

New species of the statocyst-bearing marine dalyellioid genus *Lurus* Marcus (Luridae nov. fam., Turbellaria-Rhabdoceola).

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Résumé : Trois nouvelles espèces dont deux provenant de l'Atlantique nord-ouest (*L. castor* et *L. pollux*) et une du Pacifique (*L. tyndareus*) sont ajoutées à *Lurus evelinae* Marcus, 1950. La présence d'un statocyste, caractère unique dans l'ordre Rhabdoceola, justifie la création de la nouvelle famille des Luridae. La variabilité du nombre de statolithes est comparée à celles des Catenulida-Retronectidae, et l'anatomie des organes reproducteurs est discutée au sein des Dalyellioida.

Abstract : Three new species, two from the NW. Atlantic *Lurus castor* and *L. pollux* and one from the S. Pacific, *L. tyndareus*, are added to *Lurus evelinae* Marcus, 1950. The uniqueness of *Lurus* as the only genus of the order Rhabdoceola possessing a statocyst is acknowledged with the erection of a new family, Luridae. Variability of statolith numbers is compared with that of Catenulida-Retronectidae, and the anatomy of the reproductive system is discussed within the framework of Dalyellioida.

INTRODUCTION

In 1950 Marcus described, from the coast of Brazil, the marine microturbellarian *Lurus evelinae*, which combined the general organization of the family Provorticidae with the presence of a statocyst - a character association hitherto unknown in the order Rhabdoceola. From 1968 on we have been finding further representatives of this genus, first on the east coast of the United States, and more recently in the South Pacific. We here describe three additional species of *Lurus*, two from the North Atlantic off North Carolina, one from Fiji, and establish the new family Luridae within the order Rhabdoceola. The fine structure of the statocyst will be the topic of a separate paper (Rieger *et al.*, in press).

MATERIAL AND METHODS

A total of 5 samples yielded *Lurus castor* and/or *L. pollux* ; they all came from the NW Atlantic continental shelf in the vicinity of Cape Lookout, off Beaufort (North Carolina, USA) and were taken on cruises of R/V EASTWARD. The data for the 3 most productive samples are as follows :

1. "Sample 76" : Eastward Cruise E 48-68, Station #10999 ; lat. 34°45'0, long. 75°45'0 ; 25 November 1968 ; depth 41 m. Clean coarse sand with shell particles, taken with a Pearse dredge. The associated fauna included Gnathostomulida (*Austrognatharia*, *Haplognathia*),

Turbellaria (*Retronectes*, *Nemertoderma*), Gastrotricha (*Chordodasys riedli* ; see Schöpfer-Sterrer 1969 for a more complete list), Archiannelida (*Protodrilus*), Solenogastres, Acochliadia (*Microhedyle*), nummulitiform Bryozoa (*Cupuladria doma*), and *Branchiostoma*.

2. "Sample 125" : Eastward Cruise, Station #11567 ; lat. 34°18'0, long. 76°13'6 ; 18 March 1969 ; depth 40 m. Clean coarse sand with shell particles. Associated fauna : Turbellaria (*Retronectes*, *Nemertoderma*, *Florianella bipolaris* ; see Rieger & Sterrer 1975), Gastrotricha (*Chordodasys riedli*), Archiannelida (*Diurodrilus*) Acochliadia (*Microhedyle*), Bryozoa (*Cupuladria doma*) and *Branchiostoma*.

3. "Sample D" : Morehead Harbor, off terminal pier in the turning basin ; 26 April 1969 ; depth 12-15 m. Taken with a Petersen grab. Associated fauna : Ciliata, Gastrotricha, Archiannelida (*Diurodrilus*). *Lurus tyndareus* was only found in one sample (F 13, see Sterrer 1991) : South Pacific at Fiji (Great Astrolabe Reef south of Viti Levu ; near the northern tip of the island of Ndravuni ; fine sand between sea grass at 3 m depth ; collected 9 July 1986). The associated fauna included 2 species of Gnathostomulida (*Austrognatharia pecten* Sterrer, 1991 and *Tenuignathia vitiensis* Sterrer, 1991).

Sand samples were collected by dredging (in N. Carolina) or by SCUBA using a hand-held bucket (in Fiji). Specimens were extracted with $MgCl_2$ and studied alive with phase contrast light microscopy ; scale drawings were made with a camera lucida. Some NC specimens were fixed in warm Bouin and serially sectioned according to Antonius (1965), some Fiji specimens were fixed for resin embedment according to Eisenmann & Alfert (1982).

For the description of morphological features a relative scale is used in addition to measurements in μm ; it equates the body length of each specimen with 100 units (U) and then expresses relative positions and sizes of organs in these units (Rieger & Sterrer 1968).

Type material has been deposited with the Swedish Museum of Natural History (SMNH) at Stockholm (Sweden).

DESCRIPTIONS

Lurus castor nov. spec.

(Fig. 1, 2)

Material : 28 specimens, all sexually mature, in squeeze preparation ; 5 serial sections (1 sagittal, 1 frontal, 3 cross sections).

Distribution : NW Atlantic ; subtidal sand off North Carolina.

Types : Holotype a sagittal section. Paratypes 1 frontal section and 3 cross sections.

Name : In Greco-Roman mythology, Castor and Pollux are twin deities, inseparable in the heavens and the netherworld - just as the two species of *Lurus* often occur in the same sample, in distinguishable under the dissecting microscope.

