

## Skeneimorph but not skeneid: systematics and anatomy of *Lodderena* Iredale, 1924 (Vetigastropoda: Trochoidea)

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### ABSTRACT

The genus *Lodderena* Iredale, 1924 has been classified in the Skeneidae by most recent authors. However, this family, originally characterized by their minute size, lack of nacre in the teleoconch and a rhipidoglossate radula, is currently considered to be polyphyletic assemblage, and preliminary molecular systematic data suggest exclusion of *Lodderena* from Skeneidae. In order to shed light on the systematic position of this genus, we provide a detailed description of the anatomy and histology of the type species, *Lodderena minima* (Tenison-Woods, 1878), and of *L. ornata* (Olsson & McGinty, 1958). The anatomical data confirm the vetigastropod-trochoid nature of *Lodderena* but exclude the genus from Skeneidae. Skeneidae are mainly characterized by a propodial penis, a hermaphroditic condition with separated testis and ovary, and a large receptaculum in the mantle roof. In contrast, *Lodderena* species lack both a copulatory organ and receptaculum, and have a true ovotestis. We also provide a critical review of nominal species in the genus. Based on molecular and morphological evidence, we exclude *Lodderena* from Skeneidae, instead treating it as a genus *incertae sedis* within Trochoidea. We discuss the implications of small size for functional morphology and reproduction.

### INTRODUCTION

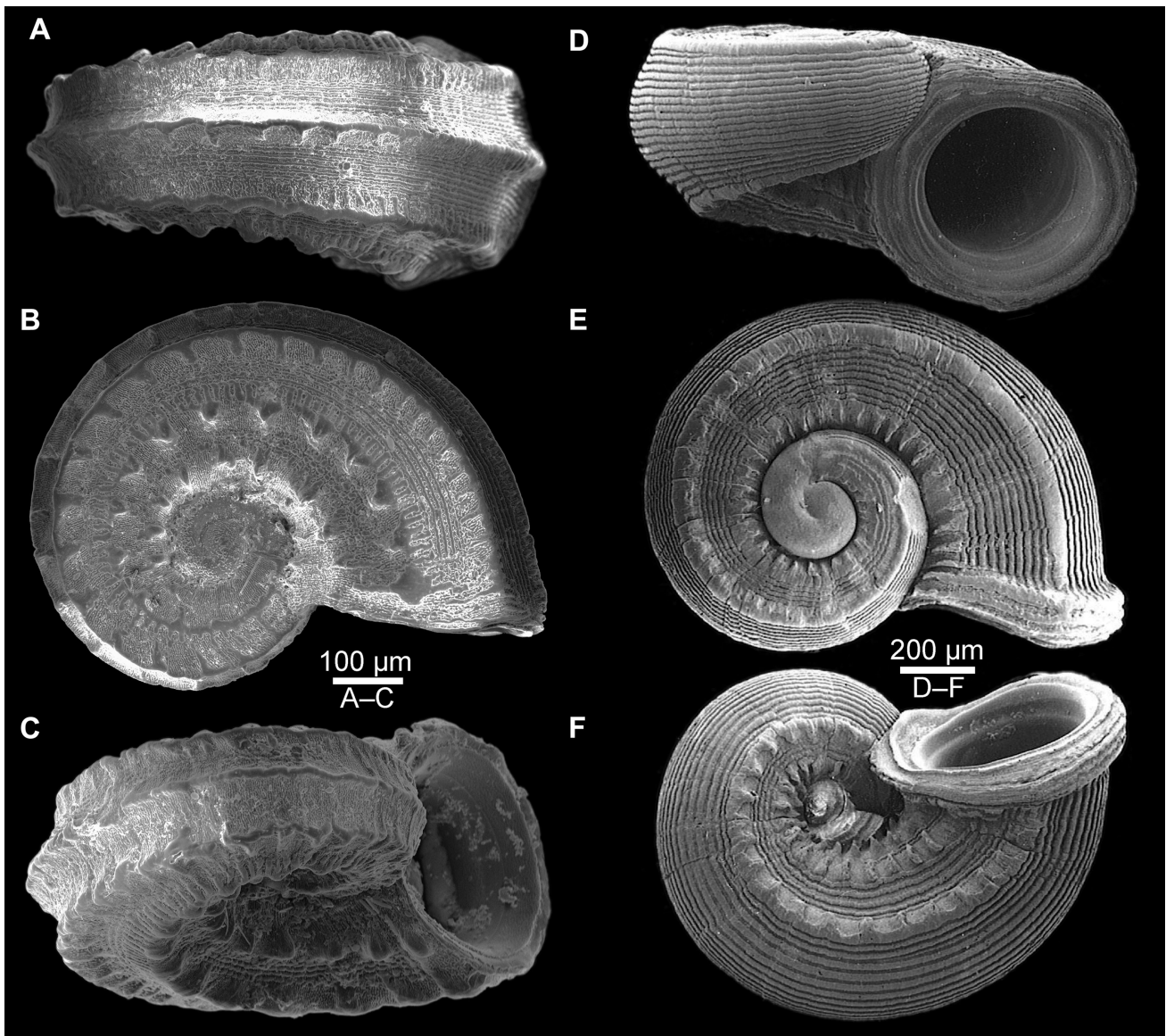
During the last decade, ‘skeneimorph microgastropods’ (small gastropods with rhipidoglossate radula but lacking a nacreous shell layer) have been shown to belong to various, phylogenetically distant gastropod clades, namely Heterobranchia-Hyalogyrinidae (Haszprunar *et al.*, 2011), Neomphalida (Heß *et al.*, 2008) and several clades of Vetigastropoda (Scissurelloidea, Seguenzioidea and Trochoidea). Recently, the family Skeneidae, formerly a notorious taxonomic catch-all, has been redefined as a clade on the basis of several synapomorphies: a hermaphroditic gonad with separated testis and ovary, a propodial penis and a large receptaculum in the mantle roof, in addition to a (strongly homoplastic) monopectinate ctenidium and a monotocardian heart condition (Haszprunar *et al.*, 2016). There is little doubt that the soft-part anatomy or molecular systematics of many of the over 40 genera currently assigned to the family (MolluscaBase, 2019; World Register of Marine Species, WoRMS; Worldwide Mollusc Species Data Base, WMSDB) have to be studied in order to confirm their inclusion in Skeneidae *sensu stricto*.

Iredale (1924) erected the genus *Lodderena* with the type species *Liotia minima* Tenison-Woods, 1878 (Fig. 1D–F) and placed it within Trochidae. At present, the WoRMS ([www.marinespecies.org](http://www.marinespecies.org)) and the WMSDB ([www.bagniliggia.it/WMSD/WMSDhome.htm](http://www.bagniliggia.it/WMSD/WMSDhome.htm)) list 12 valid species for *Lodderena*. Laseron (1954) provided the first generic diagnosis and placed *Lodderena* in Liotiidae, but most cur-

rent authors list the genus under Skeneidae. The latter assumption seemed justified, when Warén (1992) reported a propodial penis for ‘*Lodderena catenoides* (Monterosato, 1877)’, since this is currently considered a diagnostic character for Skeneidae (Warén, 1992; Kunze *et al.*, 2008; Hickman, 2013; Haszprunar *et al.*, 2016).

However, ‘*L. catenoides*’ is now considered to belong to *Skenea* (Rubio, Rolán & Redfern, 1998; Romani, Bogi & Bartolini, 2015), rather than to *Lodderena*. Furthermore, molecular systematic studies of an undetermined *Lodderena* species have placed it not in the Skeneidae, but instead indicate a closer relationship to *Tegula* (Kano, 2008) or Seguenzioidea (Williams, 2012), albeit with weak support. To date, the soft-part anatomy of *Lodderena* is poorly known. The available data are preliminary and scarce (Brückner, Ruthensteiner & Haszprunar, 2004; Kunze *et al.*, 2008; Haszprunar *et al.*, 2016), again raising doubts about the skeneid nature of *Lodderena* Iredale, 1924.

Due to the generosity of Anders Warén of the Swedish Natural History Museum, we were given access to well-preserved soft bodies of *L. minima*, the type species of the genus *Lodderena*. In addition, we also examined the soft anatomy of another species, *L. ornata*, which was described originally from the Caribbean; this species was found alive in sediments of a tropical aquarium in Munich (Fig. 1A–C), where it had been introduced with living corals. In order to infer the systematic position of the genus, we studied the microanatomy and histology of these two species by means of serial semi-thin sectioning and manual graphic reconstructions.



**Figure 1.** *Lodderena ornata* and *L. minima*. SEM images of the shell. **A–C.** *Lodderena ornata*. **A.** Dorsal aspect. **B.** Lateral aspect. **C.** Oblique lateral left aspect. **D–F.** *Lodderena minima*. **D.** Lateral aspect with frontal view of aperture. **E.** Dorsal aspect showing the protoconch. **F.** Ventral aspect. Image credits: **D–F,** A. Warén.

## MATERIAL AND METHODS

### *Lodderena minima* (Tenison-Woods, 1878)

The specimens under investigation (DLG706) were collected by Daniel Geiger from shallow water at low tide on 14 November 2001 by rock washing at Manly Beach, Sydney (New South Wales, Australia), and were originally fixed and preserved in 75% ethanol. The shell was dissolved by immersing the specimens in Bouin's fluid. Two section series of two complete specimens have been deposited in the Bavarian State collection of Zoology (ZSM) (SNSB-ZSM Mol 20190000 and 20190001).

