs dubia</td></tr>
<tr><td>Phonorhynchus helgolandicus</td><td>Coronhelmis lutheri</td></tr>
<tr><td>Paraschizorhynchoides glandulis</td><td>Coronopharynx pusillus</td></tr>
<tr><td></td><td>Halammovortex nigrifrons</td></tr>
<tr><td colspan="2">Maehrenthalia agilis</td></tr>
<tr><td colspan="2">Bresslauilla relicta</td></tr>
</table>

Routine measurements of salinity show that strong salinity variations are common in the Alaskan coastal area. The species living here are necessarily adapted to short-term salinity changes. Salt marsh samples mostly showed a rather stable but low salinity. On the other hand, because of weather dependent differences in the water exchange between the coastal waters and the adjacent sea, and variable amounts of melting water from coastal glaciers, salinity of most of the beaches showed strong short-term fluctuations (shock-biotopes, DEN HARTOG 1964). The brackish water species common with the European coastal waters predominantly occurred in the rather stable low-salinity habitats although some of them also entered shock-habitats to a variable degree. On the other hand, the typical (i.e. numerically dominant or widely distributed) species of the shock-biotopes seem to belong to a distinctly separated Pacific fauna – see Proseriata and Kalyptorhynchia in Table 5.

The existence of some marine plathelminth species in both the northern Atlantic and northern Pacific (Tables 5, 6) may be a consequence of a continuous distribution in the northern seas. This is especially true for phytal inhabitants like *Phonorhynchus helgolandicus* which often occur in coastal plankton samples (REISINGER 1932) and which may easily be dispersed by drifting objects such as algae and sea grasses. However, for brackish water species such a kind of dispersal is merely speculative. There is no indication that brackish water plathelminths are able to endure a long time in an entirely marine environment. A high degree of faunal similarity was also observed between the SE Canadian and European brackish water Plathelminthes (AX & ARMONIES 1987). This led to the idea of a circumpolar connection of brackish water plathelminth populations. It is an open question, however, if these "connections" are the result of ancient dispersal, or stations of a present continuous distribution.

Kotzebue Sound in Alaska, the N Canadian coastline, the southern part of the Canadian Archipelago, S Greenland, Iceland, and the entire Sibirian coastline have a climate (subartic tundra climate) comparable to each other. Glaciers that supply fresh water or large rivers are present at the same sites (Fig. 71). Thus, suitable brackish water habitats may exist at the coastlines around the entire Arctic Circle (Fig. 71), allowing the same plathelminth species to live there even at present conditions. Many of the brackish water plathelminths in the more temperate North Sea salt marshes prefer the winter months for activity (ARMONIES 1987) and the winter temperatures in this region are comparable to, or even lower than, the summer temperatures in an subarctic tundra climate. Therefore temperature is presumably not a limiting factor for these species.

A present faunal connection is particularly probable alongside the Sibirian coastline. Between the Canadian Atlantic coast and Europe, Alaska represents an intermediate station. In Alaska, fewer stable brackish water habitats (such as salt marshes) have been studied than was the case in Canada, and the plathelminth abundance was rather low compared with European and Canadian salt marshes. This may be the reason for the lower absolute number of typical brackish water species found. Nevertheless, there are 9 brackish water species common to Europe and Alaska. This corroborates the hypothesis of a circumpolar connection of both regions along the Sibirian route. It is striking, however, that only two brackish water species are common for all three stations and there is only a single species common to Alaska and Canada which has not been found in Europe, up to now (Table 7).

In the taxon *Macrostomum* three brackish water species are common to Canada and Europe, and four to Alaska and Europe. But neither of these seven species has been found at both the Pacific and Atlantic coast of N America. This supports the hypothesis of both a Sibirian and a N Atlantic connection of brackish water plathelminths with Europe. For further tests for the hypothesis of the existence of a boreal to subarctic brackish water community of Plathelminthes with a circumpolar distribution we particularly suggest investigations along the Sibirian coastline. General meiofauna studies showed that Plathelminthes are present as far north as the Novosibirsk Islands (SHEREMETEVSKIJ 1977).