External features : Free-swimming adults measure 380-500 μm in length and are about 60 μm wide at U 80. They are slender, with a tapering, pointed anterior end and a more conical posterior end which may be drawn out into a sharp tail. The body is colorless ; in transmitted light the anterior and posterior portions appear translucent while the bulk of the body is dark-opaque. The anterior end is beset with sensory cilia. The animal swims steadily yet slowly, moving its head from side to side in a regular pendulum swing.

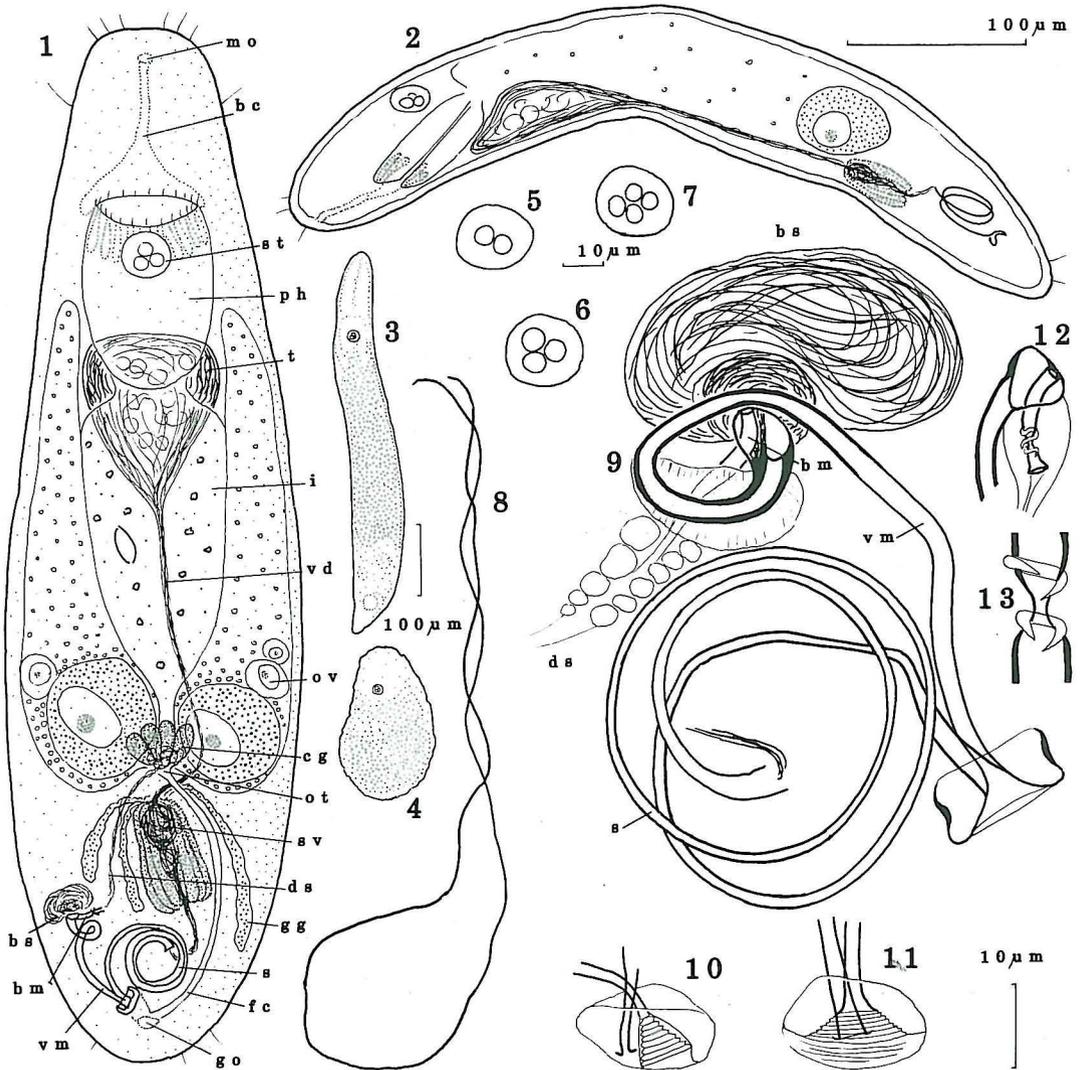


Fig. 1: *Lurus castor* nov. spec. 1.1. organization, dorsal view; 1.2. left lateral view; 1.3. free swimming animal; 1.4. contracted animal; 1.5.-1.7. statocysts of 3 specimens; 1.8. sperm; 1.9. cuticular parts of reproductive system; 1.10.-1.11. distal end of stilet and bursa mouthpiece of 2 specimens; 1.12. junction between vagina mouthpiece and bursa mouthpiece; 1.13. detail of bursa mouthpiece nozzle. The scales apply to 1-2, 3-4, 5-7, 8-12, respectively.

Epidermis : Thickness 4-5 μm ; neither in phase contrast of live animals nor in light histological sections can cell borders be distinguished (but see *L. tyndareus*, below).

Nervous and sensory system : Serial sections reveal that the brain is situated above the pharynx, just anterior to the statocyst. A more or less spherical statocyst of 15-20 μm diameter is found above the pharyngeal canal at U 17-24. In 23 specimens (82 %) it contained 3 statoliths ; in 4 (14 %), however, there were 4, and in one specimen (4 %) there were 2 statoliths (Table I). Statoliths are round to slightly irregular-elongated, homogeneous, translucent, and without a discernible plasma cap. They touch but are not connected with each other. Live observations suggest there is one dorsally located nucleus near the statocyst wall (the statolith-forming cell?). Serial sections show that the statocyst is situated behind the brain ; and the statoliths often appear as hollow spheres.