### *Lodderena ornata* (Olsson & McGinty, 1958)

In 1998, several specimens were found alive in the sediment in a tropical seawater aquarium at ZSM. Specimens were identified from scanning electron microscope (SEM) images of the shell (Fig. 1A–C) and radula (cf. Kunze et al., 2008: fig. 3; based on

Brückner, 2003) as a 'skeneimorph vetigastropod'. For soft part examination, the specimens were relaxed in an isotonic  $MgCl_2$  solution and fixed in Bouin's fluid. One complete and two fragmentary section series have been deposited at ZSM (SNSB-ZSM Mol 20080369–20080371). The complete series was used for manual graphic reconstructions of various organ systems and served as base for the drawings presented here.

### Histological methods

Rinsing of Bouin's fluid was performed with 75% ethanol containing a minimal amount of ammonia. Specimens were dehydrated in a graded series of acetone and embedded in Epon (*Lodderena minima*) or araldite (*L. ornata*). Sectioning was carried out with either Histo Jumbo diamond knife (Diatome AG, Biel, Switzerland) (*L. minima*, thickness 1  $\mu m$ ) or Ralph glass knife (*L. ornata*, thickness 2  $\mu m$ ) on a Microm HM 360 microtome (Microm International SA, Lausanne, Switzerland). Ribboned serial sections were prepared and stained with methylene blue-Azur II following Ruthensteiner (2008).

Sections were photographed using a Leica DM-RBE (Leica Microsystems, Wetzlar, Germany) compound microscope.

### Abbreviations

AM	Auckland Museum, New Zealand
ANSP	Academy of Natural Sciences of Drexel University, Philadelphia, PA, USA
BPBM	Bernice P. Bishop Museum, Honolulu, HI, USA
MIMB	Museum of the Institute of Marine Biology of Vladivostok, Russia
MNCN	Museo Nacional de Ciencias Naturales, Madrid, Spain
MNHN	Museum national d'Histoire naturelle, Paris, France
NHMW	Naturhistorisches Museum Wien, Austria
NMNZ	Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand
UCMP	University of California Museum of Palaeontology, Berkeley, CA, USA
USNM	National Museum of Natural History, Smithsonian Institution, Washington, DC, USA
ZMA	Zoologisch Museum Amsterdam, The Netherlands
ZMFU	Zoological Museum of Far Eastern Federal University of Vladivostok, Russia

## RESULTS

The anatomical and histological data for *Lodderena minima* and *L. ornata* are nearly identical; therefore, we provide a single description for both species and comment on the few differences where relevant.

### Head-foot and retractor muscles

In both species investigated, the paired cephalic (Fig. 2B) tentacles are quite long (250  $\mu\text{m}$  in living *L. ornata*), with a round profile and a diameter of only 20  $\mu\text{m}$ . Longitudinal and diagonal muscles form a complex grid within the tentacles. The epithelium of the tentacles is quite flat and lacks regular cilia, but the whole surface is provided with sensory papillae (Fig. 3A), each with a ciliary tuft at the tip. A pigmented eye is situated at the outer base of each cephalic tentacle; an eyestalk is lacking, however.

Beneath the cephalic tentacles, a stout (length 55  $\mu\text{m}$ , diameter 25  $\mu\text{m}$ ) subocular tentacle is present at each side (Fig. 3B). The cubic epithelium lacks cilia except at the tip, which is densely ciliated; papillae are lacking.

*Lodderena minima* shows three pairs of papillate epipodial tentacles. The ventral base of the first epipodial tentacle bears an epipodial sense organ (ESO) with a ciliary tuft at the blunt tip, but without papillae (for terminology of epipodial structures, see Haszprunar *et al.*, 2017). A row of small and sparsely ciliated lappets is situated about 20  $\mu\text{m}$  above the foot edge of the epipodium.

The epipodium of *L. ornata* also bears three pairs of tentacles (Fig. 4B, C). The anterior tentacles are long (120  $\mu\text{m}$ ) and, like the cephalic tentacles, are papillate. The second tentacle is much shorter (60  $\mu\text{m}$ ), bears only two small papillae and the tip is densely ciliated. The posterior tentacles are the shortest ones (30  $\mu\text{m}$ ); they have a broad base, are non-papillate and show terminal ciliation, and thus fulfil the criteria of an ESO (see also the 'Discussion' section). As in *L. minima*, the lateral epipodium shows small (length 70  $\mu\text{m}$ , diameter 20  $\mu\text{m}$ ) and sparsely ciliated lappets (Fig. 4C: ta), which lie *c.* 20  $\mu\text{m}$  above the foot edge.

The foot sole is composed of densely ciliated cells (Fig. 2A), interspersed with subepithelial mucous cells (sole glands). In both species, there is a prominent pedal gland (Fig. 3A), which opens at the central, anterior end of the foot via a short and ciliated channel. The posterior end of the pedal gland fills space between the pedal ganglia and the buccal apparatus. The foot as such is highly mus-

cular, without large haemocoel spaces. Both the intercrossed muscle fibres of the foot and the muscular wall of the head are continued backwards, forming two smooth retractor muscles (Fig. 3F) with distinct attachment zones.

### Mantle cavity

The mantle rim is smooth and lacks papillae; the epithelium of the inner mantle roof is extremely thin (1–2  $\mu\text{m}$ ) and is underlain by haemolymph sinuses. The mantle cavity (Figs 2A, B, 4B, 5C) is moderately deep (*c.* 400  $\mu\text{m}$ ).

The most prominent organ in the mantle cavity is the monopectinate ctenidium with six large lamellae forming a row from right anterior to left posterior (Figs 2A, 3F, 5C). The densely ciliated epithelium of the ctenidial lamellae consists of isoprismatic cells and is quite thick (10  $\mu\text{m}$ ). A respiratory zone with a nonciliated, flat epithelium is entirely lacking, however. Each lamella is equipped with paired skeletal rods enclosing a nerve. Distally there is a prominent bursicle (Fig. 5C), and a blind, ciliated channel (length 30  $\mu\text{m}$ , width 4  $\mu\text{m}$ ) along the efferent axis. Opposite the row of ctenidial lamellae, the central mantle floor shows a long ciliary band (Fig. 6A), the cells of which are much higher (8  $\mu\text{m}$ ) than the adjacent ones (1–2  $\mu\text{m}$ ); the cells of the ciliary band show distal nuclei and a dense microvillous border between the cilia.

An oval, relatively small pallial gland (50  $\mu\text{m}$   $\times$  25  $\mu\text{m}$ ) is located at the centre-left of the mantle cavity. This gland is at the same level as the hypobranchial gland, and its few, cubic cells have a fibrous content. The prominent hypobranchial gland (length 150  $\mu\text{m}$ ) is located at the right side of the posterior third of the mantle cavity and consists of several different regions (Figs 2B, 3E, 4D). The anteriorly located epithelial cells, which occupy about 15% of the length, show heavily stained, grape-like inclusions. The central third of the hypobranchial gland is composed of highly prismatic cells with variably stained content, probably reflecting various stages of merocrine secretion. The posterior part (about half the hypobranchial gland) consists of large, voluminous cells that are poorly stained in the sections.

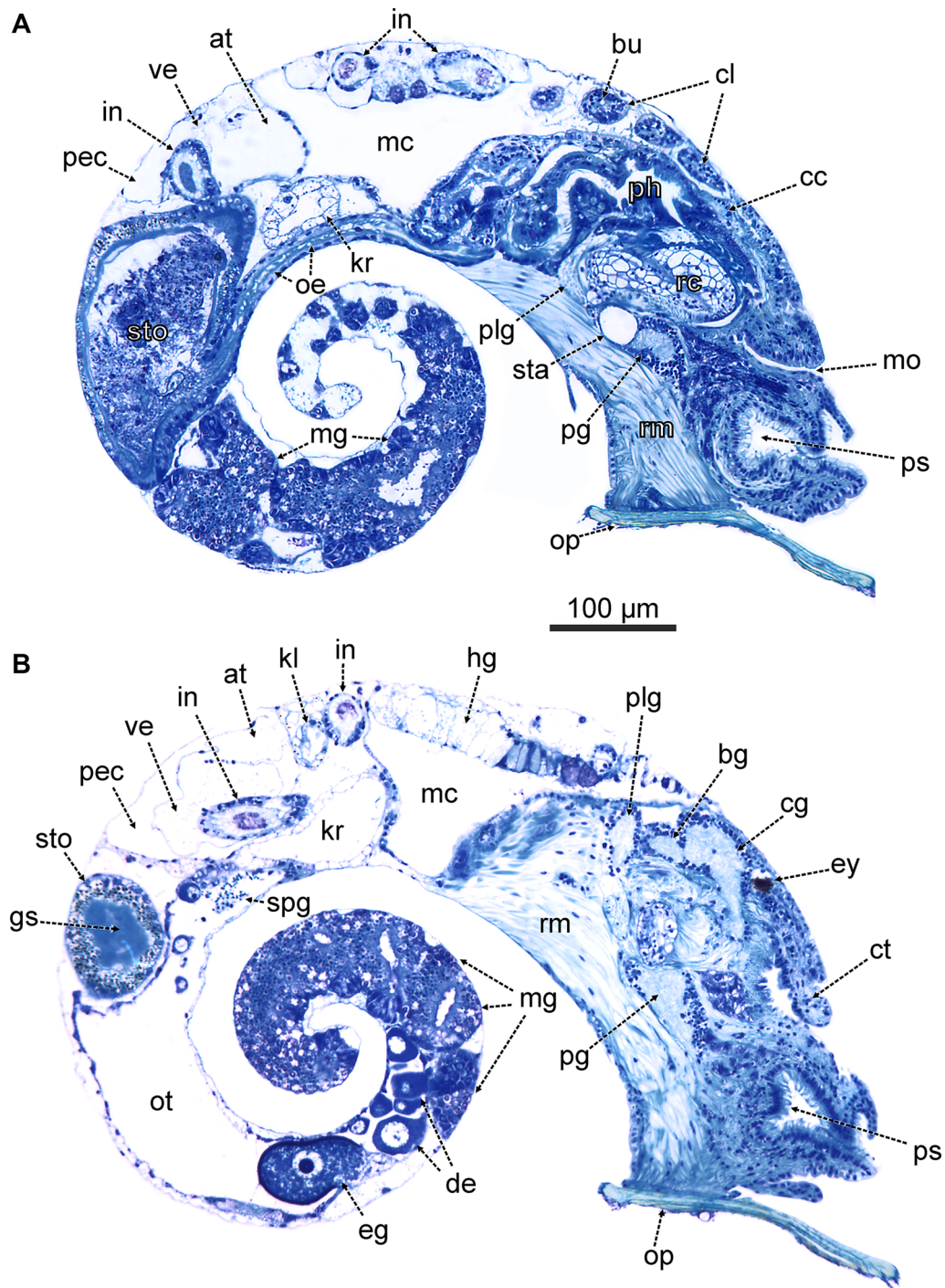
The rectum, together with the afferent blood sinus, extends forwards along the right side of the posterior mantle cavity.