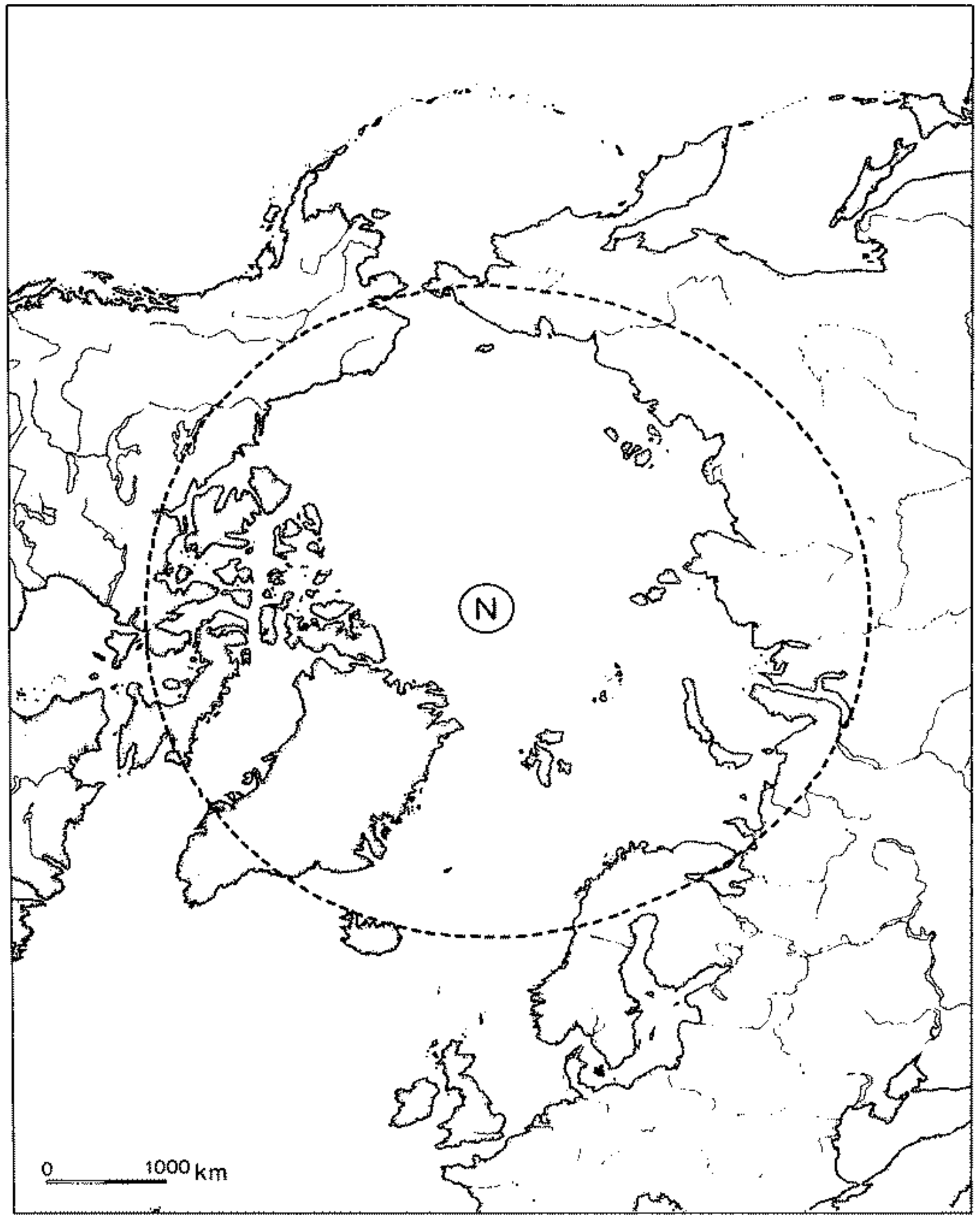

Fig. 71. Polar projection of the Arctic and surrounding continents with major freshwater supplies. Broken line: Arctic circle.

Table 7: Brackish water plathelminth species which have been found in at least two of the three regions Alaska (this study), SE Canada, and Europe (AX & ARMONIES 1987). Because of a lack of salinity data the classification into either brackish water species or euryhaline marine species is rather arbitrary in some species and the list is certainly not complete.