Digestive system : The mouth opening (mo) is subterminal-ventral and opens into a 50-100 μm long buccal canal (bc) at the end of which the pharynx (ph) is located. About 60-80 μm long and barrel-shaped, the pharynx is directed rostro-ventrally. Caudodorsally it opens into the intestine (i) which extends to about U 75. A diatom was seen in one specimen. About 2/3 down the length of the pharynx, the pharyngeal lining epithelium contains a few intraepithelial nuclei. In the one specimen sectioned sagittally the pharynx showed a distinct concentration of pharyngeal glands in a distal and a proximal ring. In one section the glands of the proximal ring seemed to be located extrapharyngeally.

Reproductive system : Of 6 squeezed specimens analyzed in detail, 5 had both male and female organs fully developed ; the sixth had only male organs. Since this was the first specimen encountered, however, it is possible that the female organs were simply overlooked.

Male organs : Triangular both in dorsal and lateral view and 50-65 μm long, the single testis (t) stretches from U 22 to U 42, ventrally behind the pharynx. The testis tapers caudally into a single, medio-ventral vas deferens (vd) which in turn enters a seminal vesicle (sv) at about U 70. Urn- or barrel-shaped, the seminal vesicle is situated within the copulatory bulb ; the latter is surrounded by circular muscles and lined with longitudinally arrayed packets of finely granular prostatic gland cell necks. Irregularly flask-shaped prostatic glands containing coarse granules (gg) fill most of the animal's tail section and empty frontally into the seminal vesicle, together with the vas deferens. The seminal vesicle usually contains a bundle of tightly coiled sperm. A short canal leads from the caudal end of the copulatory bulb to the proximal opening of the male copulatory stylet (st). The male stylet is a strongly sclerotic (see Karling 1986 for terminology), narrow tube of 1 μm diameter, which forms about 2 1/2 coils of 35 μm diameter. Proximally it begins with a short funnel ; distally it unites with another cuticular structure, the vagina mouthpiece (vm), to form a joint end piece with a broad, recurved rim. The lumina of the two stylets open separately within this end piece : the stylet as a simple pore, the vagina mouthpiece as a flaring funnel with concentric ridges. The sperm is a thin, 340-370 μm long filament that, in phase contrast, appears devoid of any differentiations but is capable of undulating motion.

Female organs : The vagina mouthpiece (vm), 100 μm long and 2.5 μm in diameter, is a more or less straight tube except for an almost circular proximal part where it opens into the



Fig. 2: *Lurus castor* nov. spec. Phase contrast photographs of live specimens. 2.1. left lateral view ; 2.2.-2.4. statocysts of 3 specimens. 2.5. sclerotic parts of reproductive system (strongly squeezed) ; 2.6. junction between vagina mouthpiece and bursa mouthpiece.

bursa (Better : the seminal receptacle : bs). It is here that it joins, and forms a common sclerotic basis with the bursa mouthpiece (bm), which connects the bursa (bs) with the ductus spermaticus (ds) that leads to the ootype (ot). The latter is surrounded by a rosette of shell glands (cg). The bursa mouthpiece is tubular, 12-18 μm long and 2 μm in diameter. It has a circular restriction (nozzle) near its free end ; externally, the nozzle is flanked by 2 spiral ribs. This nozzle was absent in at least 2 specimens. The seminal receptacle is round or kidney-shaped (20 μm x 35 μm) and filled with sperm. The ductus spermaticus is often accompanied by large granules or vacuoles (Fig. 1. 9).

There are 2 female gonads (ov) which stretch from U 27 to U 80 on either side of the body. They are vitellaria in their larger anterior section, and germaria in the posterior section which open into a median ootype (ot) surrounded by cement glands. The female canal (fc) runs from the ootype to the gonopore. Oviducts connecting the female gonads were not observed.

Lurus pollux nov. spec.

(Fig. 3, 4)

Material : 14 specimens of which 13 were sexually mature, in squeeze preparation ; 2 serial (cross) sections.

Distribution : NW Atlantic ; subtidal sand off the coast of N. Carolina.

Types : Holotype a series of cross sections. Paratype a series of cross sections.

Name : In Greco-Roman mythology, Pollux is the inseparable twin of Castor.

External features : Free swimming adults measure 350-400 μm in length and 65 μm in width at U 65. They are slender, with a gently tapering yet blunt anterior and a more conical posterior end. Color is lacking ; the body is opaque in transmitted light except for the pre-pharyngeal and postgenital regions which are more translucent. The animal swims slowly and contracts to a sphere when disturbed, often attaching itself with its posterior end to the substratum.

Epidermis : Thickness about 3 μm , increasing to 5 μm at the ends of the body. Rhabdites and frontal glands are lacking.

Nervous and sensory system : All specimens had a spherical statocyst of 15-20 μm diameter behind the brain, at U 15-23. It contained 2-5 statoliths ; one specimen had 2, six had 3, four had 4, and two specimens had 5 statoliths. Statoliths are usually clustered together but not connected. They are mostly near-spherical and 5-6 μm in diameter ; a few were elongated to the point where it looked as if each had originated from the fusion of two statoliths. In sections, the statocyst looks identical to that of *L. castor*. In one specimen we observed 4 concretions outside the statocyst, which may correspond to the "crystalloid bodies" observed by Marcus (1950 ; Fig. 55) in *L. evelinae*.