### Circulatory and excretory systems

The monotocardian heart is located just behind the mantle cavity and to the right of the middle of the visceral hump. It consists of a single (left) atrium and a (thicker) ventricle, both of which are surrounded by a thin pericardium (Figs 2A, B, 4E). The atrium lies anteriodorsally and is connected ventrally with the ventricle. Two large sinuses, the wide efferent ctenidial sinus and a second one from the viscera (rectal sinus; Fig. 5C), enter the atrium (diameter at point of entry *c.* 50  $\mu\text{m}$ ). Figure 4E shows the connection between the atrium and the ventricle in *L. ornata*. The ventricle is larger (diameter 80  $\mu\text{m}$ ) than the atrium and its ventral portion is penetrated by the rectum. The aorta emerges from the posterior ventricle and shortly after emergence splits into three branches: two branches continue forwards to supply the head region and one runs backwards into the visceral hump.

Both kidneys are connected to the pericardium via ciliated renopericardial ducts. The left kidney is small and oval; it lies adjacent to the anterodorsal end of the pericardium (Fig. 2B). The left nephropore lies opposite the opening of the renopericardial duct.

The right kidney (Figs 2B, 4E, F, 5D) is much larger and partly encloses the pericardium at its ventral side. Two large posterior branches ramify between the other viscera. The epithelial cells are large (diameter 15  $\mu\text{m}$ ) and appear empty except for a few, very small granules. The dorsal end of the right kidney connects to the renopericardial duct. The gonoduct opens into the right



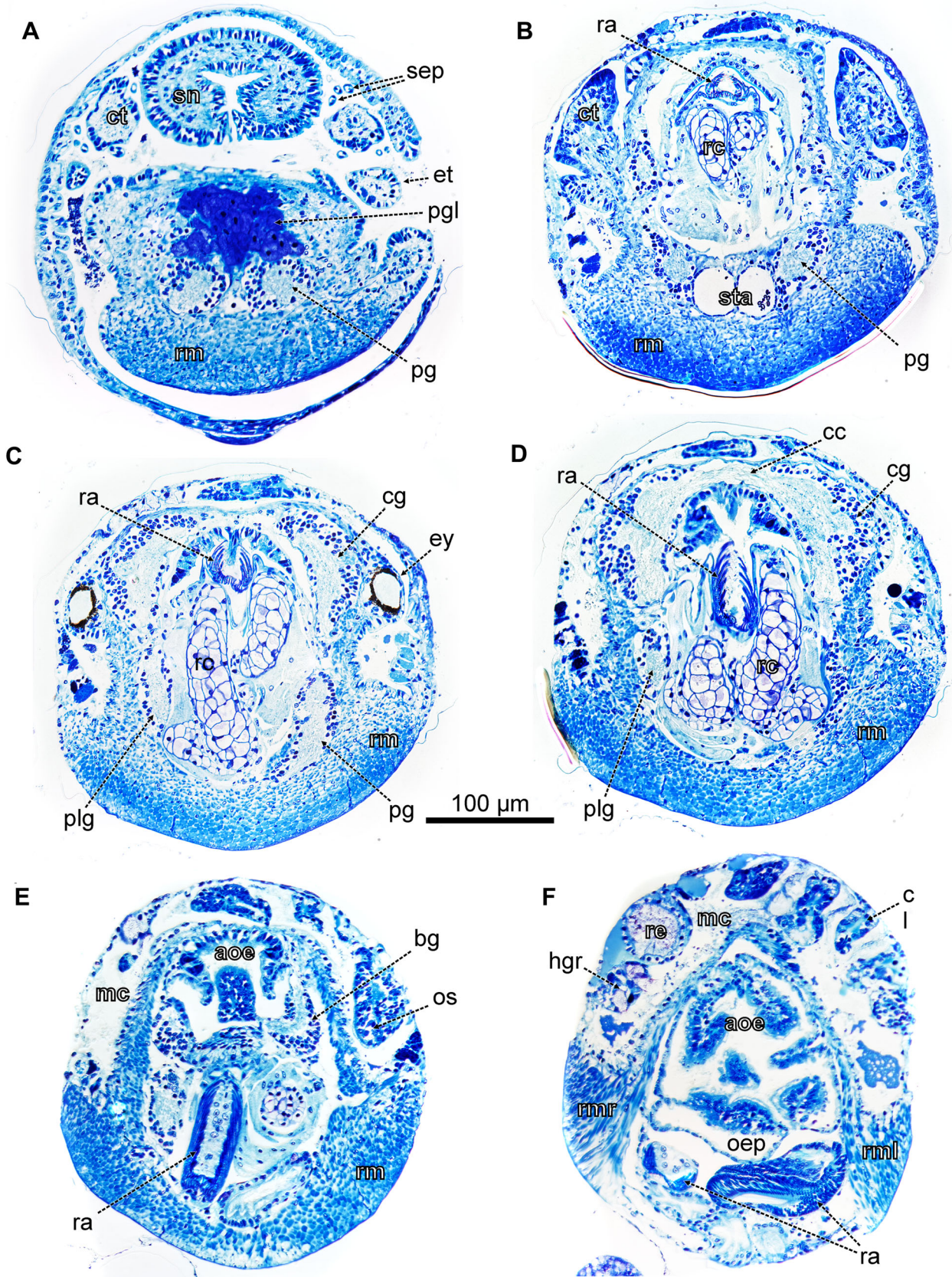
**Figure 2.** *Lodderena ornata*. Parasagittal sections. **A.** Close to the median plane. **B.** To the right of the median plane. Abbreviations: at, atrium; bg, buccal ganglion; bu, bursicle; cc, cerebral commissure; cg, cerebral ganglion; cl, ctenidium leaflet; ct, cephalic tentacle; de, developing egg; eg, egg; ey, eye; gs, gastric shield; hg, hypobranchial gland; in, intestine; kl, left kidney; kr, right kidney; mc, mantle cavity; mg, midgut gland; mo, mouth opening; oe, oesophagus; op, operculum; ot, ovotestis; pec, pericardial cavity; pg, pedal ganglion; ph, pharynx; plg, pleural ganglion; ps, pedal sole; rc, radula cartilage; rm, retractor muscle; spg, spermatogonia; sta, statocyst; sto, stomach; ve, ventricle.

kidney on the anterior right. The opening of the urinogenital pore into the mantle cavity lies opposite the entrance of the gonoduct.

