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NEW AND KNOWN NEMERTODERMATIDA (PLATYHELMINTHES-ACOELOMORPHA) – A REVISION –

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Abstract. Described in 1930-31 by Steinböck who considered it the most primitive bilaterian, the turbellarian genus *Nemertoderma* is known for its role in platyhelminth phylogeny as much as for its muddled taxonomy. On the basis of material collected in the Mediterranean, Atlantic and Pacific Oceans since 1964 this paper re-diagnoses the known 4 genera and 7 species (*Nemertoderma bathycola* Steinböck, 1930-31; *N. westbladi* Steinböck, 1938; *N. psammicola* Sterrer, 1970 (syn. *N. rubra* Faubel, 1976); *Meara stichopi* Westblad, 1949; *Meara* sp. (see SMITH *et al.*, 1994); *Nemertinoides elongatus* Riser, 1987; and *Flagellophora apelti* Faubel & Dörjes, 1978), describes one new genus with 2 new species (*Ascoparia neglecta* n. g., n. sp. and *A. secunda* n. sp.), and provides observations from living material on morphological variability, body size *vs.* reproductive state, statocyst structure and statolith variability, and sperm morphology and dimorphism. The paper concludes with diagnoses for the known taxa of Nemertodermatida, including the new family Ascopariidae.

Key words: Platyhelminthes, free-living, marine; systematics, new species.

INTRODUCTION

In 1930-31 Otto STEINBÖCK described *Nemertoderma bathycola* from a single tiny worm which he and Erich Reisinger had dredged from a muddy bottom, at 300-400 m depth, off Greenland. *Nemertoderma* caused a small sensation, not only because Steinböck, a meticulous observer, was also an assertive character (who liked to express himself double-spaced, with exclamation marks added) but because *Nemertoderma* was indeed unusual. Steinböck insisted that he had hit upon the ur-acoel, the «mother of all turbellarians»: with a novel, two-stoned statocyst, an unusually thick and gland-rich epidermis, a peripheral nervous system, and a mixed, lacunar gonad without accessory organs. A heated argument ensued when, in 1937, Einar WESTBLAD described a similar worm from the Swedish west coast suggesting, not unreasonably, that STEINBÖCK's specimen had been immature, and adding that his «speculations... seemed to originate to an alarming degree from preconceived notions.» WESTBLAD left it open whether his and STEINBÖCK's were the same species, and the assignation of the name *N. westbladi* by

STEINBÖCK in his 1938 reply was not generally accepted. WESTBLAD kept the heat on by describing, in 1949, *Meara stichopi*, endocommensal of a holothurian, and clearly related to *Nemertoderma*. The initial nomenclatural muddle was exacerbated by subsequent authors who variously referred to «*Nemertoderma*, Westblad's form», «North Sea form», «Skagerrak form» and «Adriatic form» (RIEDL, 1960), «species I & II» (STERRER, 1966), and «species A, B, C & D» (TYLER & RIEGER, 1975, 1977). Additional taxa were described by STERRER (1970: *Nemertoderma psammicola*), FAUBEL (1976: *Nemertoderma rubra*), FAUBEL & DÖRJES (1978: *Flagellophora apelti*), and RISER (1987: *Nemertinoides elongatus*).

My observations of living material of Nemertodermatida, gathered since 1964 in the Mediterranean, Atlantic, and Pacific Ocean, include all described species as well as new ones (Table I). The purpose of this paper is to (1) clarify the species problem in *Nemertoderma*, largely on the basis of sparse but consistent finds over more than 30 years, (2) provide observations on morphological variability, body size *vs.* reproductive state, statocyst structure and statolith variability, and sperm morphology and dimorphism, (3) describe a new genus with two new species, and (4) present an analysis and diagnoses of the currently known taxa, including the erection of a new family. Throughout the paper I emphasize features observable in living specimens, and consider micro-anatomical and ultrastructural features only where necessary.

There are a number of reasons why species identification in Nemertodermatida is problematic. First, with the exception of *Meara stichopi* and *Nemertoderma westbladi*, most species are known by only few specimens, which are often only partially mature, or fragments (as especially in the filiform species *Nemertoderma psammicola* and *Nemertinoides elongatus*). In addition, characters seem to vary widely even within a population. This applies to size in relation to sexual maturity (*e.g.*, *N. westbladi*), statolith numbers (most species), colour (*e.g.*, *N. psammicola*), presence or absence of epidermal glands and rhabdoids (*e.g.*, *M. stichopi*), differences between auto- and allosperm, etc. On the other hand, there is a high degree of similarity, even in details such as sperm dimensions, between specimens from geographically distant locations, *e.g.*, *N. psammicola* from Sweden, Florida and New Zealand. Finally, several species may co-occur, as for instance *N. westbladi* and *Flagellophora apelti* (the latter quite unexpectedly) in a mud sample from Kristineberg, or *N. psammicola*, *N. elongatus* and *Ascoparia neglecta* in Florida. The result is that each specimen may present a slightly different aspect, which aggravates the diagnosing of species that lack hard, measurable characters in the first place.

In view of these difficulties I have chosen to define few but broadly distributed species, all the while emphasizing differences that may eventually lead to their splitting. At this time I consider *M. stichopi, N. westbladi* and *A. neglecta* to be reasonably well characterized whereas *N. bathycola* is still insufficiently contrasted against *N. westbladi*, and *N. psammicola*. The species *F. apelti, N. elongatus* and *Ascoparia secunda* may turn out to be clusters of sibling species.

TABLE 1

Date	*Sample number*	*Country/ ocean*	*Region*	*Locality detail*	*Depth*	*Substrate*	*Species (of specimens)*
10/13/1964	461-64 (E3)	Norway	Bergen	Raunefjord	250 m	mud	*M. stichopi* (20)
10/13/1964	462-64 (E4)	Norway	Bergen	Kors Fjord	690 m	mud	*N. bathycola* (1)
10/17/1964	467-64 (E6)	Norway	Bergen	Fana Fjord, NW of Korsnes	260 m	mud	*N. bathycola* (3)
10/17/1964	468-64 (E7)	Norway	Bergen	Raune Fjord, off Sletta	120 m	mud	*N. bathycola* (7)
10/29/1964	488-64 (E12)	Norway	Bergen	off Steinneset	620 m	mud	*N. westbladi (1)*
11/5/1964	K64-17	Sweden	Kristineberg	Essvik	30 m	mud	*N. westbladi* (115)
11/8/1964	K64-18	Sweden	Kristineberg	Klubban beach	0.5-2 m	fine sand	*N. psammicola* (11)
3/29/1965	R65-14	Adriatic	Rovinj	Punta Croce	6 m	clean coarse sand	*N. elongatus* (5), *F. apelti* (7)
4/2/1965	R65-19	Adriatic	Rovinj	Punta Croce	5 m	medium sand	*N. psammicola* (1)
5/25/1965	V (Rieger coll.)	Adriatic	Venice	Lido at Alberoni	1 m	fine sand	*N. psammicola* (5)
Jul-Oct 65	K65	Sweden	Kristineberg	Klubban beach	1-5 m	fine sand	*N. psammicola* (5)
Jul-Oct 65	K65	Sweden	Kristineberg	Essvik	30 m	mud	*N. westbladi* (2), *F. apelti* (1)
5/8/1966	R66 (Rieger coll.)	Adriatic	Rovinj	off train station	3-4 m	coarse sand with detritus	*N. psammicola* (1)
8/25/1966	P66-D	N. Ireland	Portaferry			sand	*N. psammicola* (1)
8/26/1967	R67-17	Adriatic	Rovinj	Val di Cuvi	3 m	coarse sand	*F. apelti* (1)
9/19/1967	F67-44	Mediterranean	Marina di Carrara	in harbour	3-4 m	sand	*N. psammicola* (1)
9/24/1967	F67-52	Mediterranean	Fiascherino	in harbour	1-2 m	sand	*N. westbladi* (2)
9/25/1967	F67-53	Mediterranean	Portovenere	in mid-bay	5-6 m	sand	*N. psammicola* (2)
11/25/1968	NC76 (E 48-68)	off US E coast	34°45.0'N, 75°45.0'W		41 m	clean sand	*F. apelti* (4), *A.secunda* (1)
11/27/1968	NC81 (E48-68)	off US E coast	34°28.6'N, 76°43.4'W		20 m	sand	*A. secunda* (1)
12/29/1968	FL15	Florida	Big Pine Key	patch reef	3 m	fine sand	*N. psammicola* (1), *N. elongatus*(2), *A. neglecta* (4)
3/18/1969	Eastward 4	off US E coast	off Beaufort, NC		130 m	sand	*N. westbladi* (1)
7/19/1969	D69-1	Adriatic	Dubrovnik	offshore	340 m	mud	*N. westbladi* (1)
7/25/1969	D69-8	Adriatic	Dubrovnik	offshore	400 m	mud	*N. westbladi* (1)
7/20/1969	D69-2	Adriatic	Dubrovnik	Lapad	5 m	sand between *Zostera*	*N. psammicola* (1)
9/1/1969	B66-23	W Mediterranean	Banyuls-sur-Mer	Cap Ouilleret	20 m	medium sand	*N. westbladi* (1)
2/13/1973		Bermuda	Castle Harbour	Castle Roads	8 m	clean coarse sand	*F. apelti* (2)
5/1/1974	Eastward 24303-3D	off US E coast	34°07.3N, 75°57.7W)	(cf. Coull et al. 1977)	400 m	fine sand	*F. apelti* (1)
7/2/1986	NZ 5	New Zealand	N Island	N of Leigh	upper intertidal	fine, clean sand	*N. psammicola* (1)
2/16/1996	Can 1	Gran Canaria	Las Palmas	Playa de Las Canteras	2-3 m	fine sand with *Cymodocea*	*N. psammicola* (1)
2/17/1996	Can 1	Gran Canaria	Puerto de San Nicolas	harbour	2 m	fine sand	*F. apelti* (1)
2/20/1996	Can 9	Gran Canaria	Las Palmas	Playa de Las Canteras	2-3 m	fine sand with *Cymodocea*	*N. psammicola* (1)
2/21/1996	Can 10	Gran Canaria	Arinaga	inside harbour	4-5 m	fine sand with *Cymodocea*	*N. psammicola* (1
8/13/1996	W7	Queensland	Stradbroke Island	sand flat by lab	intertidal	fine sand	*N. psammicola* (2)
8/27/1996	LZ9	Queensland	Lizard Island	Watson's Bay, S end	intertidal	fine sand with fine sea grass	*N. psammicola* (1)
9/25/1996	PNG6	Papua New Guinea	Madang	Wongat Island	8 m	*Halimeda* debris	*N. psammicola* (7), *Ascoparia sp.* (2)

MATERIAL AND METHODS

Sediment samples were taken in the intertidal by means of a spade, in the shallow subtidal by snorkeling or SCUBA, and by various dredges (Mortensen, Ockelmann) in deeper waters. Animals were extracted from sand samples with the magnesium chloride method (STERRER, 1971). Mud samples from deep bottoms, kept in tubs at 4° C in a dark room, were superficially stirred up every few days, and the suspension was filtered through a 100-200 μm plankton net mounted on a plexiglass ring (RIEGER & STERRER, 1968). The filter was then placed in a petri dish with chilled seawater from where specimens were pipetted out under a dissecting microscope. Individual specimens were photographed, and drawn and measured by means of a drawing tube. Wherever several specimens were measured, a range is given, in addition to the mean (in brackets). A relative scale is used for body length and positions; it takes the total body length of a specimen as 100 units (U), U 0 being at the anterior tip of the animal (RIEGER & STERRER, 1968). A «body index» (length divided by width) is used as an indicator of body shape (*i.e.*, the greater the body index, the more filiform the animal). Mean, relative scale (U) and body index are expressed with one or two decimals, not only to distinguish them from individual measurements but also to express the often surprisingly high constancy of morphometric characters in these soft-bodied worms. I use the term «autosperm» for «autochthonous sperm», *i.e.* sperm found in the specimen which has produced it, and «allosperm» for «allochthonous sperm», *i.e.*, sperm found in a specimen that has not produced it, *e.g.*, a functional female.

The long time period over which these observations were gathered (and exchanged with colleagues) is invoked as an excuse for the loss of many of the preserved specimens and some photo negatives, which means that in some cases (Figs. 10.1-3, 15, 16) original prints must substitute for type material.

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TAXONOMIC PART

Meara stichopi (Bock) Westblad, 1949

(Figs 1.1-7, 2.1-5)

Meara stichopi (BOCK); WESTBLAD, 1949: 43-57, Figs 1-6, plates I-III
Meara stichopi; HENDELBERG, 1977: Figs 1-4
Meara stichopi; HENDELBERG, 1983: Fig. 2
Meara stichopi; SMITH *et al.* 1994: (rhabdoids)
Meara stichopi; LUNDIN & HENDELBERG, 1995: Figs 1-6
Meara stichopi; LUNDIN & HENDELBERG, 1996: Figs 1A-D

Meara stichopi; LUNDIN (in press a): Figs 1A-C'
Meara stichopi; LUNDIN & HENDELBERG (in press): spermiogenesis.

New material. About 20 specimens in squeeze preparation.

Locality. Espegrend, near Bergen, Norway. In the holothurian *Parastichopus tremulus* (Gunnerus) collected 13 Oct. 1964 in Raunefjord (250 m).

Organization and behaviour. The three adult specimens (Figs 1.1, 2.1) ranged from 1700 to 2100 µm (mean 1916.6 µm) in length and 450 to 640 µm (570.0 µm) in width at U 27.6 (body index 3.40). The statocyst (Figs 1.2, 2.2) is located at U 2.7, only 55 µm behind the anterior tip of the animal. The statocyst (Figs 1.2, 2.2) is elliptical, somewhat more convex anteriorly than posteriorly, 20-21 (20.5) µm long and 32-35 (33.5) µm wide. It is bisected by a septum that projects at least halfway down from the dorsal wall, incompletely dividing the statocyst into a left and a right chamber. Each statolith is 12-13 (12.5) µm in diameter, near-spherical but dorsally slightly flattened, and capped by a 4 µm thick cell (the lithocyte) that appears as if composed of regular spherical blisters of about 1 µm diameter. The statoliths normally sit on the bottom of the statocyst, with the blister cap upward, as if buoyed by it. If the animal is slowly rotated around its longitudinal axes the statoliths do not follow suit but always come to rest at the deepest part of the statocyst, blister cap on top.