Digestive system : The mouth is located slightly ventrally to the anterior tip of the animal. It opens into a buccal canal, up to 100 μm long, in which the pharynx moves back and forth. The barrel-shaped pharynx is 60 μm long ; its anterior end is set with stiff, simple bristles, and its muscular wall contains granular glands. In one squeezed specimen 3 girdles

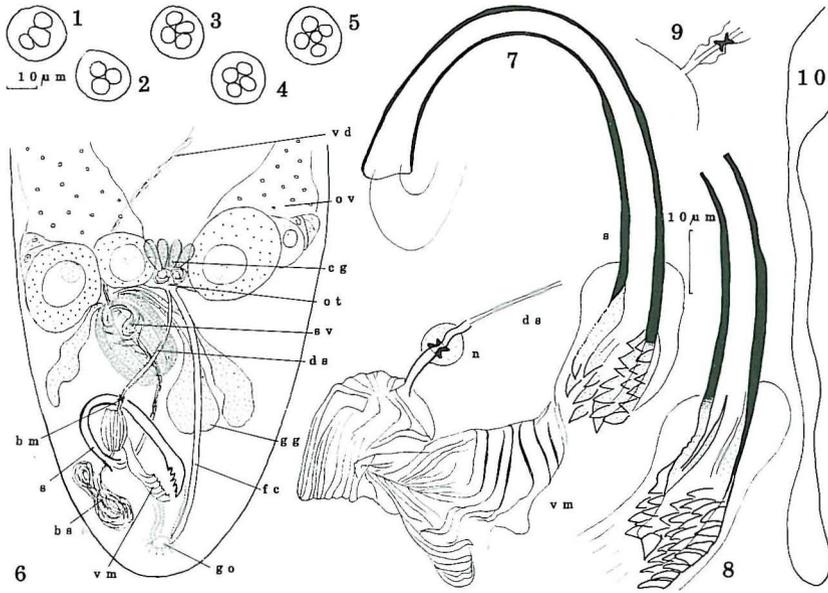


Fig. 3 : *Lurus pollux* nov. spec. 3.1-3.5. statocyst of 5 specimens ; 3.6. organization of reproductive system, dorsal view ; 3.7. cuticular parts of reproductive system ; 3.8. distal part of stylet of another specimen ; 3.9. bursa mouthpiece ; 3.10. sperm. The scales apply to 1-5 and 7-10 respectively.

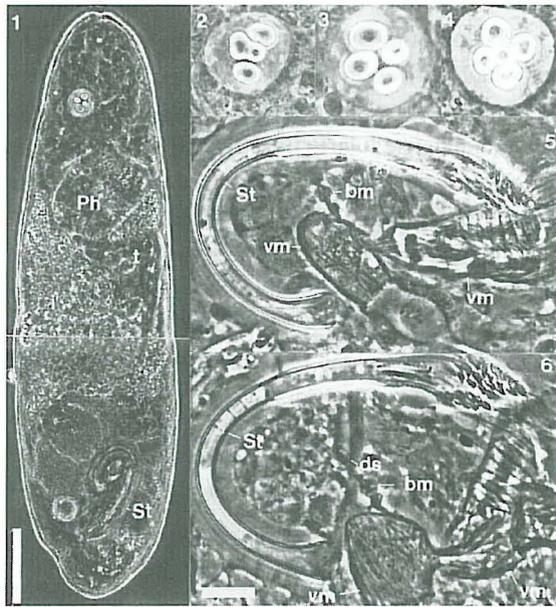


Fig. 4 : *Lurus pollux* nov. spec. Phase contrast photographs of live specimens. 4.1. right lateral view ; 4.2.-4.4. statocysts of three specimens ; 4.5.-4.6. sclerotic parts of reproductive system. Scale bar for 1 is 50 µm, scale bar for 2-6 is 10 µm.

of pharyngeal glands were obvious (a distal ring, also confirmed in another specimen ; a smaller median, and a proximal ring). The gut is often filled with large (to 5 μm diameter), round reddish inclusions.

Reproductive system : Of 13 squeezed specimens examined, 12 had both male and female organs.

Male organs : The single, conical testis (t) extends from U 35 to U 50, ventrally to the pharynx ; its pointed caudal end continues into the single, medioventral vas deferens (vd). The sperm, in phase contrast, is an unstructured filament of 200 μm length which performs undulating motions ; only a 13 μm long end piece (head? tail?) appears stiff. At U 70, the vas deferens enters a bulbous seminal vesicle (sv), which in turn is situated in the copulatory bulb and lined with finely granular secretions connected to the irregularly flask-shaped glands that surround it. The proximal lumen of the vesicle usually contains a bundle of sperm which tapers distally into the short canal that connects the vesicle to the male stylet. The male stylet (st) is a sclerotic tube of 4-5 μm diameter and 110-125 μm length, curved somewhat like a fish hook. It widens proximally into a short, 8 μm wide funnel ; distally its wall thickness increases, and it ends in a complex array of 3-5 μm long teeth arranged in 4 longitudinal rows.

Female organs : There are 2 germaria (g) around U 65, with eggs maturing caudally ; although not seen in detail we suspect paired vitellaria (v) extending latero-frontally. The germaria join medially at the ootype (ot) which is surrounded by a rosette of glands, usually contains loosely coiled sperm, and is connected to the bursa mouthpiece (bm) via a ductus spermaticus (ds). The bursa mouthpiece, 11-15 μm long, is a more or less straight cuticular tube of 1 μm diameter which carries an externally reinforced nozzle about 2/3 of its length from where it connects to the vagina mouthpiece (vm). The latter consists of 2 parts : a barrel-shaped proximal part and an irregularly tube-shaped distal part ; the barrel is entered by the tube at its widest girth. Together, the 2 parts measure 50-56 μm in length ; both are lined, accordion-style, with longitudinal folds. The folds of the distal, tube-shaped part are loosely connected with the distal portion of the male stylet, both sharing a common genital opening, ventrally at U 95. The barrel-shaped part of the mouthpiece is thus open at 3 places : in the middle (where it connects with the tube-shaped part), and at both ends where it connects with the bursa mouthpiece and the bursa proper, respectively. The bursa appears as an unstructured chamber filled with sperm.