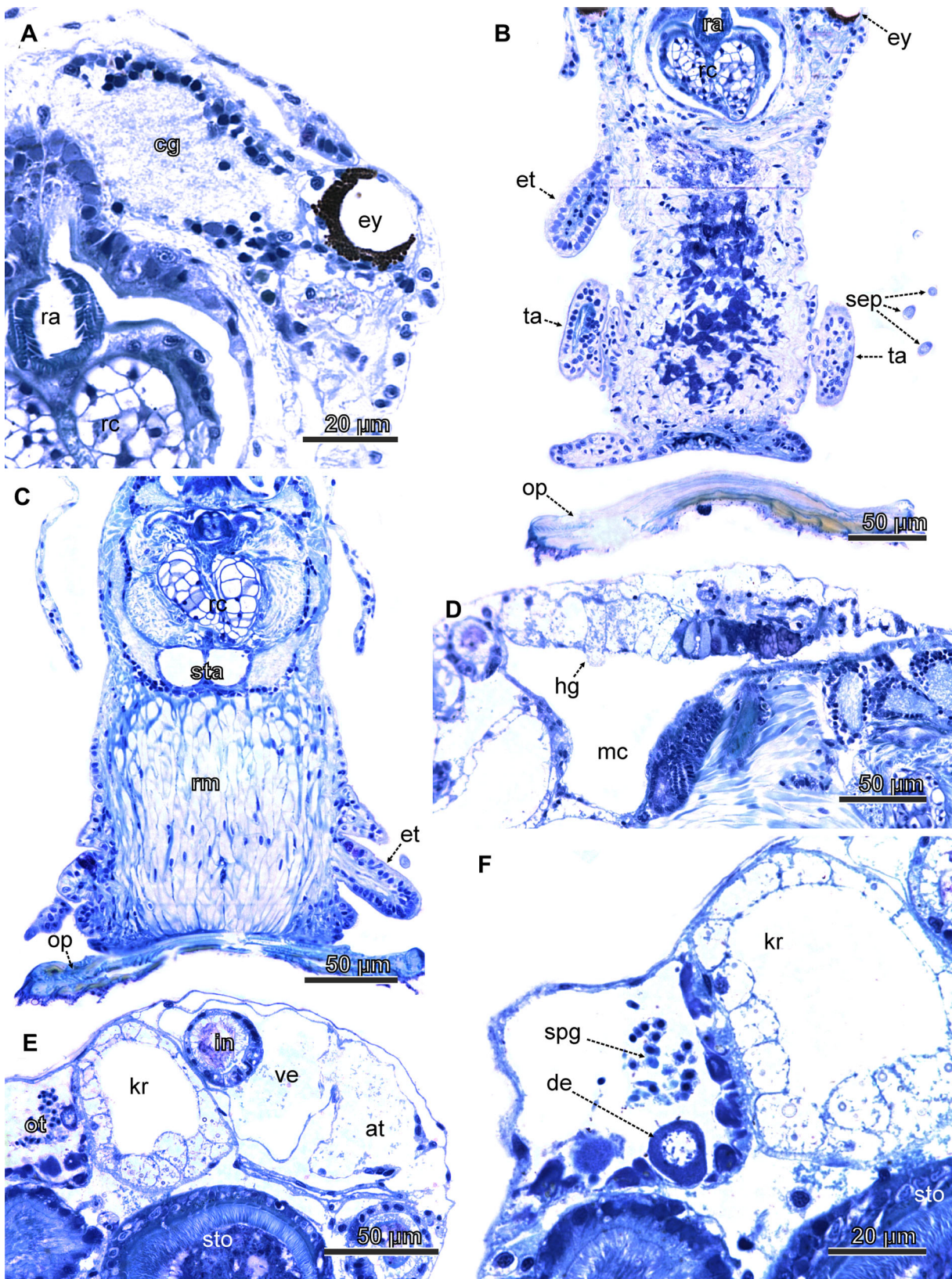
#### Genital system

The genital system of *L. ornata* shows an ovotestis (Fig. 2B) (length 400 µm, diameter 80 µm) that occupies the right side of the

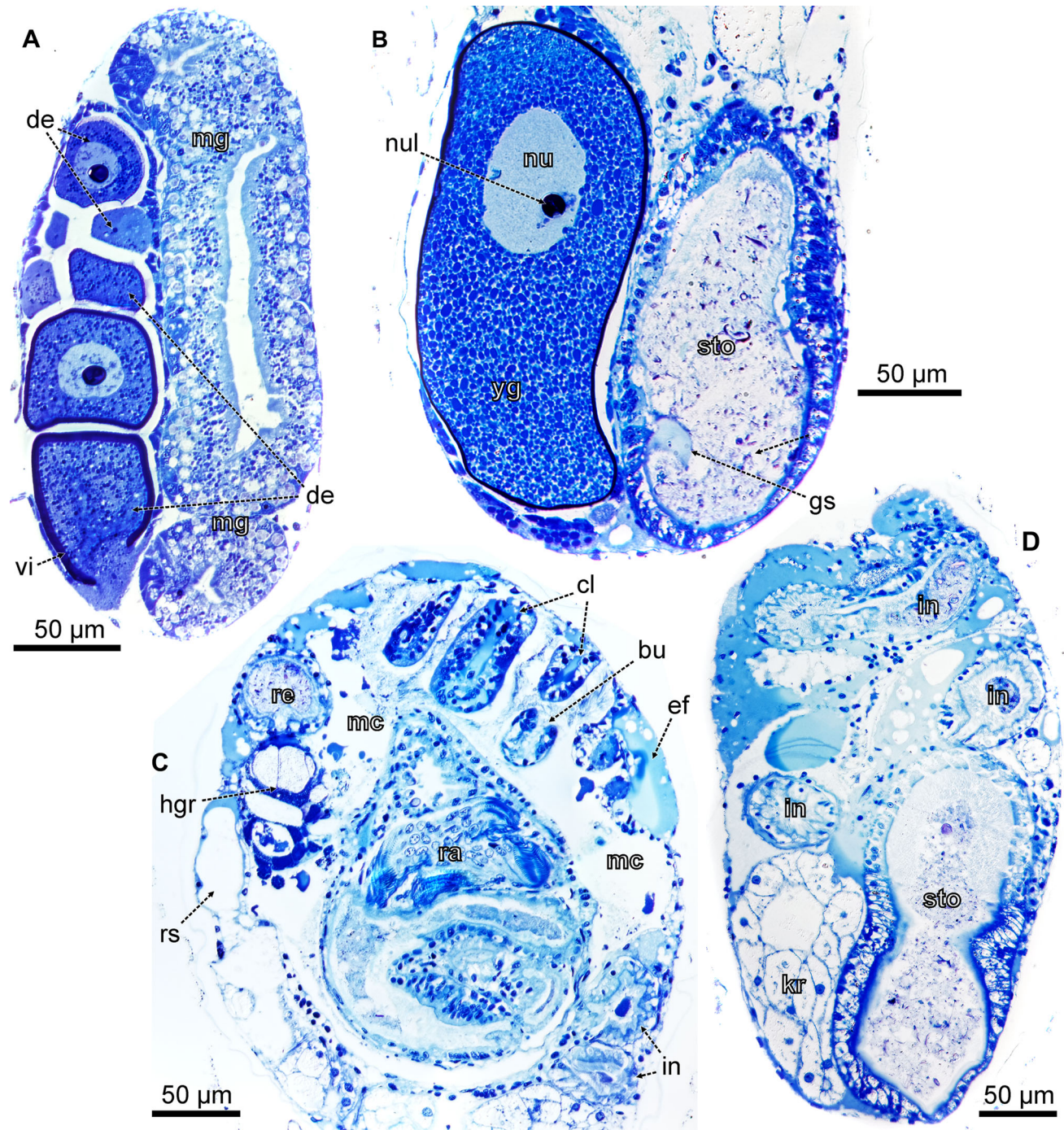
visceral part of the body. There are less than 10 eggs, which are successively larger towards the anterior portion of the gonad (Fig. 2B). Mature eggs are attached to the gonadal wall, where the otherwise very flat cells are enlarged and polygonal. These eggs are large (150 µm × 60 µm × 60 µm) and very yolky (Fig. 5B). They each contain a huge nucleus (diameter 25 µm), with a nucleolus (diameter 8 µm), and are enveloped by a 3-µm thick vitelline layer (Fig. 5A, B).



**Figure 3.** *Lodderena minima*. **A–F.** Cross-sections in anterior region, anterior (**A**) to posterior (**F**). Abbreviations: aoe, anterior oesophagus; bg, buccal ganglion; cc, cerebral commissure; cg, cerebral ganglion; cl, ctenidium leaflet; ct, cephalic tentacle; et, epipodial tentacle; ey, eye; hgr, right hypobranchial gland; mc, mantle cavity; oep, oesophageal pouch; os, osphradium; pg, pedal ganglion; pgl, pedal gland; plg, pleural ganglion; ra, radula; rc, radula cartilage; re, rectum; rm, retractor muscle; rml, left retractor muscle; rrm, right retractor muscle; sep, sensory papilla; sn, snout; sta, statocyst.



**Figure 4.** *Lodderena ornata*. Cross-sections. **A–C.** Head region. **E–G.** Posterior body region. Abbreviations: at, atrium; cg, cerebral ganglion; de, developing egg; et, epipodial tentacle; ey, eye; hg, hypobranchial gland; in, intestine; kr, right kidney; mc, mantle cavity; op, operculum; ot, ovotestis; ra, radula; rc, radula cartilage; rm, retractor muscle; sep, sensory papillae; spg, spermatogonia; sta, statocyst; sto, stomach; ta, sparsely ciliated lappet with tentacle-like appearance; ve, ventricle.



**Figure 5.** *Lodderena minima*. **A, B, D.** Cross-sections in posterior region. **C.** Cross-section through posterior pharynx. Abbreviations: bu, bursicle; cl, ctenidium leaflet; de, developing egg; ef, efferent ctenidium sinus; gs, gastric shield with tooth; hgr, right hypobranchial gland; in, intestine; kr, right kidney; mc, mantle cavity; mg, midgut gland; nu, nucleus of egg; nul, nucleolus of egg; ra, radula; re, rectum; rs, rectal sinus; sto, stomach; vi, vitelline layer of ripe egg; yg, yolk granules.