Of 20 specimens checked, only 5 had bundles of 3-6 needle-shaped rhabdoids of 7-10 µm length (Fig. 1.6) that were more or less evenly distributed throughout the epidermis; the remainder had no rhabdoids at all.

Of 12 specimens of *Parastichopus tremulus* investigated, 7 contained from 1 to 40 individuals of *M. stichopi,* most of them in the foregut immediately behind the mouth, only rarely in the body cavity. When not actively moving, animals are slightly bent, with an anterior dorsal hump (Fig. 1.7). Specimens could be kept alive in a refrigerator in *Parastichopus* body fluid or seawater for up to 6 days. Maintained this way, mature specimens regularly laid eggs; they first bend into a dorsally-convex shape, then protrude the circum-oral body surface (like puckered lips) to disgorge, via the mouth, an egg of about 120 µm diameter.

Digestive tract. One specimen was seen with a nematode in its gut.

Reproductive system. The follicular testes occupy most of the preoral part of the body (Figs 1.1, 2.1, 2.3, 2.4). The male copulatory organ (mco) opens terminally to slightly supraterminally. Autosperm (Figs 1.3-5, 2.5) is filiform, about 45-60 µm long; in phase contrast a division into head, middle piece and tail is not obvious. Some sperm were coiled, corkscrew-fashion, over half of their length; none showed any movement. Allosperm was not observed.

The ovary (Figs 1.1, 2.1, 2.4) occupies most of the postoral part of the body.

Discussion. The fact that statoliths, buoyed by their lithocyte cap, always orient themselves vertically explains WESTBLAD's puzzling observation that in histological sections of *N. westbladi* (WESTBLAD, 1937: 67, and fig. 7b) the two statoliths, like a pair of eyes, invariably pointed in the same direction. Bundled rhabdoids, which SMITH *et al.* (1994) suggest «are histochemically and ultrastructurally similar to true rhabdites», were also found by LUNDIN & HENDELBERG (1995); their spotty occurrence (in only 25% of specimens) may explain Westblad's failure to find «mucous cells with formed secretion, *e.g.*, rhabdite glands». I did not notice «pulsatile bodies» (LUNDIN & HENDELBERG, 1996). My observation of oviposition via the mouth corroborates WESTBLAD's (1949) statement that the «matured eggs are lying in the innermost part of the ovary, near the intestine», and might be «emptying by the intestine». K. LUNDIN (pers. comm.) confirms WESTBLAD's finding that masses of spermatozoids, presumably from copulation, are «in all tissues of the postoral part of the body, in the epithelium as well as in the parenchyma, particularly abundant in the neighbourhood of the ovocytes». HENDELBERG (1977) gives a sketch and TEM micrographs of what is presumably autosperm, confirming its single, 9+2 axoneme which is partly surrounded by helically coiled mitochondrial derivatives; his measurements (Fig. 1) are about 20 µm for the head, 35 µm for the middle piece, and 5-10 µm for the tail. We do not know yet whether allosperm differs from autosperm in this species (see LUNDIN & HENDELBERG, in press).

Meara sp.

Meara sp.; SMITH *et al.* 1994 (rhabdoids)
Meara sp.; LUNDIN 1997: Fig. 1D
Meara sp.; LUNDIN (in press a): Fig. 1D' (in the «foregut» of *Holothuria lentigenosa enodis* Pawson & Miller, 1979, collected near Cockburn Town, San Salvador, Bahamas, at approximately 330 m depth).

SMITH *et al.* (1994) mention *Meara* sp. in addition to *M. stichopi*. HENDELBERG (pers. comm.) says that it is not clear yet if they both belong to the same species. Their occurrence in different hosts and the symbiosis with bacteria of similar ultrastructure but of quite different size (LUNDIN, in press a) makes it seem probable that we are dealing with two species. Three specimens of *M.* sp. from the Bahamas all had rhabdoids though much more densely occurring than in *M. stichopi* (LUNDIN, 1997).

Nemertinoides elongatus Riser, 1987

(Figs 1.8-17, 3.1-4, 4.1-26)

N. sp.; SMITH & TYLER, 1985: Figs 8.7, 8.8
Nemertinoides elongatus; RISER, 1987 (NW Atlantic)
Nemertinoides elongatus; SMITH *et al.* 1994 (serous glands).

New material: 7 specimens in squeeze preparation.

Localities: Adriatic and NW Atlantic.

Organization and behaviour. Colorless to yellowish or reddish. At 4200 µm length and 300 µm width at U 42.85 (body index 14), my only intact adult specimen is below the range of 6-10 mm given by RISER (1987); all other specimens were anterior fragments. A head region (Figs 1.8, 3.1, 3.4) is often set off against the rest of the body by a shallow restriction in the region of the statocyst. An abundance of bottle-shaped mucous glands make the animal rather opaque in transmitted light (Fig. 3.4). Bottle glands are rounded and 10-12 µm in diameter in the head (Fig. 1.11), but more elongated and larger (17 µm) in the posterior body region (Fig. 1.12). A different, rather hooklet-shaped type of epidermal gland of up to 23 µm length may also be present, especially in the posterior body region (Fig. 1.14). A pair of ropey glandular strands filled with tiny rhammoids, 1.5-3 µm in length (Fig. 1.9), originate in front of the pharynx and open close to the anterior tip of the animal. Located about 100-200 µm behind the anterior tip of the body, the statocyst (Figs 1.10, 3.2, 3.3) is 15-25 (20.14) µm long and 17-30 (25.00) µm wide; it contains two statoliths of 10-12 (10.5) µm diameter, which have a lithocyte cap in blisters. Intact animals glide and writhe animatedly, seemingly tying themselves into knots.

Digestive tract. The mouth is located at about U 25. The post-oral part of the gut contains numerous granular club cells of 10-15 µm diameter (Fig. 1.13).

Reproductive system. The only intact adult had paired testes and vasa deferentia, and a dorsal, ciliated male pore at about U 42 (Fig. 1.8). Autosperm (or possibly a late spermatid, Fig. 1.16) consisted of 46 µm long head with a spiral tip and oblique striation, a 48 µm long opaque middle piece, and a 45 µm long tail. Figs 1.15, 4.1 and 4.2 show a late spermiogenesis stage consisting of a tubular part whose posterior portion is surrounded by spirally-arranged granular precipitates, and a tail. Allosperm (Figs 1.17, 4.3, 4.4) is thinner but has a pronounced head spiral of 40 µm length, and a middle piece of 29 µm. Single allosperm are found throughout the body, even in the head and between testes follicles.

Discussion. My only intact adult (from the Adriatic) agrees well enough with RISER's (1987) original description to be assigned to this species, which cannot be said for several other specimens (*e.g.*, Fig. 3.4), many of which were fragments. *N. elongatus* differs from *N. psammicola* primarily in its larger, plumper body and head constriction; much smaller rhammoids (2 µm vs. 11.5 µm), and the reproductive system, particularly the far forward, dorsal position of the male copulatory organ, the position of the ovary posterior to the male reproductive system, and the much larger sperm.

***Nemertoderma psammicola* Sterrer, 1970**

(Figs 5.1-26, 6.1-3, 7.1-4)

Nemertoderma sp. I; STERRER, 1966: Fig. 1, 3 (North Sea and Adriatic)
Nemertoderma psammicola; STERRER, 1970 (in Riedl 1970: 197, diagnosis; and plate 58) (Adriatic)
?*Nemertoderma* sp.; TYLER, 1976: 57, Fig. 30A (Eilat, Red Sea)
Nemertoderma rubra; FAUBEL, 1976: 2730, Fig. 5 (Sylt, NE Atlantic)
Nemertoderma sp. B; TYLER & RIEGER, 1977: Fig. 1A, 4A, 5A, C-E (N. Carolina, NW Atlantic)
Nemertoderma rubra; BUSH, 1981: 88, Fig. 184 (key)
?*Nemertoderma* sp.; RISER, 1984: 242, 246 (Christchurch, New Zealand)
Nemertoderma sp. B; EHLERS, 1992: Figs 1-4 (N. Carolina, NW Atlantic).

New material: About 35 specimens in squeeze preparation.

Localities: Mediterranean (Rovinj, Venice, Dubrovnik, Marina di Carrara, Porto Venere), Atlantic (Canary Islands, N. Ireland, Sweden, Florida), Pacific (New Zealand, Australia and Papua New Guinea).

Organization and behaviour. Adults in male and female maturity (Figs 5.1, 6.2) to 3100 µm long and 160 µm wide at U 47 (body index 19.37); adults with male gonads only

(Figs 1.3-4, 2.1) are usually smaller. The mean values for 6 adults from Kristineberg and Leigh (New Zealand) were 1838.33 µm by 141.66 µm at U 63.07 (body index 12.83). The anterior part of the body, to somewhat behind the statocyst, is medio-dorsally flattened (Fig. 5.2). Most Swedish, and many Adriatic specimens were distinguished by a salmon- or crimson-coloured stripe that extends from behind the statocyst to about the pharynx, where it turns to brownish and blends into outline of the intestine. Canaries specimens were faintly red, whereas most others were greyish or brownish. In many but not all specimens the skin contains bottle-shaped mucous glands, to 12 µm in diameter (Fig. 5.7); in the New Zealand specimen I also noted additional glands with a rod-shaped content in the caudal region (Fig. 5.8). A pair of rhammoid glands open frontally and extend posteriorly to about U 23, i.e., the region anterior to the mouth. Individual rhammoids are needle-shaped, 8-22 (11.5) µm long and 1 µm wide (Figs 5.5-6). The animal moves serpent-like. Many individuals encountered were anterior fragments.

Located at U 8.31, the statocyst is oval, 14.25 µm long and 20.75 µm wide (Figs 5.23-26, 6.3). Each of the two statoliths is spherical, 6-9 (7.28) µm in diameter, and covered dorsally with a lithocyte in blisters. The statocyst is not bisected by a septum but constricted by one or two shallow ridges. Statoliths normally rest at the bottom of the statocyst, and are held in upright position by the blister cap. A statocyst with only one statolith (Fig. 5.24) was found in 2 of 9 specimens from Kristineberg 1964 (22.2%), one of 12 from Kristineberg 1965 (8.3%), one of 7 specimens (14.3%) from Stradbroke, and one of 3 specimens (33%) from Lizard Island.

Digestive tract. Mouth ventrally, at U 37.8, opening into a shallow, ciliated pharynx bordered anteriorly by a horseshoe-shaped group of glands (Figs 5.1, 5.4).

Reproductive system. Testes paired, extending posteriorly from about U 45, not far behind the mouth, to about U 60 where they continue as a pair of vasa deferentia that merge just anterior to the male pore (Figs 5.1, 5.4). Located dorsally at U 93.4 the male pore (Fig. 5.20) is ciliated, and receives rod-shaped rhabdoids (Figs 5.21-22). Autosperm was recorded from Kristineberg (Figs 5.12, 7.3), New Zealand (Fig. 5.13) and Lizard Island specimens; it is composed of a 18-22 (17.6) µm long, apically slightly spiralized head, a 9-10 (9.7) µm long middle piece, and 16-22 (19.3) µm long tail. It appears that the axoneme runs through the entire length of the middle piece. In addition to this type of sperm, several Kristineberg specimens had also thinner, less regionalized and somewhat lumpy sperm (Fig. 5.14). Spermiogenesis stages, as observed in Kristineberg and Portaferry specimens, are shown in Figs 5.9-5.11 and 7.4.

Paired ovaries from about U 50 to U 70, with oocytes maturing posteriorly, reaching more than 100 µm in diameter (Fig. 5.1). There is no vagina or bursa. Numerous specimens, even juveniles, contained allosperm in the epidermis in all body regions, including the head (Fig. 7.1). Presumably resulting from hypodermal impregnation, such allosperm was found to be remarkably similar in specimens from all localities (Figs 5.16-19, 7.2). It is about 30 µm long, consisting of a strongly spiralized head 15-22 (18.9) µm long, with a central filament (Fig. 5.15), and a middle piece 10-16 (12.8) µm long; a tail is reduced or lacking. In living animals individual allosperm could be seen rotating around their axis and moving back and forth in what appeared to be short, preformed canals in or immediately underneath the epidermis.

Discussion. A diagnosis for this species, which I first mentioned (STERRER, 1966) as *Nemertoderma* sp. I, was given by me in RIEDL (1970) under the name *N. psammicola*. It is clearly identical, in all its features including the unusual red colouration, with *N. rubra* Faubel, 1976, which thus becomes a junior synonym. FAUBEL's (1976) description was based on specimens in male maturity only. Although my material contains but a few intact and fully mature specimens, it appears that this species is remarkably homogeneous throughout its global distribution range, particularly with regard to gross anatomy, and the size and proportions of body, statocyst, and auto- and allosperm. Variability between specimens, and possibly between geographically distant populations, is found in the colouration, and the presence and structure of glands. Male maturity seems to precede female maturity. The presence of allosperm throughout the body even of juveniles suggests that the latter may serve as the passive recipients in copulation, and then possibly store allosperm until they mature themselves. The different aspect of allosperm, and their movement in the host individual have yet to be explained.

Nemertoderma westbladi (Westblad) Steinböck, 1938

(Figs 8.1-5, 9.1-9)

Nemertoderma sp.; WESTBLAD, 1937: Drøbak (Norway), Sweden
N. westbladi; STEINBÖCK, 1938: p. 21 (species name)
N. «Nordseeform» (Norway and Sweden), *N.* «Skagerrakform» (Sweden), *N.* «Adriaform» (Adriatic); RIEDL, 1960: Fig. 1-7
N. sp.; KARLING, 1967: Figs 3-6
N. spec.; DÖRJES, 1968: 217-218, Figs 58-59 (Helgoland)
N. cf. *bathycola*; EHLERS, 1991: Figs 2, 3B (no locality given)
N. sp. D; TYLER & RIEGER, 1977: Figs 2, 7A-F (N. Carolina)
N. westbladi; LUNDIN, 1997: Fig. 3A (Kristineberg)
N. westbladi; LUNDIN (in press a): Fig. 3 (Kristineberg).