Species which have been found in Canada and Europe

Macrostomum hamatum
Macrostomum hystricinum
Macrostomum rubrocinctum
Monocelis lineata
Minona baltica
Coelogynopora schulzii
Stygoplanellina halophila
Pratoplana salsa
Coronhelmis multispinosus
Ptychopera spinifera
Ptychopera hartogi
Proxenetes deltoides
Proxenetes unidentatus
Beklemischeviella angustior
Haloplanella curvistyla
Thalassoplanella collaris
Parautelga bilioi
Acrorhynchides robustus
Polycystididae spec.
Placorhynchus dimorphis
Placorhynchus octaculeatus
Placorhynchus ?echinulatus
Baicalellia brevituba
Vejdovskya pellucida
Halammovortex macropharynx

Species which have been found in Alaska and Europe

Macrostomum bicurvistyla
Macrostomum curvituba
Macrostomum spirale
Macrostomum tenuicauda
Byrsophlebs dubia
Haloplanella obtusituba
Coronopharynx pusillus

Species which have been found in Alaska and Canada

Maehrenthalia americana

Species which have been found in Alaska, Canada, and Europe

Coronhelmis lutheri
Halammovortex nigrifrons

Provided a circumpolar connection of Alaskan and European brackish water Plathelminthes does exist, we expect that all species found in both Alaska and Europe do also occur in brackish waters of the Sibirian coastline. Wide areas without a corresponding plathelminth colonization would contradict the idea of an ongoing connection. And wide areas which are exclusively occupied by plathelminth species which are unknown from both Europe and Alaska would falsify the hypothesis. We argue that this potential for falsification is a decisive advantage of our hypothesis as compared with speculations like dispersal by continental drift.

Summary

From the material studied during a 5 weeks stay in Seward, Alaska in 1988, 37 species of free-living Plathelminthes are presented. 18 species are described: *Macrostomum extraculum, Archiloa tajikai, Archiloa duplaculeata, Minona gigantea, Coelogynopora sewardensis, Archotoplana macrostylis, Alaskaplana velox, Orthoplana sewardensis, Maehrenthalia americana, Promesostoma alaskana, Proxenetes arctica, Ptychopera alaskana, Placorhynchus paratetraculeatus, Progna-*

thorhynchus dividibulbosus, Pogaina alaskana, Baicalellia anchoragensis, Baicalellia sewardensis, and *Jensenia parangulata.*

Nine species also occur in European brackish waters, and 3 in Canadian brackish waters. *Maehrenthalia americana* is common to Alaska and S Canadian habitats but has not been found in Europe. Only three species, *Macrostomum pusillum, Coronhelmis lutheri,* and *Halammovortex nigrifrons* are known from Alaska, Canada, and Europe.

The results corroborate the hypothesis of the existence of a boreal to subpolar brackish water community of Plathelminthes with circumpolar distribution. The respective European, Canadian, and Alaskan populations seem to be connected both via the N Atlantic and the Sibirian coastline, but single species may be restricted to either route.

Zusammenfassung

Von dem während eines fünfwöchigen Aufenthalts (1988) in Seward, Alaska, studierten Material werden 37 Arten freilebender Plathelminthen behandelt. 18 Arten werden neu beschrieben: *Macrostomum extraculum, Archiloa tajikai, Archiloa duplaculeata, Minona gigantea, Coelogynopora sewardensis, Archotoplana macrostylis, Alaskaplana velox, Orthoplana sewardensis, Maehrenthalia americana, Promesostoma alaskana, Proxenetes arctica, Ptychopera alaskana, Placorhynchus paratetraculeatus, Prognathorhynchus dividibulbosus, Pogaina alaskana, Baicalellia anchoragensis, Baicalellia sewardensis* und *Jensenia parangulata.*

Neun der in Alaska gefundenen Arten kommen auch in europäischen und 3 in kanadischen Brackwasserhabitaten vor. *Maehrenthalia americana* tritt sowohl in Alaska als auch in Kanada auf, ist aber nicht in Europa nachgewiesen. Nur drei Arten, *Macrostomum pusillum, Coronhelmis lutheri* und *Halammovortex nigrifrons* sind von Alaska, Kanada und Europa bekannt.

Die Ergebnisse bestärken die Hypothese der Existenz einer borealen bis subpolaren Lebensgemeinschaft von Brackwasser-Plathelminthen mit circumpolarer Verbreitung. Die betreffenden Populationen in Europa, Alaska und Kanada können entweder über den Nordatlantik oder über die Sibirische Polarküste miteinander in Kontakt stehen.