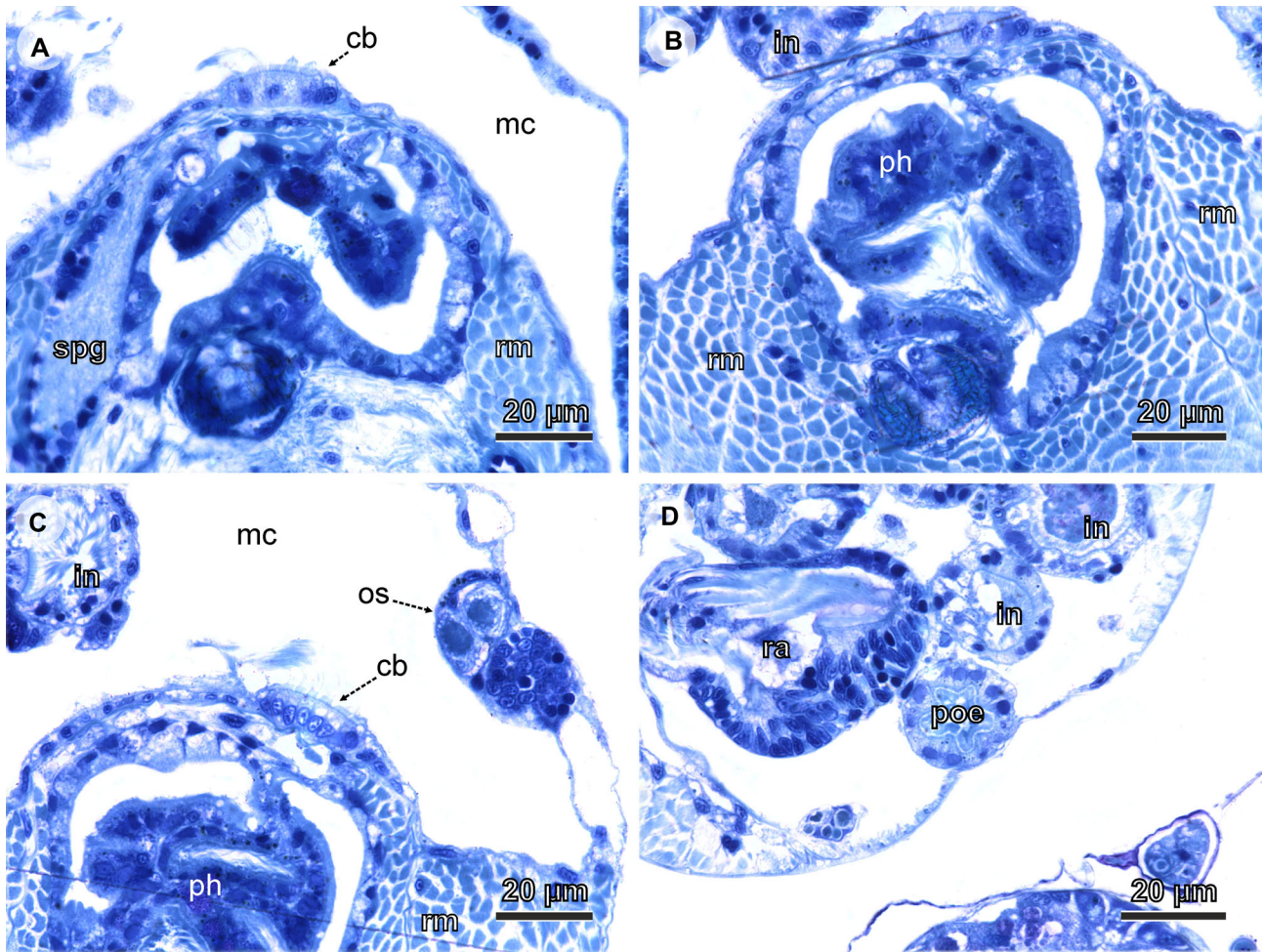
The epithelium of the anterior portion of the gonad consists of oogonia (i.e. bubble-like cells, each with very large nuclei that occupy about half the cell volume) (Fig. 5A). Here, the lumen contains small, elongate (4 µm) cells, each with an eccentric nucleus; these cells are probably spermatogonia (Figs 2B, 4E, F). The anterior end of the gonad forms a narrow opening into the right kidney.

A receptaculum and copulatory organs are absent.

#### Alimentary tract

The alimentary tract of both species is identical (Fig. 7A, B). The narrow (diameter 20 µm) mouth opening is situated at the lower side of the snout, which lacks oral lappets. The lumen of the short oral tube is star-shaped in cross-section (Fig. 3A) and its epithelium is slightly cuticularized; jaws and salivary glands are lacking.

The radula as a whole is about 300 µm long and is embedded in a prominent radular sheath. The latter runs between the two



**Figure 6.** *Lodderena ornata*. **A–D.** Cross-sections of head-neck region, anterior (**A**) to posterior (**D**). Abbreviations: cb, ciliary band; in, intestine; mc, mantle cavity; os, oesophagus; ph, pharynx; ra, radula sheath; rm, retractor muscle; spg, supraoesophageal ganglion.

slender pairs of radular cartilages; the anterior ones (100  $\mu\text{m}$ ) are about three times larger than the posterior ones (30  $\mu\text{m}$ ). The position of the buccal commissure marks the transition of the pharynx into the anterior oesophagus. Already the anterior pharynx shows a dorsal food channel flanked by two prominent folds, the inner side of which is densely ciliated. The opposing epithelium of the pharyngeal floor is also heavily ciliated, whereas the lateral parts have a squamous epithelium (Figs 3E, F, 6A, B). The anterior oesophagus is broad and shows small oesophageal pouches (Fig. 3F). In the region of oesophageal torsion, the tube bends towards the ventral side; the posterior oesophagus has a star-shaped lumen in cross-section and is uniformly ciliated (Fig. 6D). The diameter of the posterior oesophagus narrows in the central region (25  $\mu\text{m}$ ) and widens again (50  $\mu\text{m}$ ) in the most posterior area. Finally, the oesophagus enters the ventral side of the stomach (Fig. 7B).

The stomach (160  $\mu\text{m}$   $\times$  200  $\mu\text{m}$ ) shows a densely ciliated epithelium with long (10  $\mu\text{m}$ ) cilia in its anterior and dorsal region (Fig. 4D); the posterior/ventral part, in contrast, is cuticularized, forming the thick (7  $\mu\text{m}$ ) gastric shield with a prominent tooth (Fig. 5B). The epithelium of the gastric shield consists of isoprismatic cells, with all cells having nuclei in the same basal position; the apical parts are filled with small, heavily stained granules. The opening of the lobular midgut gland lies adjacent to that of the oesophagus. The single midgut gland (Fig. 5A) occupies the left side of the visceral part of the body. All cells are highly prismatic and show two distinct types: the cells of the basal area are filled with granules

and an amorphous apical part; the other cells are homogeneously stained.

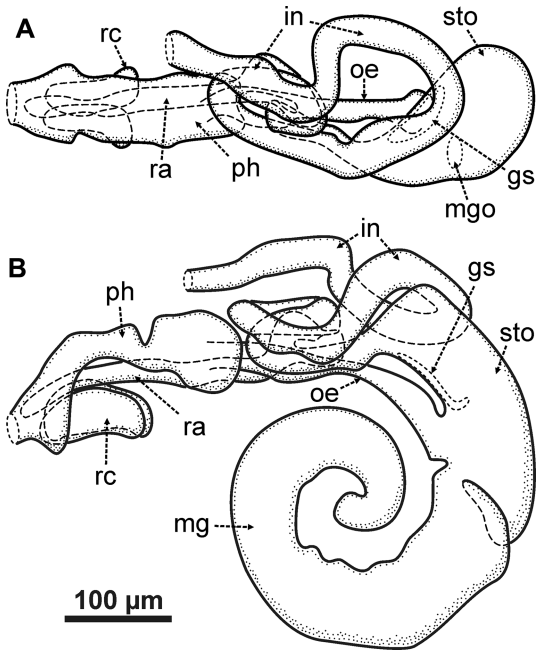
The stomach narrows at its anterior and ventral end and continues via the intestine; the intestine has a deep longitudinal furrow (Fig. 5D) that continues into the rectum. The intestine first forms two anterior loops, after which it curves to the right, runs upwards and then passes through the ventricle. From there the rectum runs a short distance within the roof of the right side of the mantle cavity towards the anal opening. This opening lies about 200  $\mu\text{m}$  behind the mouth opening (Fig. 7).

#### *Nervous system and sense organs*

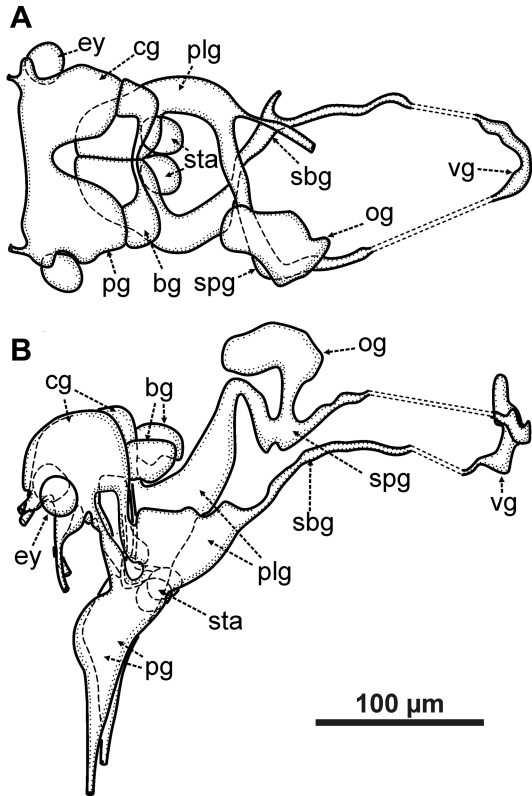
The central nervous system (Fig. 8) consists of four paired ganglia (cerebral, buccal, pleural and pedal ganglia) and four unpaired ganglia (oesophageal, suboesophageal, supraoesophageal and visceral/genital ganglia). Both the posterior pedal nerves and the visceral loop are cord-like (i.e. show many nuclei of nerve cells). As a whole, the central nervous system occupies a considerable volume of the soft body.

The cerebral ganglia are the largest ganglia and are situated below the bases of the cephalic tentacles (Figs 2B, 3C, D, 4A). Due to their relatively large size, they are close to each other; accordingly, the cerebral commissure is short and thick. The tentacle nerves show a small swelling at their origin; these swellings are largely fused with the cerebral ganglia and appear as bulges of the latter.