New material: About 125 specimens in squeeze preparation.

Localities: Atlantic (Sweden, N. Carolina), Mediterranean (Dubrovnik, Fiascherino, Banyuls).

Organization and behaviour. Very opaque in transmitted light, especially intestine and ovary, less so the epidermis, which creates a «halo» impression (Fig. 8.1-5). Epidermis with numerous mucous bottle glands (Fig. 9.8-9). Free-swimming animals are plump-sausage shaped (Fig. 8.1) or bottle-shaped (Fig. 8.4). The following phases can be distinguished in squeeze preparation: juvenile (without any reproductive structures), male (with copulatory organ and/or testes), female (with eggs), and hermaphrodite (both male and female organs present). My measurements of 107 specimens from the same sample (Kristineberg, Essvik, 30 m) confirm Westblad's observation that body size does not increase with maturity; on the contrary: 96 juveniles measured 240-950 (mean 539.12) µm in length and 140-550 (314.20) µm in width (body index 1.75) whereas 11 adults (Table 1) measured 360-750 (500.45) µm in length and 200-520 (311.80) µm in width (body index 1.65). The smallest male, also from a Kristineberg sample, was 245 µm long and 140 µm wide; the smallest female was 315 µm long and 200 µm wide. Similarly, Westblad (1937: 48) recorded 12 immature specimens with an average length of 600 µm and width of 400 µm, but 9 mature specimens with an average length of 400 µm and width of 250 µm. Beyond the fact, however, that sexually mature individuals are smaller on average than immature ones there is no correlation between male, female or hermaphrodite stages and body size, and thus no clear evidence for protandry or protogyny (Table 2).

TABLE 2

Nemertoderma westbladi. *Body length (in µm) of 11 mature specimens in relation to the presence of male copulatory organ, testes and eggs.*

specimen	length	male organ	testes	eggs
1	360	+		
2	410	+		+
3	410	+	+	
4	425	+	+	
5	430			+
6	440	+		+
7	450	+		
8	500	+	+	
9	590	+		+
10	740			+
11	750	+		+

The statocyst (Fig. 9.1-5) is located at U 14.25 and measures 18-24 (21.11) µm in length and 22-36 (27.22) µm in width. It normally contains two spherical statoliths of 8-14 (11.09) µm diameter, each covered with a «blister cap» (Fig. 9.1-2). The statocyst lumen is not bisected by a septum but slightly constricted by one or two shallow ridges along the sagittal plane of the animal. Of 112 specimens taken from the same sample (Kristineberg, Essvik, 30 m), 3 had only one stone (2.7%; Fig. 9.4), and one specimen had 3 (0.9%; Fig. 9.3). A specimen taken from the same locality but on a separate occasion contained 4 statoliths (Figs 8.5, 9.5). Statocysts with aberrant statolith numbers tend to be more spherical than the normal two-stoned ones, and statoliths may be smaller.

Reproductive system. A pair of globular testes is located in mid-body region, from which sperm bundles lead to a massive vesicula seminalis in front of the male copulatory organ, which opens at or above the posterior end of the animal (Fig. 8.5). Autosperm is filiform, 83-105 µm long, slightly spiralized only at the very tip, and not conspicuously divided into a head-middle piece of 67-75 µm length, and a tail of 55-62 µm length.

Specimens in male and female maturity (Fig. 8.4-5) and those in female maturity often contain more than one large egg in the posterior body region, sometimes up to 10. Allosperm (Fig. 9.6-7) was seen in only 2 specimens, both juveniles from Fiascherino. Located throughout the body, in or immediately under the epidermis and slowly rotating, allosperm is 40 µm long, of which the head takes up 30 µm, the middle piece (plus tail?) 10 µm. Strongly spiralized around a central filament, the head is very thin for the anterior 10 µm, then swells to a diameter of 2 µm posteriorly.

Discussion. My data support WESTBLAD's (1937: 69) conclusion that, because sexually mature individuals are not only smaller than immature ones but also seem to lack a functional mouth opening, animals stop feeding at a certain age and then draw on body substance for reproduction. The presence of allosperm in juveniles also confirms WESTBLAD's (1937: 82) supposition that animals may be inseminated, by subdermal impregnation, before they reach maturity. My statocyst data suggest that aberrant statolith numbers, as encountered by RIEDL (1960), are to be expected in large enough samples and cannot be used as a diagnostic character. Thanks to WESTBLAD's careful original description, *N. westbladi* is one of the best defined species in the order.

Nemertoderma bathycola Steinböck, 1930

(Fig. 10.1-3)

Nemertoderma bathycola; STEINBÖCK, 1930 (Greenland)
N. bathycola; STEINBÖCK, 1938 (discussion)
N. cf. *bathycola*; HENDELBERG, 1977 (Norway)
N. cf. *bathycola*; LUNDIN, 1997: Fig. 3B (Kristineberg, Sweden)
N. cf. *bathycola*; LUNDIN (in press a) (Kristineberg).

New material: 12 specimens in squeeze preparation.

Locality: Norway.

Organization and behaviour. Body length of adults (Fig. 10.1-3)is 260-400 (mean 330.0) µm, body width 35-130 (87.5) µm at U 55.0 (body index 4.88). Freeswimming animals may be even more slender than that (to a body index of 9). Specimens range widely in transparency, mostly due to abundance or absence of bottle-shaped mucous glands. Located at U 12.16, the statocyst is 11 µm long and 17 µm wide. Statoliths are 8 µm in diameter, with the lithocyte cap in blisters. Of 12 specimens, one (8%) had only a single statolith in an otherwise normal statocyst.

Digestive tract. One specimen contained a large prey turbellarian.

Reproductive system. Of 7 adults, 5 contained both a male organ and a mature egg, whereas two were in male phase only. The conical male copulatory organ, often with sperm bundles on its anterior end, is located at U 89.3 (Fig. 10.3), and opens slightly supraterminally. A single mature egg was found in five individuals; it may reach 120 µm in length, or 40% of the total body length (Fig. 10.1).

Discussion. The 12 Espegrend specimens differed from *N. westbladi* in the following: adults were considerably smaller on average (X=330.00 µm vs. X=500.45 µm), more fusiform and slender (body index 4.88 vs. 1.65), and more transparent. Significantly, adults had only one mature egg, all of which agrees with the description given by Steinböck (1930: 48, Fig. 1) for *N. bathycola.* This species also seems to prefer deeper bottoms, although it is not alone at such sites, since specimens with the characteristics of *N. westbladi* were also occasionally encountered at depths below 100 m. While I am reasonably sure that the Espegrend specimens do not belong to *N. westbladi*, and that at least some of them are conspecific with *N. bathycola*, they may well represent more than one species.

Flagellophora apelti Faubel & Dörjes, 1978
(Figs 11.1-14, 12.1-5, 13.1-4)

Nemertoderma sp. II; STERRER, 1966 (Adriatic)
Flagellophora apelti; FAUBEL & DÖRJES, 1978 (North Sea off Helgoland and Scotland)
Nemertoderma sp. A; TYLER & RIEGER, 1975: fig. 1-4 (NW Atlantic)
Nemertoderma sp. A; TYLER & RIEGER, 1977 (NW Atlantic)
Flagellophora; TYLER, 1984: Fig. 13 (integument)
Flagellophora sp.; SMITH & TYLER, 1985: Fig. 8.9
F. sp.; SMITH *et al.*, 1986: Figs 5, 12
Flagellophora sp.; TYLER, 1986 (broom organ)
Flagellophora cf. *apelti*; SMITH & TYLER 1986.

New material: 21 specimens in squeeze preparation.

Localities: Kristineberg (NE Atlantic), Canary Islands, Bermuda.

Organization and behaviour. Adults (Figs 11.1-5, 12.1-5) are 210-735 µm long and 105-140 µm wide at U 72.31 (body index 3.80). Animals are rounded at both ends and often somewhat bottle-shaped, with a shallow constriction at about U 20. Located at U 20.46, the statocyst (Fig. 11.7-8, 13.1, 13.3) is 10-17 (mean 13.88) µm long and 14-22 (17.77) µm wide, with a blisterless statolith of 6-8 (7.4) µm diameter. Of 21 specimens, one (4.8%) had only one statolith. The glands of the frontal organ rarely extend caudally beyond the statocyst. The epidermis is sparsely set with hooklet-shaped glands (Fig. 11.6). All specimens had a proboscis (Figs 11.1, 11.9, 13.1-2), *i.e.*, a bundle of about 30 glands whose fiber-like necks are protrusible through a canal opening at the anterior tip of the body (Tyler 1986). Once extruded, the fibers may flare into a fan, with the distal ends appearing slightly swollen and adhesive (Fig. 11.9).

Digestive tract. Neither a mouth opening nor pharynx glands were seen.

Reproductive system. The male copulatory organ opens ventrally at U 91.37, in the center of a rosette of glands, and is usually surrounded by untidy sperm bundles (Figs 11.1, 12.4). According to FAUBEL & DÖRJES (1978) there is a single testis, which «occupies the central region of the posterior half of the body». Sperm consists of a pointed head, a segmented middle piece, and a tail, but there are differences between geographically distinct populations. In autosperm (from the testis) of a Bermuda specimen (Fig. 11.10), the head: middle piece:tail dimensions were 10:10:42 µm, with the middle piece showing a faint striation of about 15 narrow bands. For the remaining specimens I cannot say whether the measurements are for auto- or allosperm. In all of them, head and middle piece are bilaterally symmetric, with one contour slightly concave and smooth, the other slightly convex, and the middle piece composed of regularly spaced segments. Specimens from Rovinj (Figs 11.13-14, 13.4) had a 6:9:57 µm sperm, with 6 segments in the middle piece. One specimen from N. Carolina (Fig. 11.13) had a 16:9:45-62 µm sperm with a 9-segmented middle piece whereas another (Fig. 11.12), from a different sample, had a 5:4:35 µm sperm with a 4-segmented middle piece. TYLER & RIEGER (1975) give measurements of 6.5 µm each for head and middle piece of their N. Carolina specimen, stating that the middle piece contains 6-8 «crescent-shaped bodies» which «are presumably mitochondrial derivatives».

The female pore opens dorsally at U 60.53; it does not seem to be ciliated, and is often filled with sperm bundles, which may also be found in nearby vacuoles. The ovary lies behind it, with the eggs maturing caudally.

Discussion. TYLER (1986) showed that the peculiar «flagellar organ» (FAUBEL & DÖRJES, 1978) is in fact composed of gland necks and not flagella; RIEGER *et al.* (1991) therefore propose to call it «proboscis». We still ignore its function but guess that it may have to do with feeding, especially in the absence of a mouth opening. Such absence may be temporary, however, and related to the reproductive cycle as in *N. westbladi*. A female pore, with associated bundles of allosperm, is not found in other nemertodermatids (except the new *Ascoparia*). FAUBEL & DÖRJES (1978) state that «a vagina is not present», but there is an «immense cyst-like bursa seminalis» (p. 7). Since my observations on living animals always show a fairly deep, well defined invagination which could be interpreted as a vagina, I use the neutral term «female pore» pending further microanatomical clarification. The observed bilateral symmetry and middle piece segmentation of sperm agrees well with the ultrastructural data of TYLER & RIEGER (1975: fig. 4), but is different from the the striated sperm figured by FAUBEL & DÖRJES (1978: fig. 4C). The remarkable range in substratum (coarse to fine sand to mud) and depth (3 m to 400 m), together with the observed geographic variation in sperm structure and proportions, may already presage the future need to split into several species what I am here calling *F. apelti* .

Ascoparia neglecta nov. gen., nov. spec.

(Figs 14.1-10, 15.1-4)

Type material: 4 adults in squeeze preparation.

Type locality: Florida, Big Pine Key, fine coral sand near a patch reef at 4 m depth, coll. 29 December 1968.

Etymology: Genus name from Lat. *scopa* (broom), and *a-* (without), in reference to the lack of a witch's broom-shaped proboscis. The species name refers to its long dormancy in my files.

Organization and behaviour. The slender, colourless worms (Fig. 14.1-4, 15.1) measure 645-750 (mean 686.25) µm in length and 90-120 (105.00) µm in width at U 47.11 (body index 6.63). The head is rounded, and set off against the body by a slight constriction at U 19; the posterior ends in a short tail. The statocyst, located at U 19.01, is 18 µm long and 22 µm wide (Figs 14.10, 15.3). It contains two statoliths of 8 µm diameter whose lithocyte is not in blisters. A bundle of frontal glands originate behind the statocyst, at U 30; like a twisted rope their long necks run under the statocyst to open subterminally, at the anterior tip of the head. There are no rhammoids, rhabdoids, nor bottle glands, but the epidermis contains sparsely arranged «hooklet» glands (Fig. 14.8).

Digestive tract. A pair of granular glands converge ventrally at U 33.83 (Figs 14.1, 14.3, 14.4), which suggests that this is where the mouth should be expected, although no actual opening was observed.

Reproductive system. A deeply invaginated, ciliated male pore is located ventrally at U 89.63 (Figs 14.1, 14.3, 14.4, 15. 4). It is surrounded by a dense rosette of glands with granular secretion. Bundles of sperm are usually found in front of the male copulatory organ, with the sperm heads pointing towards it. Sperm bundles were seen as far forward as U 70, but it was not clear whether these were autosperm or allosperm, nor could the location and number of testes be ascertained. Autosperm (Figs 14.5, 15.2) is filiform, with a slightly curved, 15 µm long head, a 10 µm long middle piece made up of 11-12 segments, and a 71-88 µm long tail. A spermatid (Fig. 14.6) was more curved, with a shorter tail.

The single ovary lies between U 43 and U 80, with eggs maturing caudally (Figs 14.1-2, 15.1). The largest egg may be 130 µm long, and extend to behind the female pore which is located dorsally at U 70.71. The female pore is ciliated, and in 2 of 4 specimens a bundle of allosperm was found protruding from it. In at least one specimen, vacuoles containing sperm bundles were seen to the left and right of the vagina. Allosperm protruding from the vagina (Fig. 14.7) had an undifferentiated, 16 µm long head-middle piece and a 65 µm long tail.