Abbreviations in the figures

ac	atrium commune
afp	acessory female genital pore
b	bursa
cg	cement glands
cop	copulatory bulb
dgi	ductus genito-intestinalis
fgc	female genital canal
fgp	female genital pore
ge	germary
go	glandular organ
gvd	germo-vitello-duct
i	intestine
mgc	male genital canal
mgp	male genital pore
od	oviduct
pg	prostatic glands
pv	prostatic vesicle
rs	receptaculum seminis
sg	shell glands
st	stylet
syn	syncytial tissue
te	testis
ut	uterus
vi	vitellary
vp	vaginal pore
vs	vesicula seminalis

References

Armonies, W. (1987): Freilebende Plathelminthen in supralitoralen Salzwiesen der Nordsee: Ökologie einer borealen Brackwasser-Lebensgemeinschaft. Microfauna Marina 3, 81–156.

Armonies, W. & M. Hellwig (1987): Neue Plathelminthes aus dem Brackwasser der Insel Sylt (Nordsee). Microfauna Marina 3, 249–260.

Ax, P. (1951): Die Turbellarien des Eulitorals der Kieler Bucht. Zool. Jb. Syst. 80, 277–378.

Ax, P. (1956 a): Les Turbellariés des Étangs côtiers du littoral Méditerranéen de la France méridionale. Vie Milieu Suppl. 5, 1–215.

Ax, P. (1956 b): Monographie der Otoplanidae (Turbellaria). Akad. Wiss. Lit. Mainz, Abh. Math.-Naturw. Klasse, Jahrgang 1955, Nr. 13, 1–298.

Ax, P. (1971): Zur Systematik und Phylogenie der Trigonostominae (Turbellaria, Neorhabdocoela). Mikrofauna Meeresboden 4, 1–84.

Ax, P. & W. Armonies (1987): Amphiatlantic identities in the composition of the boreal brackish water community of Plathelminthes. A comparison between the Canadian and European Atlantic coast. Microfauna Marina 3, 7–80.

Ax, P. & R. Ax (1967): Turbellaria Proseriata von der Pazifikküste der USA (Washington). I. Otoplanidae. Z. Morph. Tiere 61, 215–254.

Ax, P. & R. Ax (1970): Das Verteilungsprinzip des subterranen Psammon am Übergang Meer – Süßwasser. Mikrofauna Meeresboden 1, 1–51.

Ax, P., Ax, R. & U. Ehlers (1979): First record of a free-living dalyellioid turbellarian from the Pacific: *Balgetia pacifica* nov. spec. Helgoländer wiss. Meeresunters. 32, 359–364.

Ax, P. & B. Sopott-Ehlers (1979): Turbellaria Proseriata von der Pazifikküste der USA (Washington). II. Coelogynoporidae. Zool. Scr. 8, 25–35.

Blüthgen, J. (1980): Allgemeine Klimageographie, 3rd ed., revised by W. Weischet. Berlin, New York: de Gruyter, 887 pp.

Dörjes, J. (1968): Die Acoela (Turbellaria) der Deutschen Nordseeküste und ein neues System der Ordnung. Z. zool. Syst. Evolutionsforsch. 6, 56–452.

Ehlers, U. (1974): Interstitielle Typhloplanoida (Turbellaria) aus dem Litoral der Nordseeinsel Sylt. Mikrofauna Meeresboden 49, 1–102.

Ehlers, U. (1980): Interstitial Typhloplanoida (Turbellaria) from the area of Roscoff. Cah. Biol. Marine 21, 155–167.

Ehlers, U. (1990): On the morphology and amphiatlantic distribution of *Jensenia angulata* (Jensen, 1878) (Dalyelliidae, Plathelminthes). Microfauna Marina 6, 111–119.

Ehlers, U. & B. Sopott-Ehlers (1989): Drei neue Rhabdocoela (Plathelminthes) von der französischen Atlantikküste. Microfauna Marina 5, 207–218.

Fenchel, T. & B.-O. Jansson (1966): On the vertical distribution of the microfauna in the sediments of a brackish-water beach. Ophelia 3, 161–177.

Hartog, C. Den (1964): Typologie des Brackwassers. Helgoländer wiss. Meeresunters. 10, 377–390.

Hartog, C. Den (1965): A preliminary revision of the *Proxenetes* group (Trigonostomidae, Turbellaria). IV & V. Proc. Koninkl. Nederl. Akad. Wetensch. C 68, 98–120.

Hartog, C. Den (1977): Turbellaria from intertidal flats and salt-marshes in the estuaries of the south-western part of the Netherlands. Hydrobiologia **52**, 29–32.

Hellwig, M. (1987): Ökologie freilebender Plathelminthen im Grenzraum Watt – Salzwiese lenitischer Gezeitenküsten. Microfauna Marina **3**, 157–248.