Lurus tyndareus nov. spec.

(Fig. 5, 6)

Material : 5 specimens in squeeze preparation ; 1 semi-thin serial section.

Distribution : S. Pacific at Fiji ; subtidal sand south of Suva.

Types : Holotype a series of semi-thin cross sections. Paratypes 4 resin-embedded blocks.

Name : In Greco-Roman mythology, Tyndareus is the mortal father of Castor.

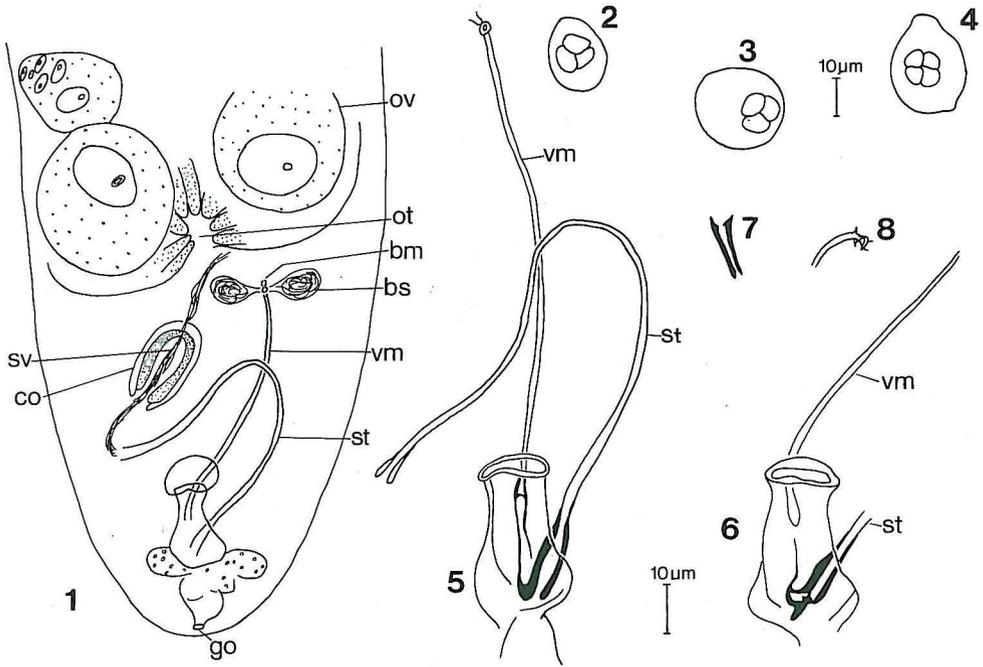


Fig. 5 : *Lurus tyndareus* nov. spec. 5.1. organization of reproductive system ; 5.2.-5.4. statocysts of 3 specimens ; 5.5. cuticular parts of reproductive system of one specimen ; 5.6.-5.8. details of cuticular parts of another specimen. The scales apply to 2-4 and 5-8, respectively.

External features : Adults are 330-340 μm long and 90 μm wide at U 50. The gut is typically filled with large (to 10 μm diameter), round, dark brown inclusions, and thus appears dark in transmitted light.

Epidermis : Preliminary low-power TEM and light microscope studies of semi-thin plastic sections show a particularly dense packing with large secretory vesicles in the cytoplasm (apparently large ultrarhabdites). Because of these vesicles cell borders are difficult to discern but appear to be present, based on tangential sections of the rostral tip. Such vesicles may also be present in the other 2 new species.

Nervous and sensory system : The statocyst is located at U 17-21. It is more or less spherical, 20-25 μm in diameter, and contains 3-4 statoliths (3 in 3 specimens, and 4 in 2 specimens). Statoliths adhere loosely to each other and are easily separated by squeezing.

Semi-thin sections clearly show that the anterior portion of the statocyst is intimately associated with the brain, while the caudal portion is completely embedded in and difficult to distinguish from the gut issue.

Digestive system : A massive pharynx, 60 μm long and 55 μm wide, extends from U 15 to U 33.

Reproductive system : The 4 adult specimens analyzed had both male and female organs fully developed.