Discussion. The absence of a proboscis as well as the probable presence of a mouth justify erecting a new genus separate from *Flagellophora*, with which *Ascoparia* otherwise shares habitus, absence of blisters on the lithocyte, hooklet glands, location of male copulatory organ and ciliated female pore, and autosperm structure. It appears that sperm is transferred from the male copulatory organ to the female pore in bundles which are then stored in vacuoles (bursae?) prior to fertilization.

Ascoparia secunda **nov. spec.**

(Figs 14.11-16, 16.1-4)

Type material: One adult in squeeze preparation.

Type locality: NW Atlantic, off North Carolina (34°28-6'N, 76°43-4'W), clean coarse sand with shell at 20 m.

Additional material: One adult in squeeze preparation, NW Atlantic, off North Carolina (34°45-0'N, 75°45-0'W), clean coarse sand with shell at 41 m depth.

Etymology: The second species in the new genus.

Organization and behaviour. The type specimen («specimen A», Figs 14.15, 16.1) was 500 µm long and 110 µm wide at U 36.58 (body index 5.12). It was pointed both anteriorly and posteriorly. The statocyst, located at U 18, was 16 µm long and 19 µm wide (Figs 14.11, 16.3); statoliths are 8 µ in diameter, with the lithocyte cap not in blisters. A short bundle of frontal glands converge on the anterior tip of the head.

A second specimen («specimen B», Fig. 14.16, 16.4), which I tentatively list with this species, measured 410 µm in length and 80 µm in width at U 36.6 (body index 5.12). It was rounded both anteriorly and posteriorly, and had a narrow bundle of ropey frontal glands that extended posteriorly to the statocyst. The epidermis contained sparse, somewhat hooklet-shaped glands which reach a higher density only in the tail region (Fig. 16.2). Located at U 24.4, the statocyst (Fig. 14.12) was 16 µm long and 20 µm wide, with a blisterless lithocyte of 8 µm diameter.

Digestive tract. No mouth was seen in either specimen.

Reproductive system. Surrounded by a gland rosette, the male copulatory organ (Figs 14.15, 16.2) is situated ventrally at U 87 (U 93 in specimen B), with bundles of sperm found dorsally from it. Sperm of the type specimen – I cannot say whether it was auto- or allosperm – consisted of an 8 µm long head with a slightly spiralized tip; a 6 µm long middle piece with 13 striations, and a 45-70 µm long tail. What may be an early spermatogenesis stage is shown in Fig. 14.13.

Specimen A (Fig. 14.15) had a female pore dorsally at U 54, which contained a bundle of allosperm that ended in a vacuole adjacent to an immature egg. The ovary extends between the female and the male pore; eggs mature caudally so that the largest egg is found immediately in front of the male copulatory organ.

Discussion. The habitus, absence of a proboscis, absence of blisters on the statoliths, location of male copulatory organ and female pore, and autosperm structure identify this species as belonging to *Ascoparia.* It differs from *A. neglecta* primarily in the location of the ovary behind the vagina. The second specimen may belong to a species yet to be described.

***Ascoparia* sp.**

Material: Two adult specimens in squeeze preparation.

Locality: Papua New Guinea; Wongat Island off Madang, *Halimeda* debris from reef slope at 8 m.

The larger of the two adults was 450 µm long and 140 µm wide at U 50. Although these specimens could not be identified to species they are listed here as the only record of the genus in the Pacific Ocean.

THE TAXA OF NEMERTODERMATIDA

First defined as a family within the Acoela (Steinböck, 1930), nemertodermatids were subsequently given the status of a suborder (and later an order, Ax, 1961) within the Archoophora (Karling, 1940). They are now considered an order within Acoelomorpha (Ehlers, 1984). The order is defined by the possession of a statocyst with two statoliths of which each is produced by a single lithocyte, and uniflagellate sperm with a 9+2 axoneme (Hendelberg, 1983b). The nemertodermatid statocyst is symmetric, in contrast to the polylithophorous statocysts of Catenulida-Retronectidae (Sterrer & Rieger, 1974) and Rhabdocoela-Luridae (Sterrer & Rieger, 1990) which often contain an irregular number of irregularly shaped statoliths, and also differ in other aspects of their ultrastructure (Ehlers, 1991). Two statoliths must be considered the norm for the order, despite the occurrence, in four species, of aberrant statocysts with one, three, or four statoliths. Nemertodermatida share with Acoela the possession of a true frontal organ (Smith & Tyler, 1986; but see Ehlers, 1992), and an interconnected system of epidermal ciliary rootlets (Smith, 1990, Lundin & Hendelberg, 1995, Lundin, 1997). But while Acoela lack rhabdites – rod-shaped, eosinophilic, epidermal secretions with a characteristic ultrastructure, histochemistry, and mode of formation (Smith *et al.*, 1994) – the rhabdoids of *Meara* «are histochemically and ultrastructurally similar to true rhabdites» of Rhabditophora, and the glands of *Nemertinoides elongatus* appear to be making the same kind of mucus as is found in true rhabdites (Smith *et al.*, 1994). Furthermore, Nemertodermatida are the only Platyhelminthes with primitive, uniflagellate sperm with a 9+2 axoneme (TYLER & RIEGER, 1975, HENDELBERG, 1983b, LUNDIN & HENDELBERG, in press). The taxon Acoelomorpha, therefore, which has also been linked to the peculiar vermiform *Xenoturbella* (SMITH, 1990; but see EHLERS, 1991, NORÉN & JONDELIUS, 1997, ISRAELSSON, 1997, LUNDIN, in press b), needs to be reassessed, especially in light of new evidence from 18S rDNA analyses (CARRANZA *et al.*, 1997, JONDELIUS, 1998).

The following features might be used for establishing relationships between the genera: epithelial *vs.* insunk brain; presence and structure of mouth and pharynx; presence of proboscis, frontal organ and other glands; paired *vs.* unpaired testes and ovaries, and their orientation to the body axes; epithelial *vs.* lacunar nature of reproductive organs; and sperm structure. Most of these, however, are still too inconsistently known to be useful, especially for field identification. This leaves mainly the auxiliary reproductive structures. The male copulatory organ, present in all genera, opens either supraterminally (as in *M. stichopi, N. bathycola*, *N. westbladi*, and *N. psammicola*), or subterminally (*F. apelti, A. neglecta* and *A. secunda*). Only in *Nemertinoides elongatus*, the male copulatory organ is located far forward dorsally, possibly in connection with the extreme elongation of the body and the need to protect this organ in the event of body fragmentation. There are two features, however, that separate the order into two groups of genera. The first is the presence of a female pore (vagina?) and auxiliary organ (bursa?) for receiving and storing sperm in *Flagellophora* and *Ascoparia*, *vs.* the absence of such organs in all other genera. I would expect differences in sperm structure, such as the bilateral symmetry in the sperm of *Flagellophora* and *Ascoparia*, and the differentiation between autosperm and allosperm in *Nemertoderma* and *Nemertinoides,* to be linked to this character. The second feature is inconspicuous yet nevertheless as consistent; it is the observation that in all species of *Meara, Nemertoderma* and *Nemertinoides*, the lithocyte which caps the statolith is organized in the form of blisters (Fig. 1.2) whereas it is smooth in *Flagellophora* and *Ascoparia.* On the basis of these differences I propose to amend the diagnosis for the family Nemertodermatidae, and erect a second family, Ascopariidae.

DIAGNOSES

(*see also Table 3*)

Order Nemertodermatida **Karling, 1940**

(*emended diagnosis*)

With or without a ventral mouth and pharynx simplex; gut with lumen and granular club glands. Statocyst symmetric, with two statoliths. Without protonephridia. Sperm uniflagellate, with 9+2 microtubular pattern. Free-living or symbiotic, marine.

Fam. Nemertodermatidae Steinböck, 1930

(*emended diagnosis*)

Nemertodermatida without a female pore; sperm radially symmetric. Male pore located supraterminally or dorsally. Lithocyte in blisters. Usually with epidermal bottle glands. Three genera:

Genus *Nemertoderma* Steinböck, 1930: Nemertodermatidae with male pore located supraterminally. Testes and ovaries in posterior two thirds of body. Three species:

- *N. bathycola* Steinböck, 1930: Mean length 0.3 mm, body index 4.9. Female phase usually with only one mature egg.

  Northeastern Atlantic; on mud, from 120 m to 690 m depth.
- *N. westbladi* (Westblad) Steinböck, 1938: Mean length 0.5 mm, body index 1.6. Statocyst 14 µm long, 21 µm wide, statolith 7 µm in diameter. Female phase usually with more than one mature egg. Autosperm with 18 µm long head, 9.5 µm long middle piece, and 18 µm long tail.

  Northern Atlantic and Mediterranean; on mud or muddy sand, from the subtidal to 620 m depth.
- *N. psammicola* Sterrer, 1970: Mean length 1.8 mm, body index 12.8. Statocyst 18 µm long, 22 µm wide, statolith 8 µm in diameter. Autosperm with 15 µm long head, 10 µm long middle piece, and 71-88 µm long tail.

  Northern Atlantic, Mediterranean and Western Pacific; in fine sand, from the intertidal to 8 m depth.

Genus *Meara* Westblad, 1949: Nemertodermatidae with male pore located supraterminally. Testes in preoral, ovaries in postoral region. Commensals in holothurians. Two species:

- *M. stichopi* Westblad, 1949: Mean length 2.2 mm, body index 3.3. Often with bundled rhabdoids of 10 µm length; bottle glands lacking. Statocyst 20 µm long, 33 µm wide, statolith 12 µm in diameter. Autosperm with 20 µm long head, 35 µm long middle piece, and 5-10 µm long tail.

  Northeastern Atlantic; in *Parastichopus tremulus*.
- *M.* sp. SMITH *et al.*, 1994.

  Bahamas (in the foregut of *Holothuria lentigenosa enodis*).

Genus *Nemertinoides* Riser, 1987: Nemertodermatidae with male pore located dorsally. Testes in postoral, ovaries in caudal region. One species:

- *N. elongatus* Riser, 1987: Mean length 6 mm, body index 14. With bottle glands and 2 µm long rhammoids. Statocyst 20 µm long, 25 µm wide, statolith 10 µm in diameter. Male copulatory organ at about U 40. Autosperm with 46 µm long head, 48 µm long middle piece, and 45 µm long tail.

  Northwestern Atlantic and Mediterranean; in coarse sand, from the intertidal to 6 m depth.

Fam. Ascopariidae nov. fam.

Nemertodermatida with a dorsal female pore; sperm bilaterally symmetric. Male pore located suberminally. Lithocyte not in blisters. Usually without epidermal bottle glands. Two genera:

Genus *Flagellophora* Faubel & Dörjes, 1978: Ascopariidae with an eversible proboscis. One species:

- *F. apelti* Faubel & Dörjes, 1978: Mean length 0.5 mm, body index 3.8. Statocyst 14 µm long, 18 µm wide, statolith 7 µm in diameter. Male copulatory organ at about U 91,

TABLE 3

Taxa of Nemertodermatida, and diagnostic characters

	av. length in mm	*body index*	*frontal organ*	*pro-boscis*	*rhabdoid length*	*bottle glands*	*hooklet glands*	*statocyst length*	*statocyst width*	*statolith diameter*	*blisters on statolith*	*mouth*	*male pore*		*female pore*		*autosperm symmetry*	*autosperm length*		
													location	*at U*	*location*	*at U*		*head*	*middle piece*	*tail*
Fam. Nemertodermatidae																				
Meara stichopi	2.2	3.3	-	-	10µm	?	-	20	33	12	+	+	supraterminal	96	-		radial	20 µm	35 µm	5-10 µm
Nemertinoides elongatus	6	14+	+	-	2 µm	+	23 µm	20	25	10	+	+	dorsal	42	-		radial	46 µm	48 µm	45 µm
Nemertoderma psammicola	1.8	12.8	+	-	11.5 µm	+	?	14	21	7	+	+	supraterminal	93	-		radial	18 µm	9.5 µm	18 µm
Nemertoderma westbladi	0.5	1.6	+	-	?	+	?	21	27	11	+	+	supraterminal	98	-		radial	(h + mp	67-75 µm)	55-62 µm
Nemertoderma bathycola	0.3	4.9	?	-	?	+	?	11	17	8	+	?	supraterminal	98	?		?	?	?	?
Fam. Ascopariidae																				
Flagellophora apelti	0.5	3.8	+	+	-	-	10 µm	14	18	7	-	-	ventral	91	dorsal	60	bilateral	5-16 µm	4-9 µm	35-62 µm
Ascoparia neglecta	0.6	6.6	+	-	-	-	10 µm	18	22	8	-	?	ventral	90	dorsal	71	bilateral	15 µm	10 µm	71-88 µm
Ascoparia secunda	0.5	4.8	+	-	-	-	15µm	16	19	8	-	?	ventral	80	dorsal	54	bilateral	8 µm	6 µm	45-70 µm

female pore at about U 60. Autosperm with 5-16 µm long head, 4-9 µm long middle piece, and 35-62 µm long tail.

Northern Atlantic and Mediterranean; in sand (occasionally sandy mud), from 2 m to 400 m depth.

Genus *Ascoparia* nov. gen.: Ascopariidae without an eversible proboscis. Two species:

- *A. neglecta* nov. spec.: Mean length 0.6 mm, body index 6.6. Statocyst 18 µm long, 22 µm wide, statolith 8 µm in diameter. Male copulatory organ at about U 90, female pore at about U 71. Autosperm with 15 µm long head, 10 µm long middle piece, and 71-88 µm long tail.

  Northwestern Atlantic; in fine sand, at 3 m depth.
- *A. secunda* nov. spec.: Mean length 0.5 mm, body index 4.8. Statocyst 16 µm long, 19 µm wide, statolith 8 µm in diameter. Male copulatory organ at about U 80, female pore at about U 54. Autosperm with 8 µm long head, 6 µm long middle piece, and 45-70 µm long tail.

  Northwestern Atlantic; in sand, from 20 m to 41 m.
- *A.* sp.

  Papua New Guinea; in *Halimeda* debris, 8 m.