**Figure 7.** *Lodderena ornata*. Digestive system. Manual reconstruction of a section series. **A.** Dorsal aspect. **B.** Lateral left aspect. Abbreviations: gs, gastric shield; in, intestine; mg, midgut gland; mgo, opening to midgut gland; oe, oesophagus; ph, pharynx; ra, radula sheath; rc, radula cartilage; sto, stomach.



**Figure 8.** *Lodderena ornata*. Nervous system. Manual reconstruction of a section series. **A.** Dorsal aspect. **B.** Lateral left aspect. Abbreviations: bg, buccal ganglion; cg, cerebral ganglion; ey, eye; og, osphradial ganglion; pg, pedal ganglion; plg, pleural ganglion; sbg, suboesophageal ganglion; spg, supraoesophageal ganglion; sta, statocyst; vg, visceral ganglion.

A second, large cerebral nerve (labial nerve) emerges ventrally from each cerebral ganglion; it is fairly prominent at its base, then becomes much thinner and supplies the area of the mouth opening and the anterior pharynx. A third, very thin nerve emerges from the posterior end of each cerebral ganglion, runs ventrally and supplies the statocysts.

The nearly spherical buccal ganglia are situated adjacent to the posterior end of the cerebral ganglia (Fig. 2B) and close to each other so that the interconnecting commissure is very short.

Two further connectives leave the cerebral ganglia. The cerebropedal connectives emerge shortly behind the labial nerves and run in a posterior-ventral direction to reach the pedal ganglia. The broader cerebropedal connectives start at the posterior ventral end of the cerebral ganglia and run just laterally of the statocyst nerve to reach the pleural ganglia.

The pedal ganglia (Figs 2B, 3B) are elongated and again are close to each other so that the pedal commissure is extremely short. The posterior cord-like nerves run backwards, but further commissures could not be detected. The depressed statocysts (see also under sense organs) sit at the posterior-dorsal side of the pedal ganglia (Figs 3B, 4C). The cerebropedal connectives are located in front of the cerebropedal connectives. The oval pleural ganglia are partly fused with the pedal ganglia and form a pleuropedal complex (hypothroid situation). The cerebropedal connectives enter the pleural ganglia at their anterior dorsal edge, whereas the contact to the pedal ganglia is situated ventrally and more posteriorly. A prominent nerve emerges from the right pleural ganglion and supplies the right mantle and retractor muscle; the left pleural ganglion lacks such a nerve.

The visceral loop is streptoneurous and cord-like throughout. The pleuro-supraoesophageal connective emerges from the posterior right pleural ganglion (Fig. 6A), crosses the anterior oesophagus dorsally and leads to the small ( $20\ \mu\text{m} \times 30\ \mu\text{m}$ ) supraoesophageal ganglion at the left side. A short and thick connective leads upwards to the large ( $50\ \mu\text{m} \times 30\ \mu\text{m}$ ) osphradial ganglion (Fig. 3E); the latter is situated in the left mantle roof directly above the supraoesophageal ganglion and supplies the osphradial epithelium as well as the ctenidial lamellae.

From the supraoesophageal ganglion, the left visceral connective runs posteriorly and reaches the visceral and genital ganglia, which are situated close to each other at the posteriormost part of the visceral loop, below the posterior end of the mantle cavity. The (right) genital ganglion is conical; the visceral ganglion shows a spherical shape.

The left pleural ganglion continues as the short pleuro-suboesophageal connective, which crosses below the oesophageal to the right side and reaches the very small (diameter  $10\ \mu\text{m}$ ) suboesophageal ganglion. Here, another thick nerve emerges and supplies the right retractor muscle; in addition, the thin connective to the genital ganglion emerges at the posterior end of the suboesophageal ganglion.

Cephalic and epipodial appendages have been described earlier. The eyes (diameter  $20\ \mu\text{m}$ ) (Figs 2B, 3C, 4A) lie below the body surface, directly adjacent to the cerebral ganglia. The eyes are closed vesicles with a thick pigment layer at the posterior side. They are filled with a homogeneous, vitreous content but lack a specific lens. The large (*L. minima*) or depressed (*L. ornata*) statocysts (diameter  $20\ \mu\text{m}$ ), which are located adjacent to the pedal ganglia, are close to each other (Figs 3B, 4C). They contain several statoconia, which show concentric layers of organic matrix in the decalcified condition. The bursicles of the ctenidial leaflets (Fig. 5C) have been described earlier. The single osphradium (diameter  $20\ \mu\text{m}$ ) is located on the very left side of the mantle roof and is directly underlain by the large osphradial ganglion (Figs 3E, 6C). The few epithelial cells are quite large and have large nuclei.

REVIEW OF *LODDERENA* SPECIES

*Lodderena* **Iredale, 1924**: 233 (type species *Lodderena minima* (Tenison-Woods, 1878); OD).

*Pachystremiscus* **Olsson & McGinty, 1958**: 32–33, pl. 4, figs 1–2a (type species *Lodderena pulchella* (Olsson & McGinty, 1958); OD).

Species are listed in alphabetic order. Radula and soft-part anatomy are unknown, unless otherwise stated.

There is little doubt that several more species of *Lodderena* need to be formally included or described. However, the list presented below reconfirms that conchological characteristics alone are an insufficient basis for identifications and that anatomical or molecular characters are also needed.

***Lodderena arifca* (Bartsch, 1915)**

*Vitrinella* (*Docomphala*) *arifca* **Bartsch, 1915**: 168, pl. 36, figs 7–9 (Port Alfred, Eastern Cape, South Africa; holotype, USNM 250554).

*Vitrinella arifca*—**Turton, 1932**: 197, no. 1367. **Barnard, 1963**: 178. **Kensley, 1973**: 68, fig. 210.

*Lodderena arifca*—**Herbert, 2015**: 42, fig. 5G–I.

*Anticlimax arifca*—WMSDB ([www.bagniliggia.it/WMSD/HtmSpecies/1030507121.htm](http://www.bagniliggia.it/WMSD/HtmSpecies/1030507121.htm)).

***Lodderena bunnelli* Redfern & Rolán, 2005**

*Lodderena bunnelli* **Redfern & Rolán, 2005**: 1–6, figs 1–9 (SEM) (Lanyard Cay, Abaco, Bahamas, 6 m; holotype, ANSP 413566; paratypes, MNCN 15.05/46685).

*Remarks*: Shell of paratype is figured at <https://minerva.usc.edu/xmlui/bitstream/handle/10347/11173/Lodderena%20bunnelli.pdf?sequence=1&isAllowed=y>.

***Lodderena emeryi* (Ladd, 1966)**

*Cyclostremiscus emeryi* **Ladd, 1966**: 80, pl. 11, figs 9–11 (Eniwetok Atoll, Marshall Islands, 630–1500 feet (192–457 m); holotype, USNM 648444; Miocene (holotype) to recent). **Okutani, 2000**: 85, pl. 42, fig. 10.

*Pachystremiscus emeryi*—**Paines, 2002**: 14, fig. 6.

**?*Lodderena eumorpha eumorpha* (Suter, 1908)**

*Cyclostrema eumorpha* **Suter, 1908**: 25, pl. 2, figs 7–9 (near the Snares Islands, New Zealand, in 50 fathoms; holotype, NMNZ, M.002155). **Suter, 1913/1915**: 153, pl. 33, fig. 20a, b.

*Lodderena eumorpha eumorpha*—[www.gastropods.com/Taxon\\_pages/Family\\_SKENEIDAE.shtml](http://www.gastropods.com/Taxon_pages/Family_SKENEIDAE.shtml).

*Remarks*: Most authors place this species/subspecies in *Lodderia* Tate, 1898 or *Parviturbo* Pilsbry & McGinty, 1945 (Skeneidae).

**?*Lodderena eumorpha cookiana* (Dell, 1952)**

*Crosseola cookiana* **Dell, 1952**: 415, pl. 85, fig. 4 (New Zealand, Mernoo Bank, Western Chatham Rise, 43°21'S, 175°E [sic], in 52 fathoms; holotype, NMNZ, M.5502; 2 paratypes, NMNZ, M.5504).

*Lodderia cookiana*—**Dell, 1956**: 49.

*Lodderia eumorpha cookiana*—**Powell, 1979**: 72.

*Lodderena eumorpha cookiana*—WMSDB (<http://www.bagniliggia.it/WMSD/HtmSpecies/5066000656.htm>).

*Remarks*: Images of holotype are available at <http://collections.tepapa.govt.nz/object/146505>. Most authors place this species/subspecies in *Lodderia* Tate, 1898 (Skeneidae).

***Lodderena formosa* Powell, 1930**

*Lodderena formosa* **Powell, 1930**: 541, pl. 87, figs 11, 12 (off Mangonui Heads, North Island, New Zealand in 6–10 fathoms; holotype, AMM; 1 paratype, NMNZ, M.002824). **Powell, 1979**: 72, pl. 21, figs 13, 14.

***Lodderena janetmayae* Rubio, Rolán & Redfern, 1998**

*Lodderena janetmayae* **Rubio et al., 1998**: 44, figs 35–40 (SEM) (Chub Rocks, Abaco, Bahamas, 14 m; holotype, USNM 880254; paratypes, MNCN 15.05/31936).

*Remarks*: Images of paratypes are available at <https://www.usc.es/gl/servizos/museohn/colecciones/paratiposrolan.html?action=detail&image=279>.

***Lodderena minima* (Tenison-Woods, 1878)**

*Liotia minima* **Tenison-Woods, 1878**: 58 (Victoria or Tasmania, exact locality not known; no data on types).