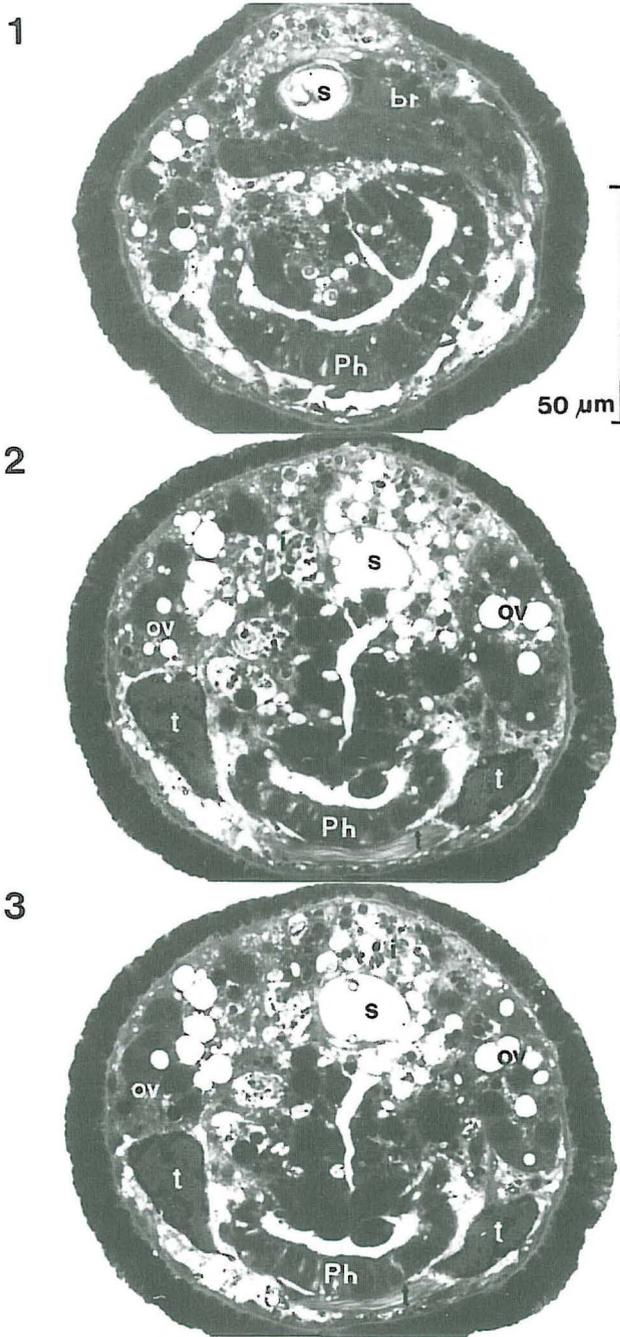


Fig. 6 : *Lurus tyndareus* nov. spec. Semi-thin cross sections through the region of the statocyst 6.1, just behind the brain ; 6.2. & 6.3. in the posterior part of the statocyst.

Male organs : The single testis extends from U 20 to U 35, ventrally and caudally of the pharynx. It continues caudally into a single vas deferens which enters a barrel-shaped copulatory bulb (co) at U 82. The seminal vesicle (sv) lies inside the copulatory bulb. The caudal end of the copulatory bulb connects with the male copulatory stylet, a simple, curved tube of 2-3 μm diameter and 140-160 μm length. The wall of the proximal end is thickened, as is that of the distal end which joins the urn-shaped structure of the genital opening.

Female organs : The vagina mouthpiece (vm) is a more or less straight tube of 105 μm length and 2 μm diameter. Distally it opens into the urn-shaped cuticular structure of the genital pore, facing the stylet opening ; proximally it merges with what must be the bursa mouthpiece (bm), an externally reinforced nozzle. The seminal receptacle (bs) appears distinctly bipartite. There are 2 female gonads (ov) which extend laterally from U 30 to U 80. They are made up of anterior vitellaria and posterior germaria which open into a central ootype (ot).

DISCUSSION

Systematics of the new species

The overall agreement between *Lurus evelinae* Marcus and our new species is so great that there is little doubt about their being related at least within the same family. Several differences between *L. evelinae* on one hand, and the 3 new species on the other, may eventually suggest a generic separation.

First of all, *L. evelinae* is unique in its possession of two vasa deferentia and two (although sometimes coalescing) testes, in contrast to the invariably single testis and vas deferens in all 3 of the new species. Second, Marcus (1950) stresses the differentiation between a vesicula seminalis and a vesicula granulorum ; in the new species, the vesicula seminalis is always surrounded by the proximal portion of the vesicula granulorum. A third difference may lie in the separation between germaria and the vitellaria in *L. evelinae*, when in the new species their interface seems to be rather continuous. However, at this time we choose to forgo a generic separation pending the discovery of further species or a detailed re-examination of *L. evelinae*.

Position of *Lurus* within the order Dalyellioida

The presence of an entirely sclerotic vagina-bursa mouthpiece system is viewed as a derived condition. On the basis of hard structures (Fig. 7.1) the 4 species form a series of increasing sclerotization of the vagina mouthpiece, from *L. pollux* in which there is a wide canal with a weakly cuticularized, many-folded wall, to the more tubular yet still weak structure in *L. evelinae* (which Marcus describes as cuticularized only in its ental, i.e., bursal, part) ; to the robust, stylet-like tube of *L. castor* in which only the accordion folds of the common distal funnel remind of *L. pollux* ; and finally the well-defined urn and tube of *L. tyndareus*. The complicated arrangement of the highly sclerotic system made up of vagina, bursa mouthpiece and male stylet in *Lurus* is similar not only to the basic design of