ABBREVIATIONS USED IN FIGURES

als	allosperm	mp	middle piece of sperm
aus	autosperm	ov	ovary
bg	buccal glands	pb	proboscis
fo	frontal orgn	rh	rhammoids
fp	female pore	sp	sperm
h	head of sperm	t	testis
m	mouth	tl	tail of sperm
mco	male copulatory organ	vd	vas deferens

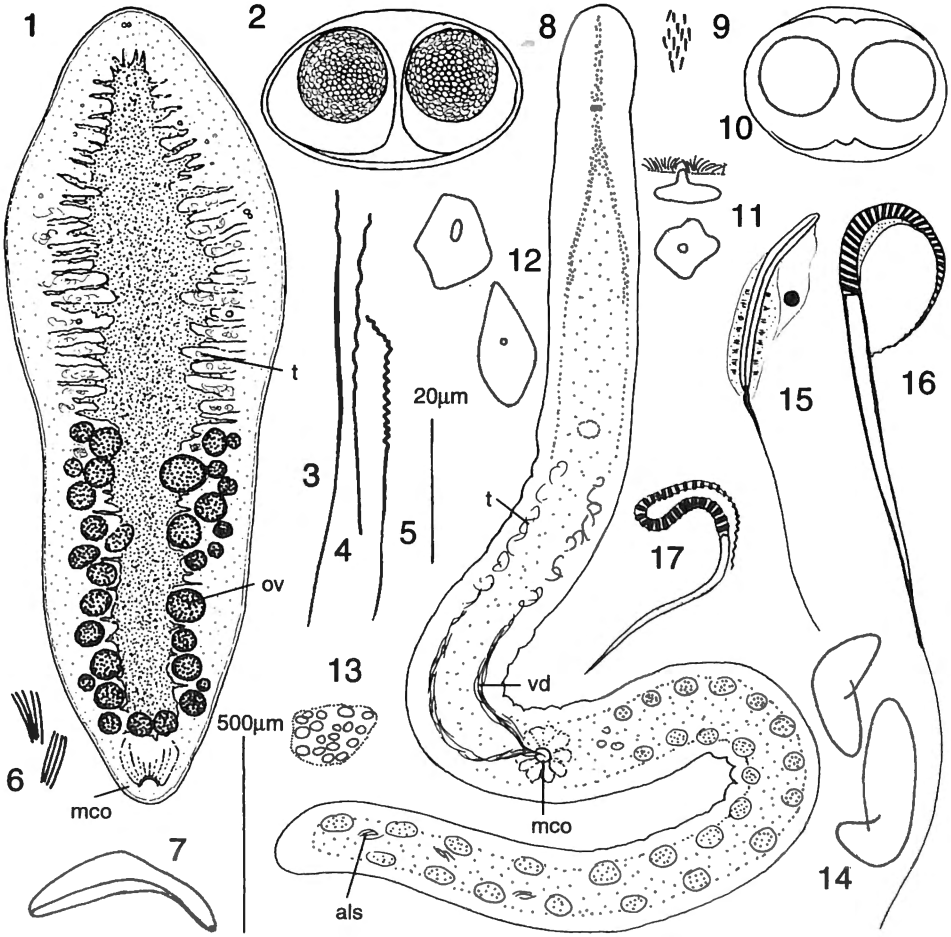


Fig. 1. – *Meara stichopi* (1-7) and *Nemertinoides elongatus* (8-17). – *Meara stichopi:* 1 mature specimen, dorsal view; 2 statocyst; 3-5 three autosperm; 6 rhabdoid bundles; 7 sketch of habitus, left ventral view. – *Nemertinoides elongatus:* 8 dorsal view of mature specimen from Rovinj (semi-schematic, with posterior body region completed after Riser, 1987); 9 rhabdoids; 10 statocyst («blister cap» omitted); 11 mucous gland of anterior body region, lateral (above) and dorsal (below) view; 12 mucous gland of posterior body region, dorsal view; 13 granular gland, and 14 «hooklet» gland of posterior body region; 15 spermatid; 16 autosperm or late spermatid; 17 allosperm. One scale applies to 1, a second to the remaining figures except 7 which is not to scale.

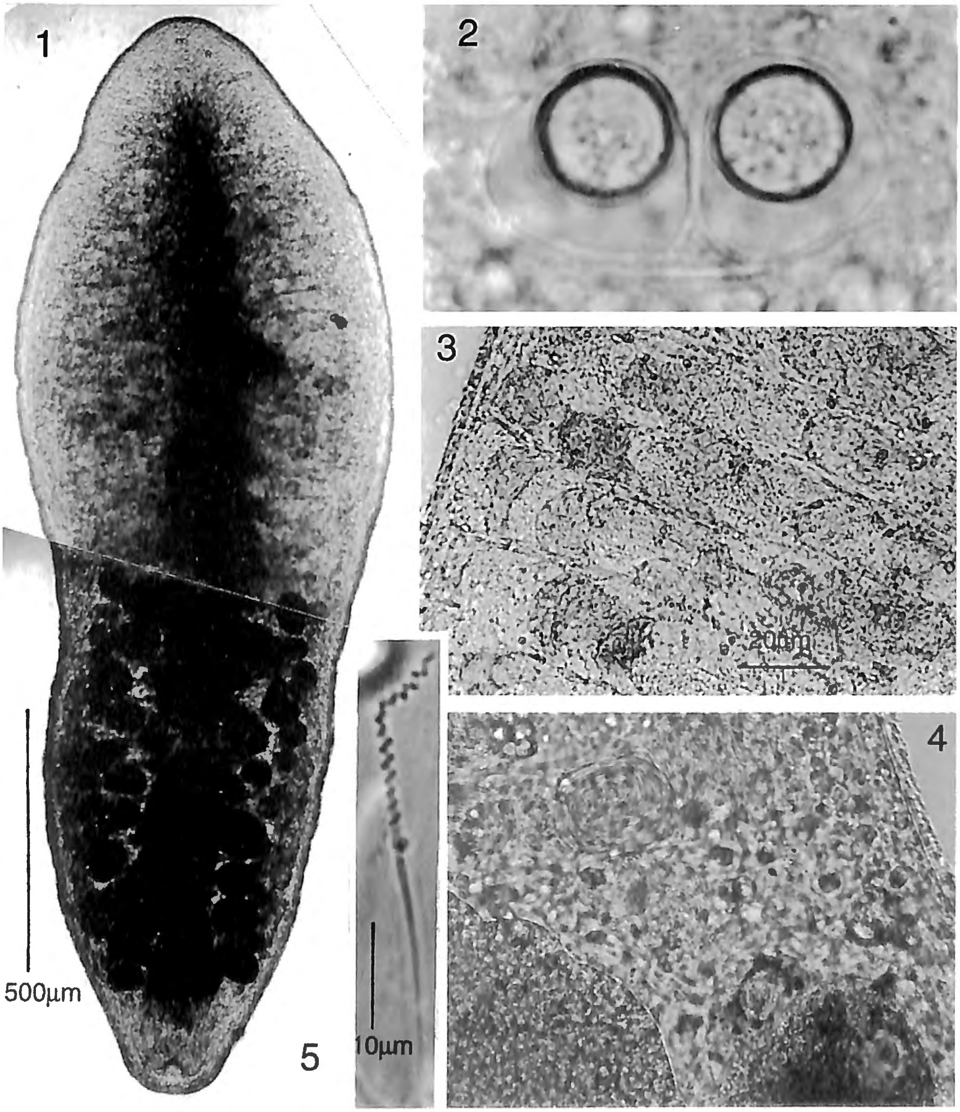
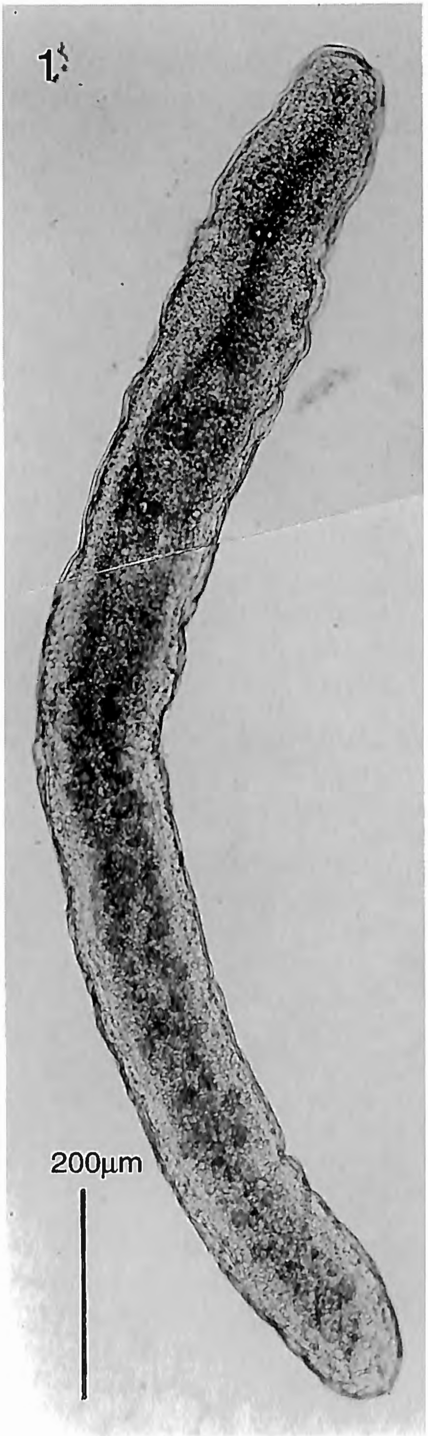
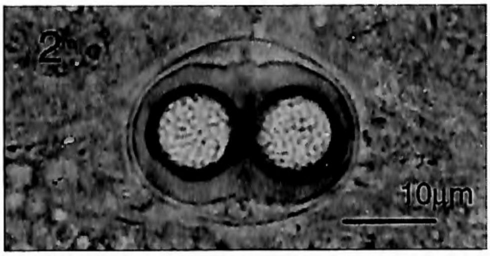


Fig. 2. – *Meara stichopi,* microphotographs of live specimens from Espegrend. – 1 habitus of adult, dorsal view; 2 statocyst, dorsal view; 3 testis follicles in left anterolateral body region; 4 sperm balls anterior to eggs in right mid-body region; 5 autosperm. One scale applies to 1; and a second to 2 and 5; and a third to 3 and 4.


1
200µm


2
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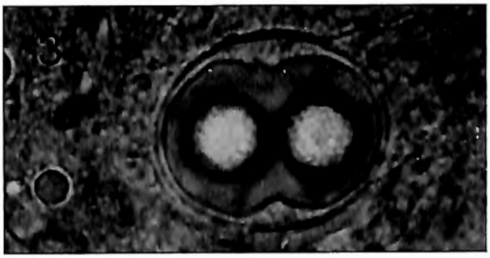
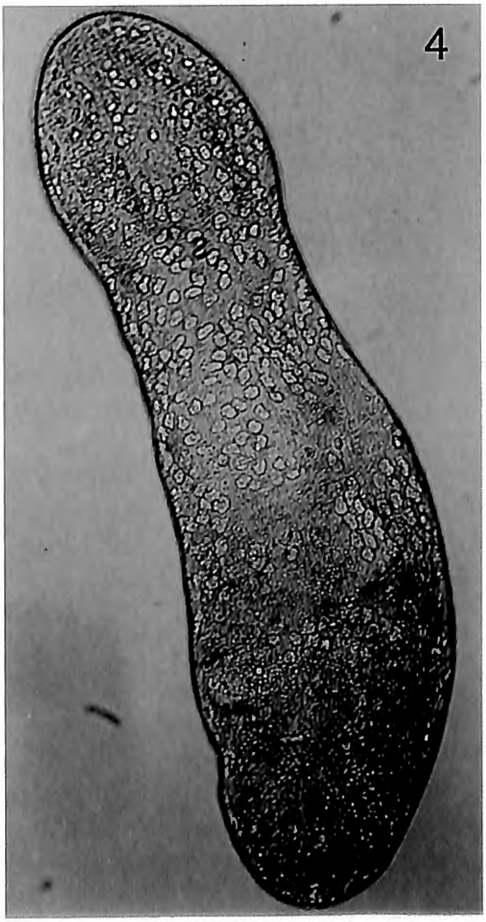

3


4

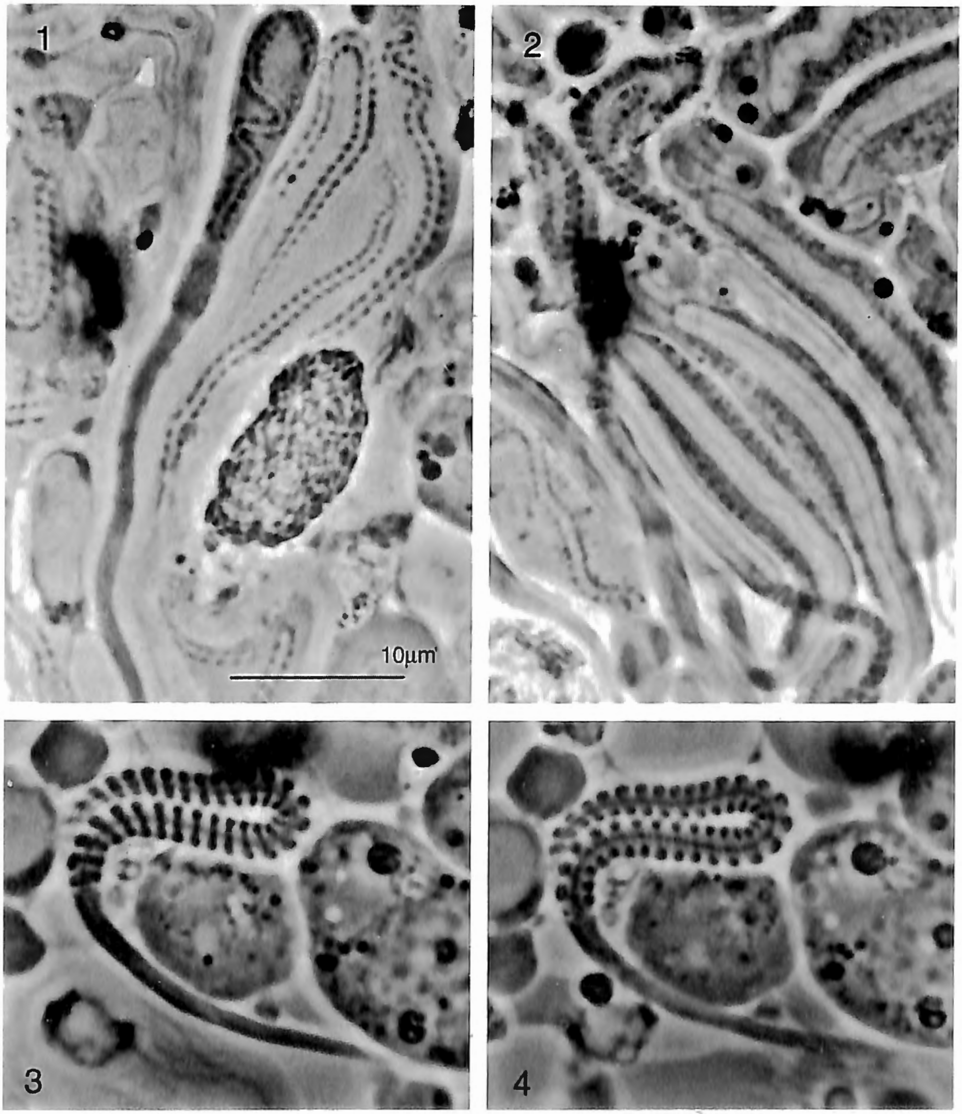


Fig. 4. – *Nemertinoides elongatus,* microphotographs of live specimens from Florida. – 1 & 2 spermiogenesis stages; 3 & 4 allosperm, at two different planes of focus. All to the same scale.