*Lodderia minima*—**Tate, 1899**: 222. **Hedley, 1900**: 94, 95, pl. 3, figs 1–3.

*Lodderena minima*—**Laseron, 1954**: 4, figs 6, 6a. **Hickman & McLean, 1990**: fig. 95E. **Warén, 1992**: 155, figs 5C, 7C, 9A. **Beechey, 2018**: [http://seashellsofns.org.au/Skeneidae/Pages/Lodderena\\_minima.htm](http://seashellsofns.org.au/Skeneidae/Pages/Lodderena_minima.htm). **Grove, 2015**: <https://mollussoftasmania.org.au/project/lodderena-minima/>.

*Remarks*: According to **Beechey (2018)**, the type locality is Brighton, Western Port, Victoria. Photos and a description of shell are provided at [http://www.gastropods.com/8/Shell\\_16378.shtml](http://www.gastropods.com/8/Shell_16378.shtml), but some photos are misidentified (A. Warén, personal communication). SEMs of rhipidoglossate radula of *L. minima* have been depicted by **Hickman & McLean (1990: fig. 97C)** and **Warén (1992: 155, fig. 5C)**.

***Lodderena nana nana* Powell, 1930**

*Lodderena nana* **Powell, 1930**: 541, pl. 87, figs 13, 14 (Mangonui Heads, New Zealand, 6–10 fathoms; holotype, AM).

*Lodderena nana nana*—**Powell, 1979**: 72, pl. 21, figs 11, 12.

***Lodderena nana pooki* Fleming, 1948**

*Lodderena nana pooki* **Fleming, 1948**: 87, pl. 8, fig. 6 (New Golden Hind Expedition station 2, Narrows, Preservation Inlet, Long Sound, Southland Fjords, New Zealand, 19–24 fathoms; location of types unknown). **Smith, 1952**: 7. **Powell, 1979**: 72.

***Lodderena omanensis* Moolenbeek, 1996**

*Lodderena omanensis* **Moolenbeek, 1996**: 24, pl. 1, figs 4–6, pl. 2, fig. 2 (main island, Al Hallaniyah, Oman; holotype and paratypes, ZMA Moll. 3.95.03 and 3.95.04).

***Lodderena ornata* (Olsson & McGinty, 1958)**

(Fig. 1A–C)

*Cyclostremiscus* (*Pachystremiscus*) *ornatus* **Olsson & McGinty, 1958**: 33, pl. 4, fig. 1 (Chiriqui Lagoon, Isla Bocas, Panama; holotype, ANSP 211880).

*Pachystremiscus ornatus*—**Rios, 1985**: 41, pl. 16, fig. 178.

*Cyclostremiscus ornatus*—De Jong & Coomans, 1988: 32, pl. 22, fig. 137. Leal, 1991: 83, 84, pl. 12, figs d–f, h (as *C. ornata*). Rios, 1994: 37, fig. 116.

*Lodderena ornata*—Moolenbeek, 1996: 1, figs 1–3, pl. 2, fig. 1. Rubio *et al.*, 1998: figs 19–25. Redfern & Rolán, 2005: figs 10–14. Rosenberg, Moretzsohn & García, 2009: 625, 687. Lima *et al.*, 2011: fig. 2A–H. Ortigosa *et al.*, 2018: figs 2–21a, b.

*Cyclostremiscus solitarius*—Hertlein & Allison, 1968: 2, 3, fig. 1a, b (Clipperton Island, Eastern Pacific; holotype, UCMP 37121).

*Pachystremiscus solitarius*—Kaiser, 2007: 29, pl. 11, figs 1, 2a, 2b.

*Cyclostremiscus emeryi*—Kay, 1979: 54, 55, fig. 15E–G. Fukuda, 1993: 28, pl. 8, fig. 95a, b (both not Ladd, 1966 = *L. emeryi*).

‘Skeneiform gastropod’—Kunze *et al.*, 2008: fig. 3C, D.

*Remarks:* The radula of *L. ornata* has been described and SEM images provided by Kunze *et al.* (2008, fig. 3; based on Brückner, 2003: fig. 30E, F). The anatomy and histology are described in the present paper.

### ***Lodderena pachynepion* (Pilsbry & Olsson, 1945)**

*Cyclostremiscus* (*Pachystremiscus*) *pachynepion* Pilsbry & Olsson, 1945: 273, pl. 29, figs 2, 2a, 2b (Isla del Gallo, north of Tumaco, Department of Nariño, Colombia; holotype, ANSP 181019). Keen, 1971: 381. Draper, 1974: 75, fig. 18.

*Lodderena pachynepion* Moolenbeek, 1996: 22.

*Remarks:* SEMs of syntypes are provided at [http://www.gastropods.com/5/Shell\\_47925.shtml](http://www.gastropods.com/5/Shell_47925.shtml).

### ***Lodderena pulchella* (Olsson & McGinty, 1958)**

*Cyclostremiscus* (*Pachystremiscus*) *pulchellus* Olsson & McGinty, 1958: 32, pl. 4, figs 2, 2a (Chiriqui Lagoon, Isla Bocas, Panama; holotype, ANSP 211897).

*Pachystremiscus pulchellus*—Rios, 1985: 41, pl. 16, fig. 179.

*Cyclostremiscus pulchellum*—De Jong & Coomans, 1988: 32, pl. 22, fig. 139.

*Cyclostremiscus* sp.—Leal, 1991: 84, pl. 12, figs J, K, L.

*Lodderena pulchella*—Rubio *et al.*, 1998: 40, figs 1–18. Rosenberg, Moretzsohn & García, 2009: 625, 687. Daccarett & Bossio, 2011: 55, pl. 100.

*Remarks:* The protoconch and radula have been depicted by Rubio *et al.* (1998: figs 15, 17, 18).

### ***Lodderena redferni* Landau, Van Dingenen & Ceulemans, 2017**

*Lodderena redferni* Landau, Van Dingenen & Ceulemans, 2017: 145, pl. 69, figs 1, 2 (Le Grand Chauverau, St-Clément-de-la-Place, Maine-et-Loire, NW France; Redonian (Upper Miocene); holotype, NHMW 2016/0103/1462; paratype 1 from Clément-de-la-Place, NHMW 2016/0103/1463; paratype 2 from Renauleau, NHMW 2016/0103/1611).

*Remarks:* This species is known only as a Miocene fossil.

### ***Lodderena striata* (Kay, 1979)**

*Cyclostremiscus striatus* Kay, 1979: 55, 56, fig. 15A–D (Honaunau Bay, Hawaii; holotype, BPBM, 9747).

*Lodderena striata*—Moolenbeek, 1996: 22. Redfern & Rolán, 2005: 4.

*Pachystremiscus striatus*—Paines, 2002: 15, fig. 7.

*Remarks:* Moretzsohn & Kay (1995: 2) stated that Ponder (1985) had classified this species in Vitrinellidae. We could not verify this statement in Ponder’s work, although *Cyclostremiscus* Pilsbry & Olsson, 1945 as defined by its type species, *Vitrinella panamensis* C.B. Adams, 1852 (type by OD), is indeed a vitrinellid genus.

### ***Lodderena tanae* Moolenbeek, 1996**

*Lodderena* n. sp. Bosch *et al.*, 1995: 38, fig. 62 (intertidal from off Masirah Island and SE coast of Oman, Arabian Sea).

*Lodderena tanae* Moolenbeek, 1996: 26, pl. 1, figs 7–9, pl. 2, fig. 3 (Al Hallaniyah, Oman, Al Hallaniyah, 17°30’N, 56°00’E; holotype, ZMA Moll. 3.95.06; paratypes ZMA Moll. 3.95.07).

*Lodderena vladimiri* Chernyshev, Rolán & Rubio, 2016: 45, fig. 1 (Pity Bay, Guam, 1 m; holotype, MIMB 30691; 1 paratype, MIMB 30392; 2 paratypes, ZMFU, XII 43792/Ga-9385; 2 paratypes, MNHN IM-2000-35641).

*Indeterminate species*

### ***Lodderena* sp. Rubio *et al.*, 1998**

*Lodderena* sp. Rubio *et al.*, 1998: 44, figs 28, 29, 32–34, 41 (St. Virgin Islands, Cape Verde Archipelago).

*Remarks:* This appears similar to *L. ornata*.

### ***Lodderena* sp. Kano, 2008**

*Lodderena* sp. Kano, 2008: 5 (intertidal of Izu, Japan). Williams, 2012: 587, table 1.

*Remarks:* Sequence data are deposited under the following DDBJ/EMBO/GenBank accession numbers: cytochrome *c* oxidase subunit I, AB365243; histone H3, AB365287 (Kano, 2008; Williams, 2012).

*Excluded species*

### **†*Lodderena anceps* Laws, 1941**

*Lodderena anceps* Laws, 1941: 140, pl. 19, fig. 43 (Pakaurangi Point, Kaipara, New Zealand; holotype originally deposited in author’s collection; Cenozoic fossil).

*Remarks:* Laws (1941) was himself uncertain about the generic placement of this species but noted its resemblance to *L. nana*. It is currently referred to as *Cyclostremiscus* (Vitrinellidae) (e.g. Maxwell, 2009).

### ***Cyclostrema catenoides* Monterosato, 1877**

*Cyclostrema catenoides* Monterosato, 1877: 417, fig. p. 417 (off Civitavecchia, Italy; type material missing).

*Lodderena catenoides*—Warén, 1992: 155, 156, figs 2C, 3F, 7D–F, 28E, F. Oliverio, 2008: 251.