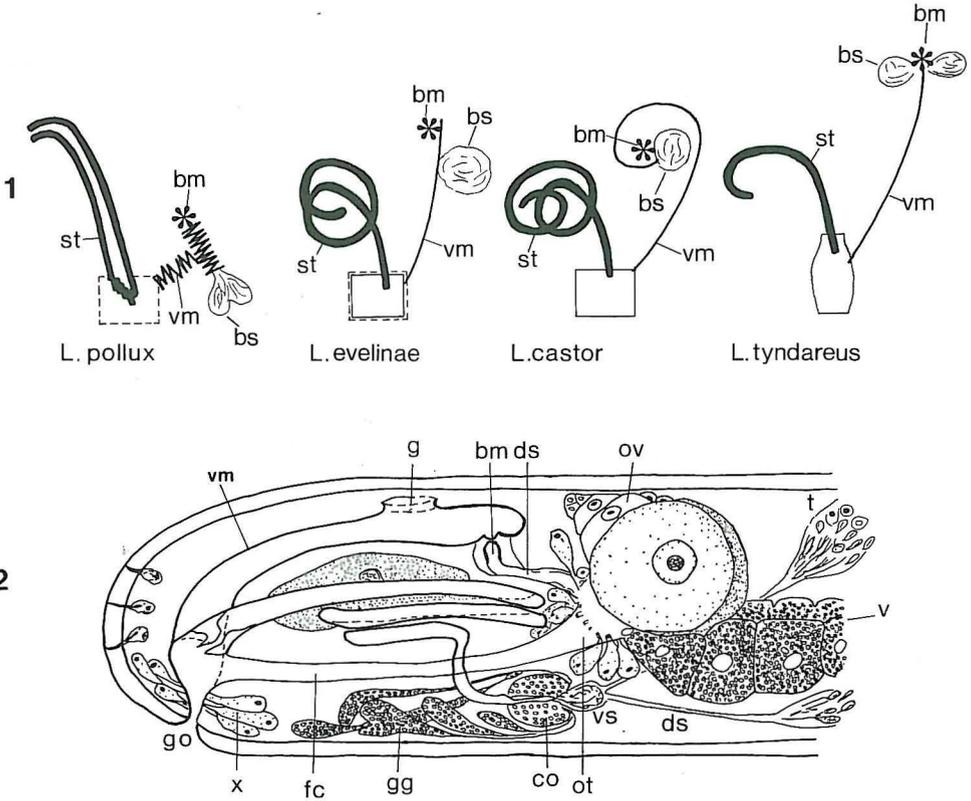


Fig 7 : *Lurus* spp 7.1. schematic comparison of sclerotic structures of reproductive system ; 7.2. *L. evelinae*, right lateral view of reproductive system (redrawn from Marcus 1950, fig. 56). We interpret the lateral opening of the vagina mouthpiece (g) as homologous with the connection to the seminal receptacle (bs) in other species.

Provorticidae (as noted by Marcus 1950), but agrees even more with that of the Umagilidae (Lehman 1946, Shinn 1982, Cannon 1987) and certain Hypoblepharidae (Karling & Nielsson 1974). It remains questionable whether the female canal for oviposition in *Lurus* (not seen in *L. tyndareus*), *Syndisyrix* and *Provortex* is homologous with the female canal in other Dalyellioida, which do not have separate canals for oviposition and transfer of foreign sperm to the ootype. Rieger (1974) has provided reasons to assume that, in the typhloplanoid *Kytorhynchus oculatus*, the canal system for oviposition may be secondary, and the original female canal had been modified into a bursal organ. One difficulty of such an assumption is that the position of the shell glands apparently has not changed in *K. oculatus* (see Rieger 1974, fig. 10). Generally the canal system in Turbellaria appears to have a dual origin (Karling 1940, Rieger *et al.* 1990), i.e., from the tunica of the gonad and from an invagination of the body wall. It seems possible, therefore, that changes in the developmental timing of the two parts of the canal system might have resulted in differences as to how they are connected.

In *Lurus*, *Provortex*, *Syndisyrix* and *Hypoblepharina* the position of the system made up of vagina, receptacle, bursa mouthpiece and ductus spermaticus in relation to the atrium genitale and the other parts of the reproductive system is rather similar to the original female canal plus seminal receptacle system in other dalyellioids, which lack a dual connection between female gonad and atrium ; instead, the original female canal enters the common genital atrium dorso-caudally and often has a small, bladder-like seminal receptacle attached dorso-caudally, just prior to its connection with the female gonad. On the basis of the relative position of genital ducts we propose the hypothesis that the female egg laying canal in *Lurus*, *Provortex*, *Syndisyrix* and *Hypoblepharina* may also be interpreted as a secondary structure, and that the original female canal system corresponds to the vagina-receptacle-bursa mouthpiece-sperm duct system. Irrespective of the homology question concerning the female canal raised here, Karling (1956, p. 340) already suggested a closer grouping of these genera :

“...In der aberranten Art *Lurus evelinae* (Marcus, 1950) tritt uns eine Art entgegen, die in ihrer Organisation den Umagilliden auffallend nahe kommt (vgl. besonders die caudale Verschiebung der Genitalöffnung, die Bursa copulatrix mit Ductus spermaticus, den langen, kutikularen Ductus ejaculatorius). Ein Zusammenführen der frei lebenden marinen Verwandten der Familie Umagillidae, d.h. der Gattungen *Provortex*, *Hypoblepharina* und *Lurus* würde sich vielleicht als ein Schritt in rechter Richtung erweisen...”

This similarity between the 3 genera in the relative position of genital ducts can be seen as a homoiology, i.e., parallel evolution from a similar ancestral organization. For this reason we do not think that *Lurus*, the Provorticidae, Umagillidae and Hypoblepharinidae should be combined into a monophyletic taxon but rather that they represent parallel lines that evolved from a similar parent stock of Dalyellioida.