Fig. 3 (page 76). – *Nemertinoides elongatus,* microphotographs of live specimens from Rovinj. – 1 anterior fragment; 2 & 3 statocyst of two specimens; 4 anterior fragment with many bottle glands. One scale applies to 1 and 4; and a second to 2 and 3.

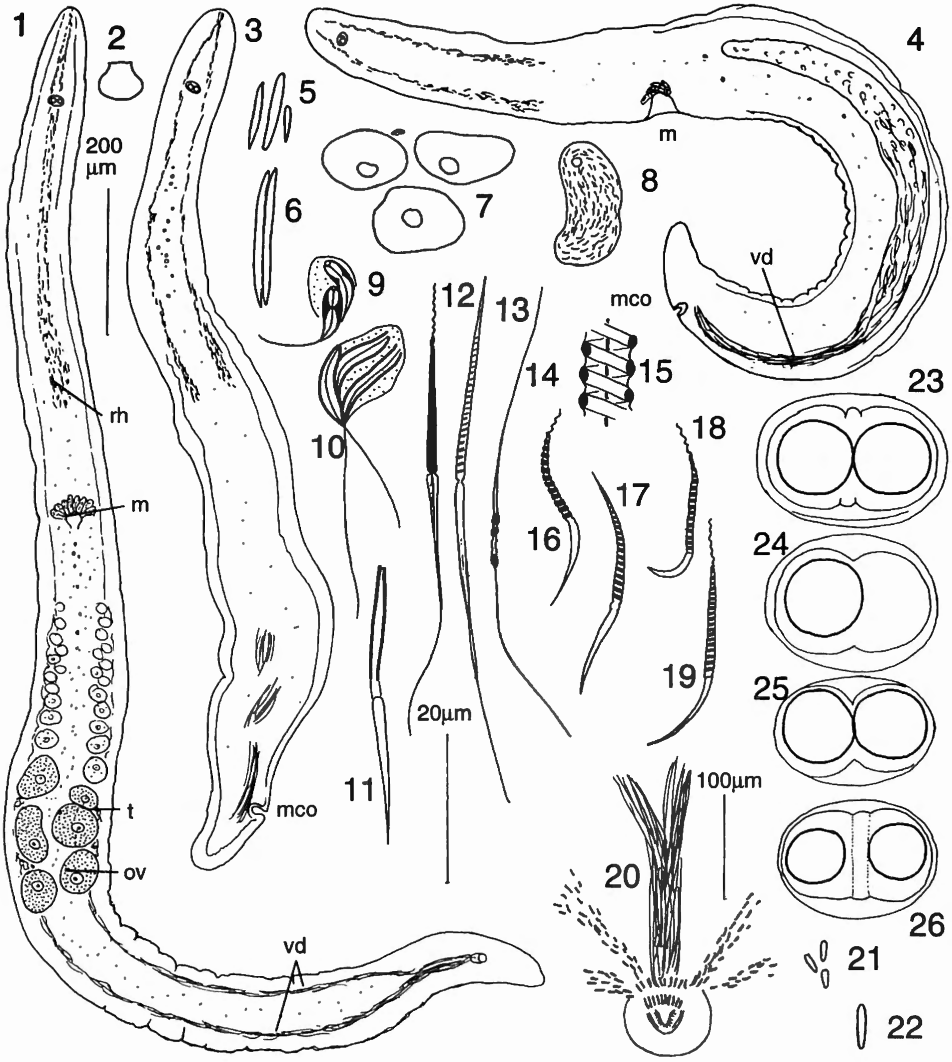


Fig. 5. – *Nemertoderma psammicola.* – 1 mature specimen from Kristineberg, dorsal view; 2 schematic cross section through the rostrum; 3 specimen in male phase from New Zealand, anterior in dorsal, posterior in right lateral view; 4 specimen in male phase from Kristineberg, left lateral view; 5 rhammoids of a New Zealand specimen; 6 rhammoids of a Florida specimen; 7 bottle glands of New Zealand specimen; 8 rod gland of New Zealand specimen; 9-11 successive spermatogenesis stages of a Kristineberg specimen; 12-13 autosperm of a Kristineberg (12) and New Zealand (13) specimen; 14 aberrant autosperm of a Kristineberg specimen; 15 schematic view of head of allosperm; 16-19 allosperm of specimens from Florida (16), New Zealand (17), Gran Canaria (18) and Kristineberg (19); 20 vasa deferentia and male pore of New Zealand specimen; 21-22 rhabdoids associated with male pore; 23-26 statocysts («blister cap» omitted) of specimens from Kristineberg (23, 24), New Zealand (25), and Gran Canaria (26). One scale applies to 1, 3 and 4; a second to 20, and a third to the remaining figures.

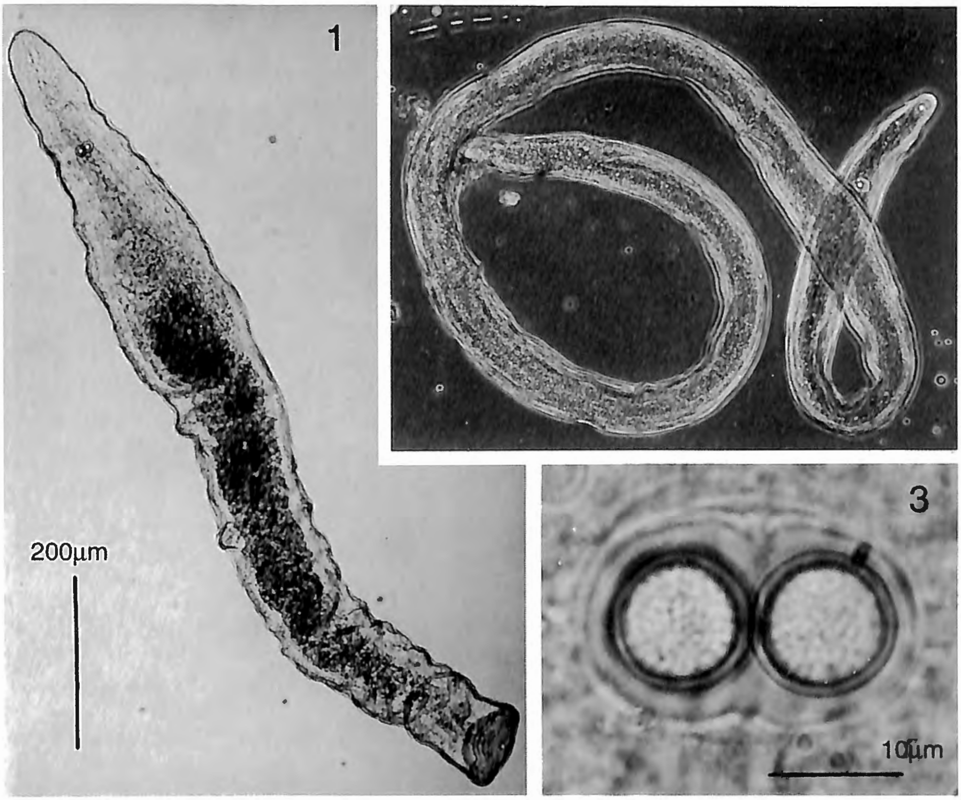


Fig. 6. – *Nemertoderma psammicola,* microphotographs of live specimens. – 1 adult from Fiascherino; 2 adult from Portaferry; 3 statocyst of specimen from Kristineberg. The same scale applies to 1 and 2.

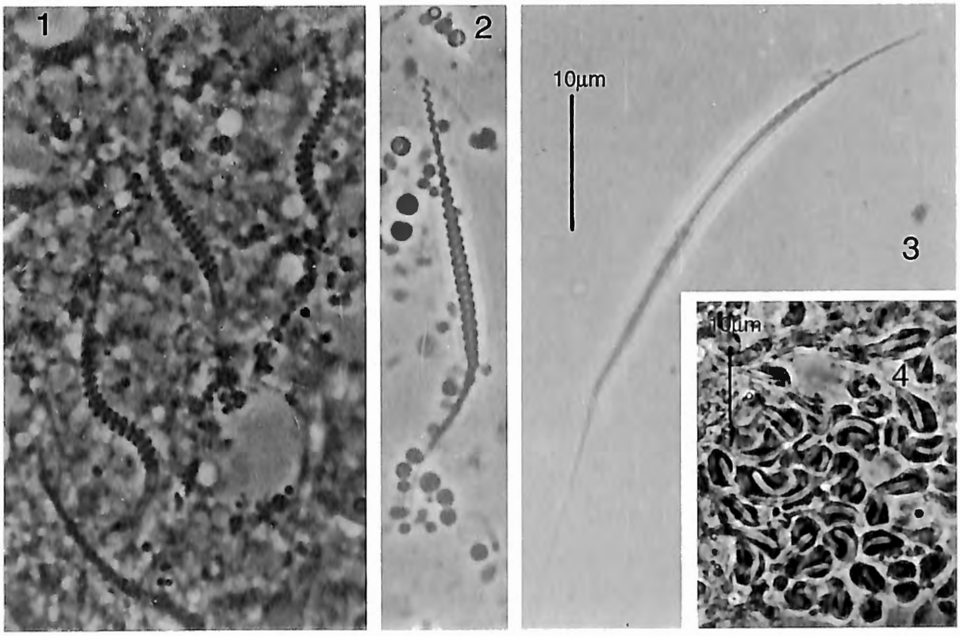


Fig. 7. – *Nemertoderma psammicola,* microphotographs of live specimens. – 1-3 sperm of the same specimen from Kristineberg: 1 allosperm in situ; 2 allosperm squeezed out of body; 3 autosperm; 4 spermiogenesis stages of a Portaferry specimen. The same scale applies to 1-3.

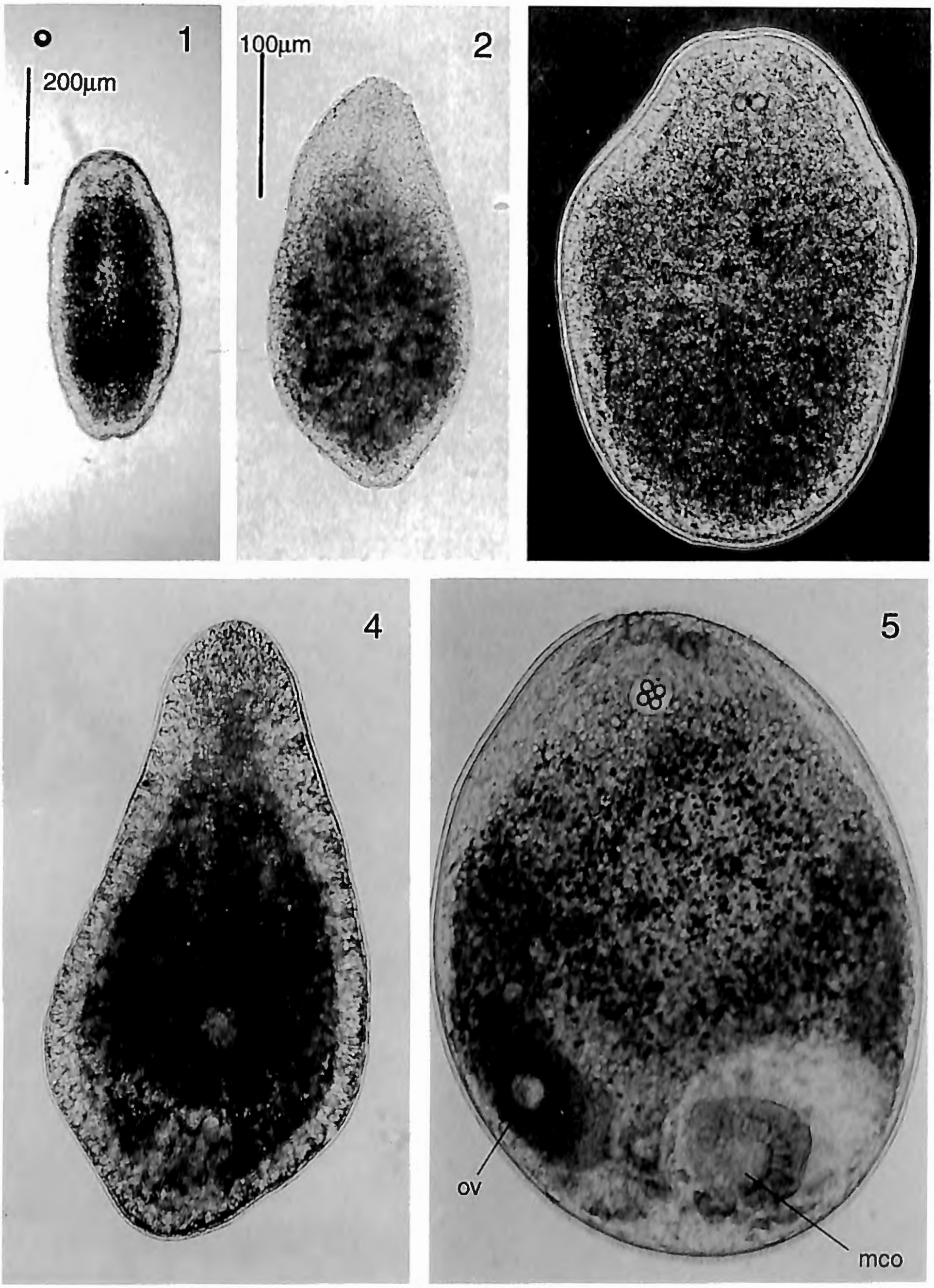
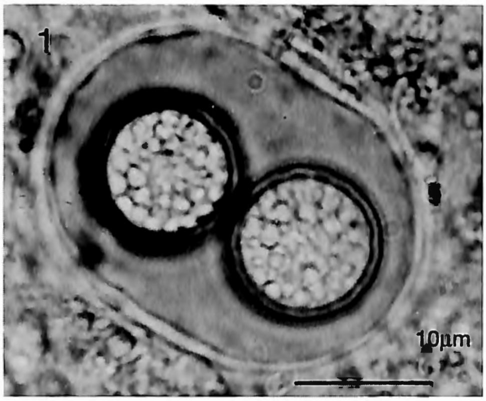
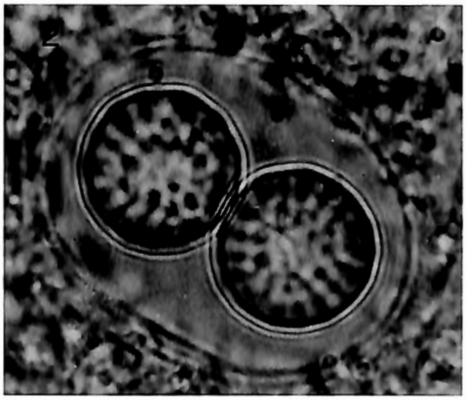
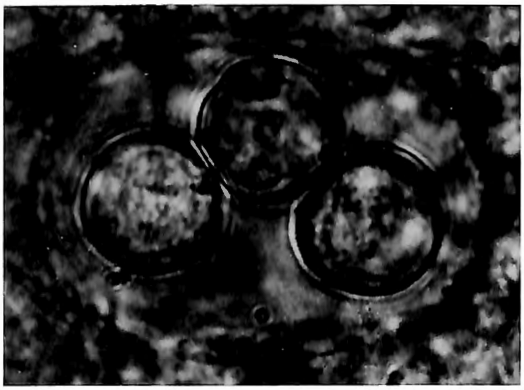
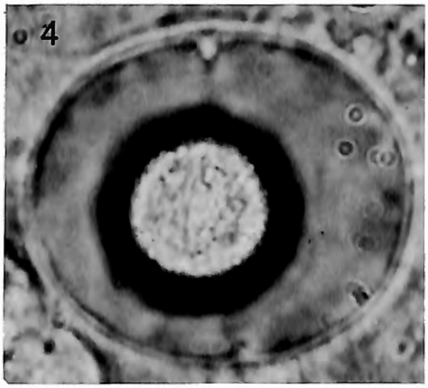