Holmquist, C. & T. G. Karling (1972): Two new species of interstitial marine triclads from the North American Pacific coast, with comments on evolutionary trends and systematics in Tricladida (Turbellaria). Zool. Scr. **1**, 175–184.

Jansson, B.-O. (1968): Quantitative and experimental studies of the interstitial fauna in four Swedish sandy beaches. Ophelia **5**, 1–71.

Karling, T. G. (1943): Studien an *Halammovortex nigrifrons* (Karling) (Turbellaria Neorhabdocoela). Acta Zool. Fenn. **37**, 1–23.

Karling, T. G. (1947): Studien über Kalyptorhynchia (Turbellaria). I. Die Familien Placorhynchidae und Gnathorhynchidae. Acta Zool. Fenn. **50**, 1–65.

Karling, T. G. (1958): Zur Kenntnis der Gattung *Coelogynopora* Steinböck (Turbellaria Proseriata). Ark. Zoologi **11**, 559–567.

Karling, T. G. (1962 a): Marine Turbellaria from the Pacific coast of North America I. Plagiostomidae. Ark. Zoologi **15**, 113–141.

Karling, T. G. (1962 b): Marine Turbellaria from the Pacific coast of North America II. Pseudostomidae and Cylindrostomidae. Ark. Zoologi **15**, 181–209.

Karling, T. G. (1963): Die Turbellarien Ostfennoskandiens V. Neorhabdocoela 3. Kalyptorhynchia. Fauna Fennica **17**, 1–59.

Karling, T. G. (1964): Marine Turbellaria from the Pacific coast of North America III. Otoplanidae. Ark. Zoologi **16**, 527–541.

Karling, T. G. (1966): Marine Turbellaria from the Pacific Coast of North America IV. Coelogynoporidae and Monocelididae. Ark. Zoologi **18**, 493–528.

Karling, T. G. (1967): On the genus *Promesostoma* (Turbellaria), with descriptions of four new species from Scandinavia and California. Sarsia **29**, 257–268.

Karling, T. G. (1973): Anatomy and Taxonomy of a new otoplanid (Turbellaria, Proseriata) from South Georgia. Mikrofauna Meeresboden **16**, 1–11.

Karling, T. G. (1974): Turbellarian fauna of the Baltic proper. Identification, ecology and biogeography. Fauna Fennica **27**, 1–101.

Karling, T. G. (1977): Taxonomy, phylogeny and biogeography of the genus *Austrorhynchus* Karling (Turbellaria, Polycystididae). Mikrofauna Meeresboden **61**, 153–165.

Karling, T. G. (1980): Revision of Koinocystididae (Turbellaria). Zool. Scr. **9**, 241–269.

Karling, T. G. (1982): Anatomy and Taxonomy of *Phonorhynchus* Graff (Turbellaria), with special reference to *P. helgolandicus* (Mecznikow). Zool. Scr. **11**, 165–171.

Karling, T. G. (1983): Structural and systematic studies on Turbellaria Schizorhynchia (Platyhelminthes). Zool. Scr. **12**, 77–89.

Karling, T. G. (1985): Revision of Byrsophlebidae (Turbellaria Typhloplanoida). Ann. Zool. Fennici **22**, 105–116.

Karling, T. G. (1986): Free-living marine Rhabdocoela (Platyhelminthes) from the N.American Pacific coast. With remarks on species from other areas. Zool. Scr. **15**, 201–219.

Karling, T. G. (1989): New taxa of Kalyptorhynchia (Platyhelminthes) from the N.American Pacific coast. Zool. Scr. **18**, 19–32.

Karling, T. G., V. Mack-Fira & J. Dörjes (1972): First report of marine microturbellarians from Hawaii. Zool. Scr. **1**, 251–269.

Karling, T. G. & E. R. Schockaert (1977): Anatomy and systematics of some Polycystididae (Turbellaria, Kalyptorhynchia) from the Pacific and S. Atlantic. Zool. Scr. **6**, 5–19.

Kotikova, E. A. & B. I. Joffe (1988): On the nervous system of the dalyellioid turbellarians. Fortschr. Zoologie **36**, 191–194.

Kozloff, E. N. (1987): Marine invertebrates of the Pacific Northwest. Chapter 5: Phyla Platyhelminthes, Gnathostomulida (pp. 84–93). University of Washington Press, Seattle, 511 pp.