The statocyst of *Lurus*

The presence of a statocyst in *Lurus* is unique in the order Rhabdozoela. Among Turbellaria, a statocyst is found in all Nemertodermatida, in most Catenulida and Acoela, and in many Proseriata (Ehlers 1985). The statocyst of Acoela and Proseriata invariably contains one statolith, that of Nemertodermatida contains two. In several respects the statocyst of *Lurus* is similar to that of Catenulida, especially the genus *Retronectes* Sterrer & Rieger (1974). The *Lurus* statocyst is round (rather than transversely oval, as in Nemertodermatida), and statoliths are somewhat irregularly shaped (rather than perfectly round, as in Acoela and Nemertodermatida). Furthermore, the statoliths themselves do not have a cap of plasma and/or cell nuclei (as is typical for Acoela, Nemertodermatida and the rather different Proseriata), but appear devoid of such, as are Catenulida. Unlike the statoliths of all other Turbellaria which are not dissolved during resin embedment, those of *Lurus* are, which suggests a quite different chemical composition (Rieger *et al.*, in press). Similar differences in the reaction to resin embedment have been described for body wall spicules in the Turbellaria Bertelliellidae and the peculiar *Acanthiella chaetonotoides* (Rieger & Sterrer 1975).

The *Lurus* statocyst usually contains two or more statoliths), with a considerable degree of intraspecific variability (Table I). Again, this is not unlike the variability found in some Retronectidae. Of 3 specimens of *Retronectes melpomene*, for instance, two had one statolith, and one specimen had five; of two specimens of *R. terpsichore*, one had one statolith and the other two (Sterrer & Rieger 1974).

TABLE I

Intraspecific variability of statolith number in *Lurus* spp.

specimens of	number of statoliths				mean
	2	3	4	5	
<i>L. evelinae</i>	30				
<i>L. castor</i>	1	23	4	0	3.11
<i>L. pollux</i>	1	6	4	2	3.54
<i>L. tyndareus</i>	0	3	2	0	3.40

The apparently close similarity between catenulid and lurid statocysts on the light microscopy level needs to be followed up with a thorough ultrastructural analysis (Rieger *et al.*, in press) before any further phylogenetic conclusions can be drawn. The available semi-thin sections suggest a distinct difference between the catenulid and lurid statocysts, mostly because of the peculiarly close association with the gut tissue in the latter. However, if one accepts the statocysts of Luridae and Catenulida as instances of parallel evolution - as we do for the time being - then the remarkable degree of similarity should warn us that there may be many more instances of structural "identity" which, on closer inspection, will turn out to be of independent origin.

DIAGNOSES

Diagnosis of Luridae nov. fam.: Dalyellioida with a statocyst. Testis and vas deferens unpaired, or paired with a tendency to coalesce. Female gonad usually paired and separated into germaries and vitellaries. With a common ventral gonopore near the caudal end of the body; copulatory organ with a sclerotic stylet; female canal usually provided with sclerotic vagina mouthpiece and bursa mouthpiece. Type genus: *Lurus* Marcus, 1950 (amend.).

Diagnosis of *Lurus* (amended from Marcus 1950): Luridae with usually polyolithophorous statocyst. Copulatory stylet and vagina mouthpiece usually united distally in common sclerotic duct. Type species: *L. evelinae* Marcus, 1950.

Diagnosis of *L. evelinae* Marcus, 1950 (amended from Marcus 1950): *Lurus* with paired vasa deferentia and testes, the latter often coalescing. Copulatory stylet tubular, forming about 2 1/2 coils. Vagina mouthpiece a slightly curved, wide tube. Seminal receptacle near but not at the distal end of the vagina mouthpiece.

Diagnosis of *L. castor* nov. spec.: *Lurus* with single testis and vas deferens. Copulatory stylet is a 1 µm wide tube forming 2 1/2 coils of about 35 µm diameter. Vagina mouthpiece

is a proximally curved, but otherwise rather straight tube 2.5 μm wide and 100 μm long. Junction between stylet and vagina mouthpiece is funnel-shaped. Bursa mouthpiece 2 μm wide, 12-18 μm long. Seminal receptacle situated at the proximal end of the vagina mouthpiece. Sperm filiform, 340-370 μm long.

Diagnosis of *L. pollux* nov. spec.: *Lurus* with single testis and vas deferens. Copulatory stylet is a fishhook-shaped tube, 4-5 μm wide and 110-125 μm long, with complex array of teeth at distal end. Vagina mouthpiece barrel-shaped proximally, irregularly tube-shaped distally. Junction between stylet and vagina mouthpiece is accordion-like. Bursa mouthpiece 1 μm wide and 11-15 μm long. Seminal receptacle situated midway of the vagina mouthpiece. Sperm filiform, 200 μm long.

Diagnosis of *L. tyndareus* nov. spec.: *Lurus* with single testis and vas deferens. Copulatory stylet a curved tube 2-3 μm wide and 140-160 μm long. Vagina mouthpiece is a straight tube 2 μm wide and 105 μm long ; bursa mouthpiece not conspicuously separate. Junction between stylet and vagina mouthpiece is urn-shaped. Seminal receptacle situated at the proximal end of the vagina mouthpiece.

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FIGURE ABBREVIATIONS

bc	buccal canal
bm	bursa mouthpiece
br	brain
bs	bursa (seminal receptacle)
cg	shell glands
co	male copulatory bulb
cs	common sclerotic basis of vagina mouthpiece and male stylet
ds	ductus spermaticus
fc	female canal
g	opening to seminal receptacle
gg	prostatic glands
go	genital pore
i	intestine
m	mouth opening
ot	ootype

ov	female gonads
ph	pharynx
s	statocyst
st	male copulatory stylet
sv	seminal vesicle
t	testis
v	vitellaria
vd	vas deferens
vm	vagina mouthpiece
x	cement glands.

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