Fig. 8. – *Nemertoderma westbladi*, microphotographs of live specimens. – 1 juvenile from Kristineberg; 2 juvenile from Fiascherino; 3 juvenile from Banyuls; adult with mature egg from Dubrovnik; 5 adult with 4 statoliths, with egg and male organ, from Kristineberg. 3 and 5 are more strongly squeezed than the rest. The same scale applies to 2-5.


1
10µm


2



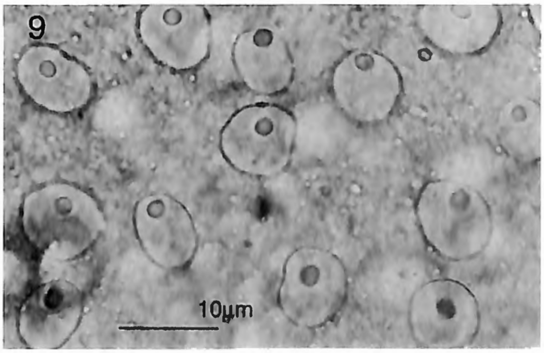

4


5
30µm


6


7
10µm


8


9
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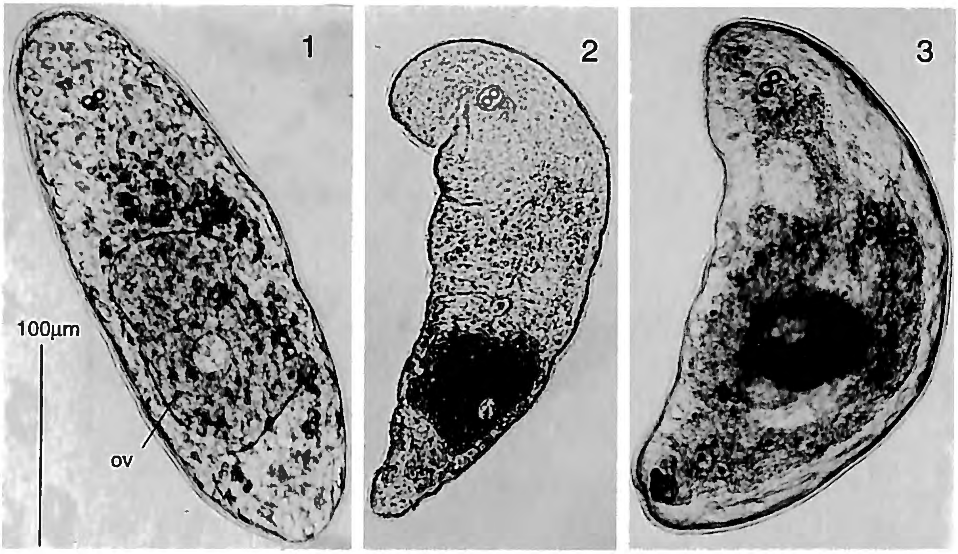

Fig. 10. – *Nemertoderma bathycola,* microphotographs of live specimens from Espegrend. – 1 specimen from 260 m depth; 2 specimen from 120 m depth; 3 specimen from 260 m depth. All to the same scale

Fig. 9 (page 82). – *Nemertoderma westbladi,* microphotographs of live specimens. – 1-2 statocyst of a Kristineberg specimen, at different planes of focus; 3-5 statocysts with aberrant statolith numbers (Kristineberg specimens); 6-7 allosperm of a Fiascherino specimen, in situ, (6) and squeezed out of specimen (7); 8-9 mucous bottle glands, lateral (8) and dorsal view (9). One scale applies to 1-4; a second to 5, a third to 6-7, and a fourth to 8-9.

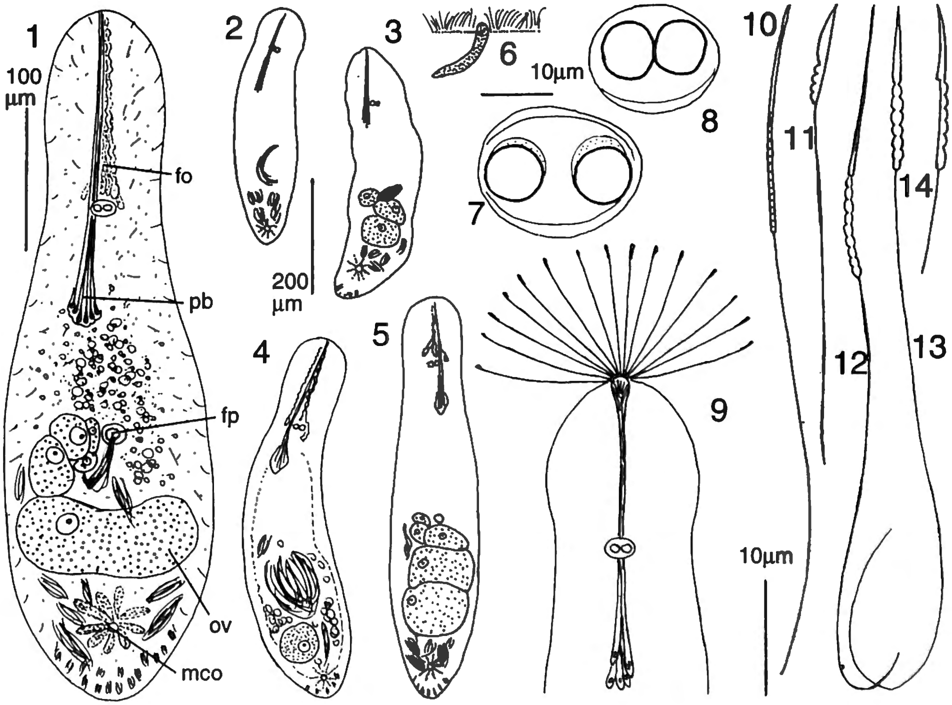

Fig. 11. – *Flagellophora apelti.* – 1 mature specimen from Bermuda, dorsal view; 2-5 habitus of specimens from Kristineberg (2) and Rovinj (3-5); 6 «hooklet gland» of specimen from North Carolina, lateral view; 7-8 statocyst of specimen from North Carolina (7) and Bermuda (8); 9 protruded proboscis; 10-14 sperm of specimens from Bermuda (10), North Carolina (11, 12) and Rovinj (13 in top view, and 14 in side view). One scale applies to 1, a second to 2-5, a third to 6-8, and a fourth to 10-14. Fig. 9 redrawn from Rieger *et al.* 1991, fig. 8J.

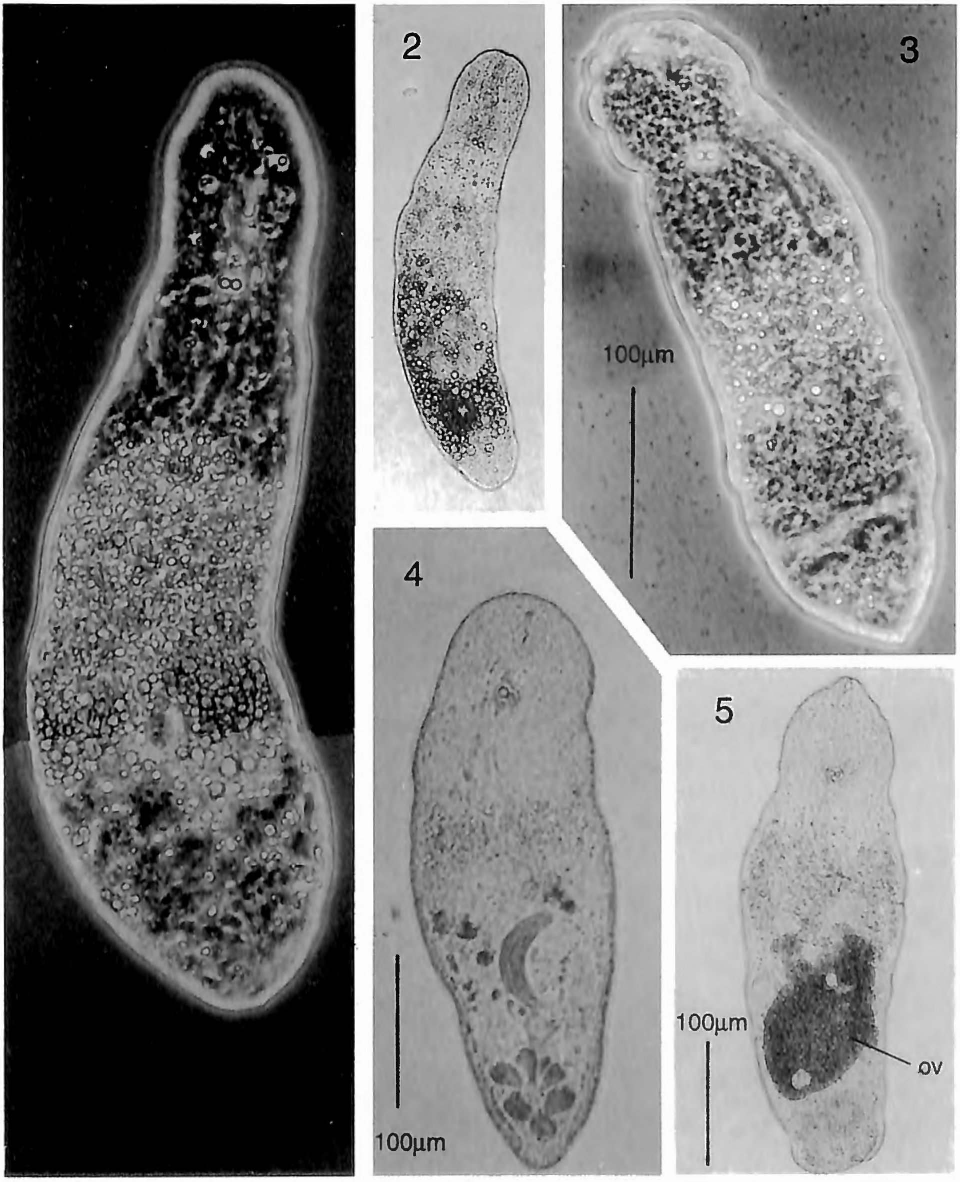

Fig. 12. – *Flagellophora apelti,* microphotographs of live, adult specimens. – 1 from Bermuda; 2 from Rovinj; 3 from North Carolina; 4 from Kristineberg; 5 from Rovinj. One scale applies to 1 and 3, a second to 2 and 5, and a third to 4.