Luther, A. (1921): Untersuchungen an rhabdocoelen Turbellarien. Acta Soc. Fauna Flora Fennica **48**, 1–59.

Luther, A. (1946): Untersuchungen an rhabdocoelen Turbellarien V. Ueber einige Typhloplaniden. Acta zool. Fenn. **46**, 1–56.

Luther, A. (1947): Untersuchungen an rhabdocoelen Turbellarien VI. Macrostomiden aus Finnland. Acta zool. Fenn. **49**, 1–40.

Luther, A. (1948): Untersuchungen an rhabdocoelen Turbellarien VII. Ueber einige marine Dalyellioida VIII. Beiträge zur Kenntnis der Typhloplanoida. Acta zool. Fenn. **55**, 1–122.

Luther, A. (1955): Die Dalyelliiden (Turbellaria Neorhabdocoela). Eine Monographie. Acta Zool. Fennica **87**, 1–337.

Luther, A. (1960): Die Turbellarien Ostfennoskandiens I. Acoela, Catenulida, Macrostomida, Lecithoepitheliata, Prolecithophora und Proseriata. Fauna Fennica **1**, 1–95.

Luther, A. (1962): Die Turbellarien Ostfennoskandiens III. Neorhabdocoela 1. Dalyellioida, Typhloplanoida: Byrsophlebidae und Trigonostomidae. Fauna Fennica **12**, 1–71.

Nasonov, N. (1932): Zur Morphologie der Turbellaria Rhabdocoelida des japanischen Meeres. Akad. d. Wiss. CCCP 1932, 65–113.

Reise, K. (1988): Plathelminth diversity in littoral sediments around the island of Sylt in the North Sea. Fortschr. Zool. **36**, 469–480.

Reisinger, E. (1932): Turbellaria. In: Nordisches Plankton Teil Zool. **10**, 43–56.

Remane, A. (1969): Wie erkennt man eine genuine Brackwasserart? Limnologica (Berlin) **7**, 9–21.

Rixen, J.-U. (1961): Kleinturbellarien aus dem Litoral der Binnengewässer Schleswig-Holsteins. Arch. Hydrobiol. **57**, 464–538.

Schockaert, E. R. & T. G. Karling (1970): Three new anatomically remarkable Turbellaria Eukalyptorhynchia from the North American Pacific coast. Arkiv Zoologi **23**, 237–253.

Sheremetevskij, A. M. (1977): Effect of some abiotic factors of environment on the distribution of littoral meiobenthos in the Laptev Sea and Novosibirsk islands. Gidrobiol. Zh. **13**, 63–70 (in Russian).

Sopott-Ehlers, B. (1976): Interstitielle Macrostomida und Proseriata (Turbellaria) von der französischen Atlantikküste und den Kanarischen Inseln. Mikrofauna Meeresboden **60**, 1–35.

Sopott-Ehlers, B. & P. Ax (1985): Proseriata (Plathelminthes) von der Pazifikküste der USA (Washington). III. Monocelididae. Microfauna Marina **2**, 331–346.

Sterrer, W. (1973): Plate tectonics as a mechanism for dispersal and speciation in interstitial sand fauna. Neth. J. Sea Res. **7**, 200–222.

Tajika, K.-I. (1981): Marine Turbellarien aus Hokkaido, Japan V. Coelogynoporidae (Proseriata). Jour. Fac. Sci. Hokkaido Univ. Ser. VI, Zool. **22** (4), 451–473.

Tajika, K.-I. (1982): Marine Turbellarien aus Hokkaido, Japan IX. Monocelididae (Proseriata). Bull. Lib. Arts & Sci. Coerse, Sch. Med. Nikon Univ. **10**, 10–34.

Tajika, K.-I. (1983): Zwei neue interstitielle Turbellarien der Gattung *Archotoplana* (Proseriata, Otoplanidae) aus Hokkaido, Japan. J. Fac. Sci. Hokkaido Univ. (IV-Zool.), **23**, 179–194.

Tulp, A. S. (1974): Turbellaria van Ameland. Levende natuur **77**, 62–69.

Westheide, W. (1977): The geographical distribution of interstitial polychaetes. Mikrofauna Meeresboden **61**, 287–302.

Prof. Dr. Peter Ax
II. Zoologisches Institut und Museum der Universität Göttingen
Berliner Straße 28, D-3400 Göttingen

and

Dr. Werner Armonies
Biologische Anstalt Helgoland,
Wattenmeerstation Sylt,
D-2282 List