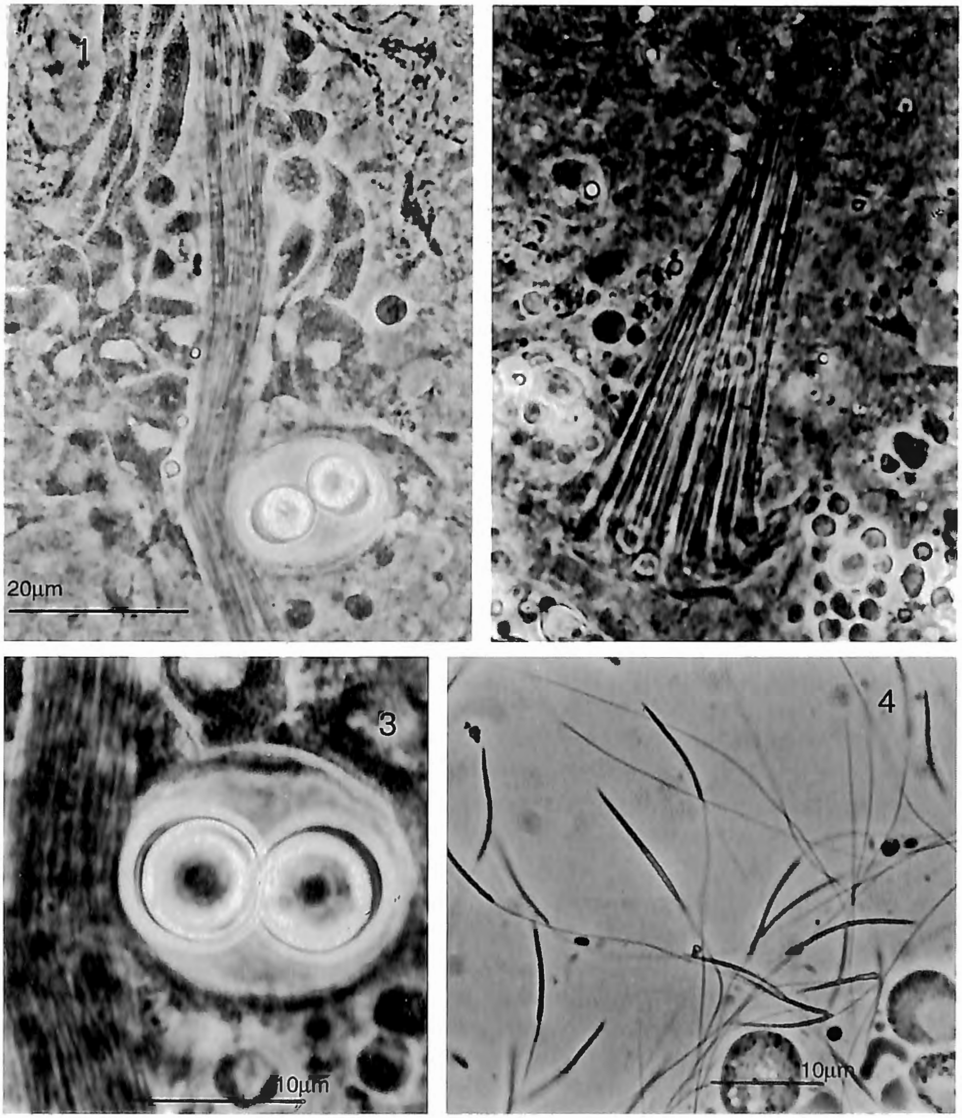

Fig. 13. – *Flagellophora apelti*, microphotographs of live specimens. – 1 statocyst, proboscis and frontal organ (Bermuda specimen); 2 posterior end of proboscis (Bermuda specimen); 3 statocyst (Bermuda specimen); 4 sperm (Rovinj specimen). One scale applies to 1-2, a second to 3, and a third to 4.

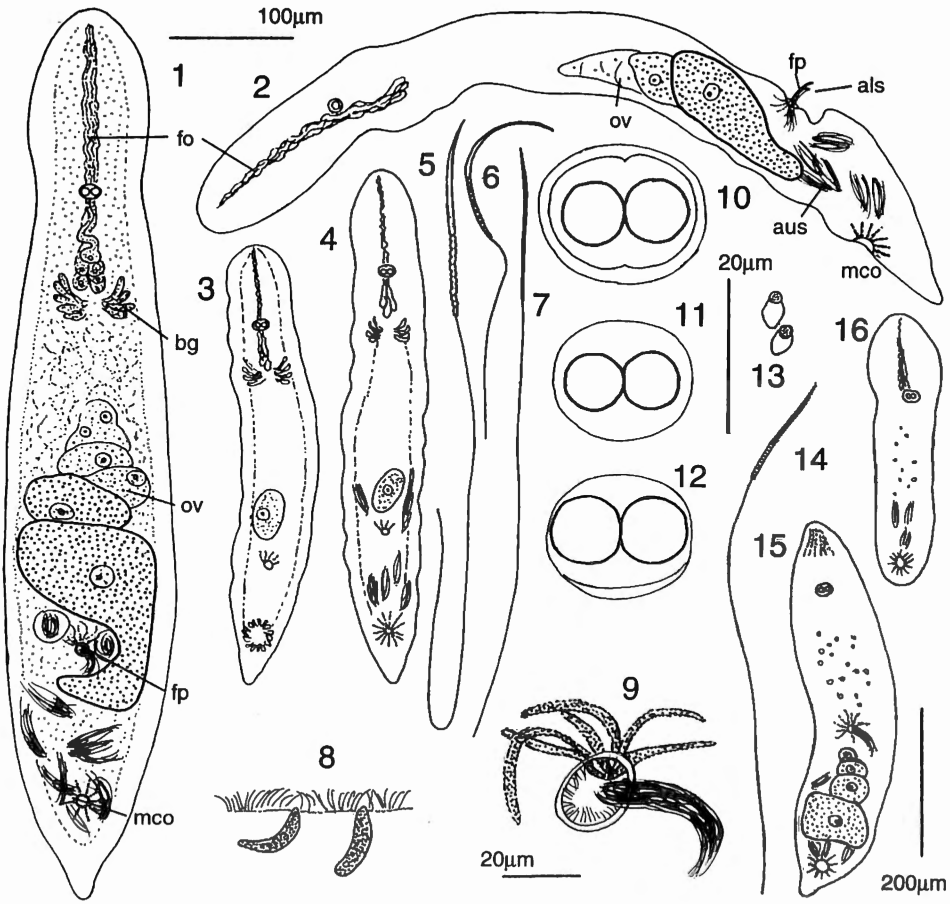

Fig. 14. – *Ascoparia neglecta* (1-10) and *A. secunda* (11-16). – *A. neglecta:* 1 mature specimen, dorsal view; 2 the same in left lateral view; 3-4 two other specimens, dorsal view; 5 autosperm; 6 spermatid; 7 allosperm; 8 epidermal 'hooklet' glands, lateral view; 9 vagina, dorsal view; 10 statocyst. – *A. secunda:* 11 statocyst of specimen A; 12 statocyst of specimen B; 13 spermatogenesis stage; 14 sperm; 15 specimen A, dorsal view; 16 specimen B, dorsal view. One scale applies to 1-2; a second to 3, 4, 15 and 16; a third to 9; and a fourth to the remaining Figs.

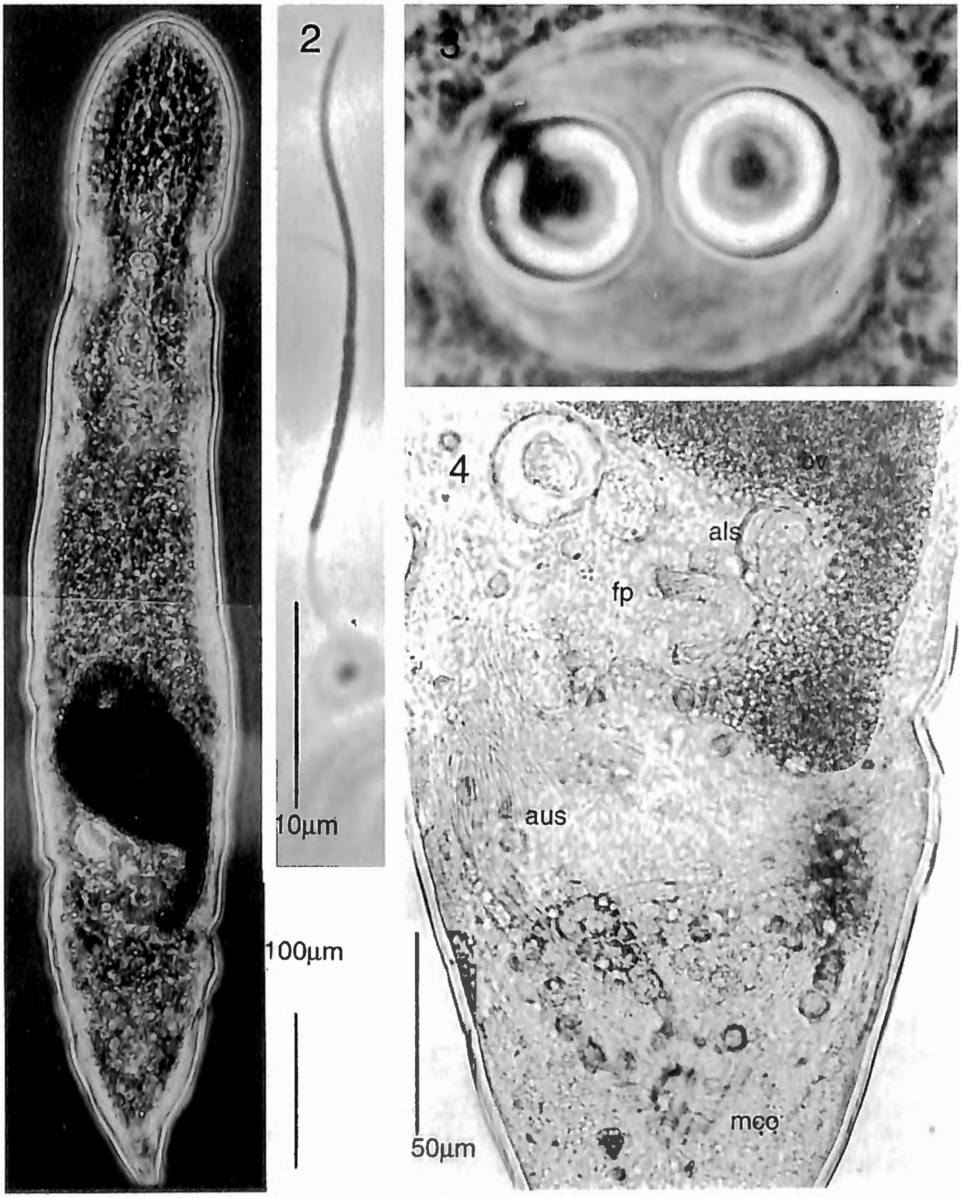

Fig. 15. – *Ascoparia neglecta*, microphotographs of live specimens. – 1 dorsal view of adult; 2 autosperm; 3 statocyst; 4 posterior body region, dorsal view. One scale applies to 1, a second to 2-3, and a third to 4.

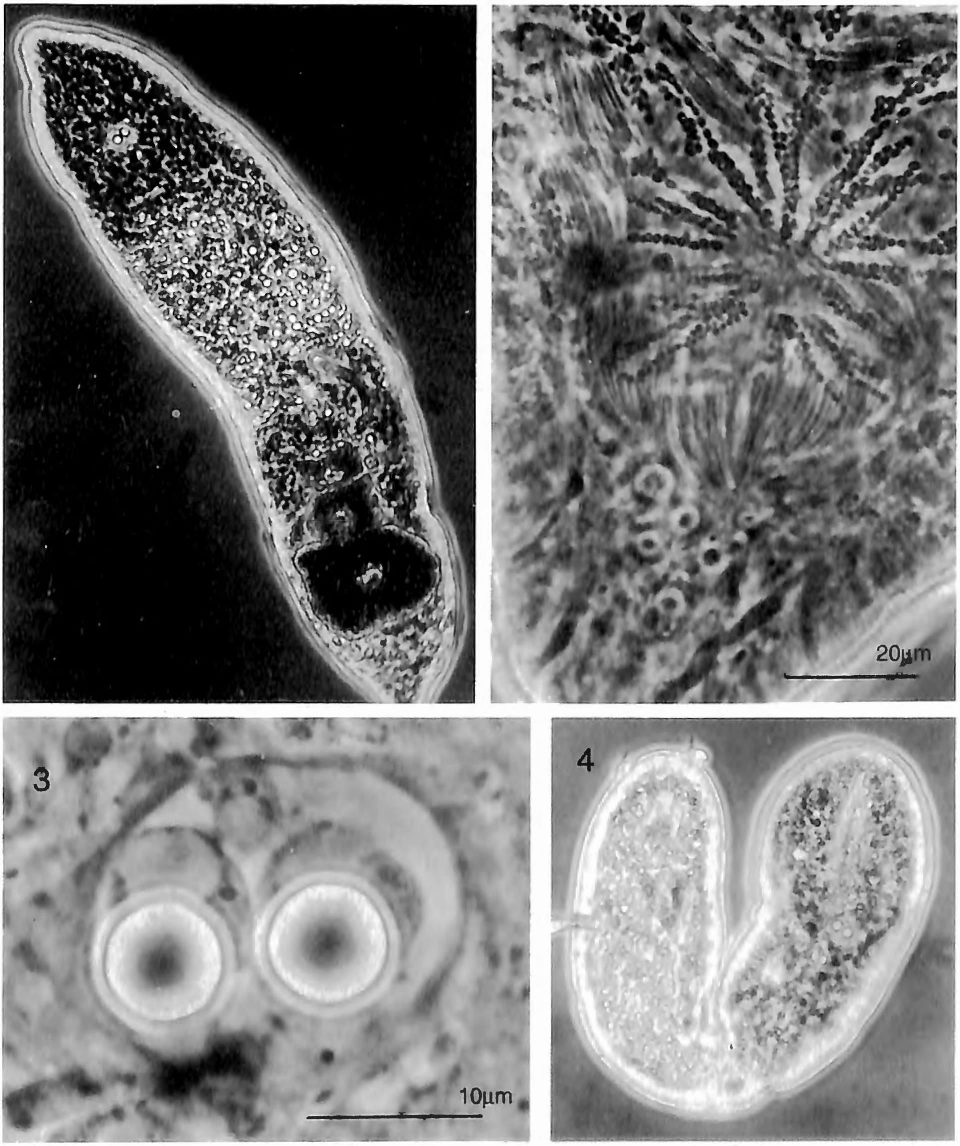

Fig. 16. – *Ascoparia secunda,* microphotographs of live specimens. – 1 specimen A, dorsal view; 2 specimen A, male pore; 3 specimen A, statocyst; 4 specimen, B dorsal view. The same scale applies to 1 and 4.

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