*Remarks:* Based on the occurrence of a propodeal penis, this species is currently considered as *Skenea* s. s. (cf. Haszprunar *et al.*, 2016).

### ***Turbo?* *sphaeroida* (Wood, 1842)**

*Turbo?* *sphaeroida* Wood, 1842: 533, pl. 5, fig. 3 (Sutton, East Anglia, UK; Coralline Crag Formation, Early Pliocene; location of type material currently not known).

*Turbo sphaeroidea*—Wood, 1848: 122, 123, pl. 15, fig. 9. Wood, 1872: 86.

?*Cyclostrema sphaeroidea*—Harmer, 1923: 752, pl. 60, fig. 15.

*Lodderena sphaeroideum*—Marquet & Landau, 2006: 23, fig. 5.2a–e. Hoeksema, Simons & Wesselingh, 2018: 16, fig. 11.

**Remarks:** Warén, 1980 (pl. 2, figs 7–9) figured a specimen (USNM 181467) as *Cyclostrema sphaeroideum* with a remark in the legend ‘this is probably not Wood’s species’. Marquet & Landau (2006: 23) identified this specimen as *Parviturbo lecointrae* (Dollfus & Dautzenberg, 1899), but this has recently been named *Parviturbo ergasticus* Rubio, Rolán & Gofas, 2015 (see Rubio, Rolán & Fernández-Garcés, 2015: 177–179, fig. 4A–I). Although the protoconch shows some similarity with that of *Lodderena*, we follow Hoeksema, Simons & Wesselingh (2018) and consider this Pliocene species as a member of *Parviturbo*.

### ***Lodderena* sp. Edelman-Furstenberg & Faershtein, 2010**

*Lodderena* sp. Edelman-Furstenberg & Faershtein, 2010: 12, 39, pl. 2, fig. 12 (Gulf of Eilat, Red Sea).

**Remarks:** The (broken) shell depicted does not at all resemble a *Lodderena*.

## DISCUSSION

### *General remarks*

Although the molecular systematic analyses (Kano, 2008; Williams, 2012) did not place *Lodderena* in the vicinity of Skeneidae, they did not offer clear alternatives. In order to understand the phylogenetic relationships of *Lodderena*, further molecular systematic data will be required. However, to infer the evolution of functional traits and environmental adaptations, morphological characters remain essential (e.g. Wake, Wake & Specht, 2011; Richter & Wirkner, 2014; Giribet, 2015).

### *Character analysis*

The papillate condition of the cephalic and epipodial tentacles and the mantle edge reflect the vetigastropod nature of *Lodderena*. Details of these papillae from transmission electron microscopy (TEM) have been provided by Crisp (1981), Herbert (1984) and Künz & Haszprunar (2001).

As recently reviewed by Haszprunar *et al.* (2017), epipodial conditions differ considerably among Vetigastropoda. In essence, there are two different structures that are variously combined. True epipodial tentacles resemble the cephalic tentacles in showing papillae and an elongated tip. In contrast, ESOs are usually shorter and thicker appendages, are usually non-papillate and are characterized by a blunt apical tip with tall prismatic sensory cells that bear ciliary ‘collar receptors’ (for TEM, see Crisp, 1981; Herbert, 1984; Haszprunar *et al.*, 2017). Haliotidae and Trochoidea show a combination of both structures, with the ESO attached to the ventral base of one, a few or all the epipodial tentacles. In contrast, Scisurrellidae (e.g. Bourne, 1910) or Seguenzioida *sensu* Kano (2008) and Kano, Chikyu & Warén (2009) show ESOs always as separated tentacles (e.g. Kunze, Heß & Haszprunar, 2016).

However, the matter is not so clear in early juveniles or in progenetic species. While adult trochids clearly have the ‘combined type’ (e.g. Crisp, 1981; Hickman & McLean, 1990), early juveniles have the ESOs separated (e.g. Robert, 1902: pl. 18, figs 83, 84). The same is true for *Haliotis* (e.g. Ino, 1952; Maxwell, 2015: figs 29, 35). According to the recapitulation concept, this suggests that among the Vetigastropoda the ‘separate condition’ is plesiomorphic and the

‘combined condition’ is apomorphic. It also may explain the observation that the tiny (0.8 mm) *L. ornata* has separate ESOs, whereas the larger (1.2 mm) *L. minima* shows the combined condition. Further species of *Lodderena* need to be studied to clarify this matter. Since small skeneimorph vetigastropods are likely to have evolved via progenesis (Haszprunar *et al.*, 2016), the state of this character remains doubtful in very small (i.e. <1 mm) representatives.

Both species investigated show a row of small and sparsely ciliated lappets along both sides of the epipodium. So far, this is a unique character among skeneiform vetigastropods. If this character is present in other species of *Lodderena*, it may serve as a diagnostic character of the genus.

The retention of left and right adult (smooth) shell muscles is a gastropod plesiomorphy (Haszprunar, 1985, 1988c; Ponder & Lindberg, 1997), a condition found in many vetigastropod taxa, including trochoideans and the phasianellid *Tricolia* (Marcus & Marcus, 1960).

The single left and monopectinate ctenidium of *Lodderena* is shared with Skeneidae (Haszprunar *et al.*, 2016) and several other Vetigastropoda. In *Lodderena*, this presumably represents a paedomorphic character; this condition is also known in early juveniles of taxa with bipectinate or zeugobranch adult conditions, such as *Haliotis* (Crofts, 1937; Ino, 1952; Oba, 1964; Page, 1997) and *Scissurella* (Strasoldo, 1991). As is typical for most Vetigastropoda and several Neomphalida, each ctenidial leaflet is equipped with a bursicle and skeletal rods (Szal, 1971; Haszprunar, 1987b, 1988c, 1989; Heß *et al.*, 2008; Kunze *et al.*, 2008).

The retention of two asymmetric kidneys with different structure and functions is diagnostic for the Vetigastropoda and Patellogastropoda (Andrews, 1985; Haszprunar, 1988c, 1993; Ponder & Lindberg, 1997; Sasaki, 1998). The release of the gametes through the visceral gonoduct and an urinogenital opening shared with the right kidney is often found in Vetigastropoda.

The two *Lodderena* species under investigation show simultaneous hermaphroditism and a true ovotestis. In contrast, in the Skeneidae, which are also hermaphroditic, the ovary/oviduct and testis/vas deferens are entirely separated (Haszprunar *et al.*, 2016). Whereas skeneid species have a propodial penis and a large receptaculum in the mantle roof, both structures are entirely lacking in *Lodderena*. Yolky eggs with a vitelline layer are diagnostic for Vetigastropoda (Ponder & Lindberg, 1997). Considering the large size of the eggs compared with the narrow passage into the right kidney and through the urinogenital opening, it is likely that these eggs are highly flexible and probably flow through the narrow passage.

Among the Vetigastropoda, an entire lack of jaws is so far restricted to lepetelloidan limpets (Lepetellidae, Cocculinellidae, Addisoniidae or *Kaiparapelta*; see Haszprunar, 1987a, b, 1988a, b; Haszprunar, Graf & Heß, 2014; Judge & Haszprunar, 2014). Although this secondary loss is paralleled in several other caenogastropod and heterobranch taxa, it may be another synapomorphy of the genus *Lodderena*.

All *Lodderena* species so far investigated (Hickman & McLean, 1990; Warén, 1992; Rubio *et al.*, 1998; Kunze *et al.*, 2008) share very similar radula. The rachidian tooth forms a plate with the anterior edge slightly curved. There are four uniform lateral teeth, each about 6 µm long and with four or five sharp denticles, which become progressively smaller from the inner to the outer edge. The fifth lateral tooth differs in having a spatula-shaped tip, which is bent backwards, and the denticles appear rounded. The marginal teeth are c. 16 µm long, quite slender (width c. 1 µm), their tip is bent backwards and they bear seven or eight denticles of similar shape. Whereas the images of the radula of *L. pulchella* presented by Rubio *et al.* (1998: figs 17, 18) and of *L. minima* by Hickman & McLean (1990: fig. 97C) both closely resemble the condition found in *L. ornata*, the radula of *L. minima* figured by Warén (1992: 155, fig. 5C) shows a separate first lateral tooth and also an appreciable distance between the outermost lateral and the innermost marginal teeth. However, it is possible that these differences are due to

overspreading in the preparation made by Warén (1992). The rhachidian tooth is very similar in all three species.

Many skeneimorph species show a broadly similar radular type. However, Warén (1990) showed that juvenile turbinids and trochids have a very similar rhipidoglossate radula, even if the radula type differs substantially in adults. This similarity of the radulae might be due to a similar diet in juveniles, namely grazing on similar substrates that differ from those of the adult (Warén, 1990), and thus might indicate convergence. Alternatively, it might be a truly homologous feature; if so, it is probably a vetigastropod plesiomorphy or may indicate that the radula of the vetigastropod (plus neomphalidan) stem species was of this type. Finally, the similar radular structures of these small species may be due to paedomorphosis and thus again a matter of parallelism; this is the most likely explanation. In any case, the similarities of the radula type of *Lodderena* cannot be used to infer systematic relationships.

Two pairs of radular cartilages are present in the majority of vetigastropod clades (e.g. Sasaki, 1998; Katsuno & Sasaki, 2008). In contrast, poorly developed oesophageal pouches are rare and deviate from the general vetigastropod pattern (Salvini-Plawen & Haszprunar, 1987), as does the single midgut gland. On the other hand, the conditions of the stomach with its ciliary field, gastric shield and tooth reflect basic gastropod conditions. This is also the case for the intestine, with its longitudinal furrow, and the complete encircling of the rectum by the heart ventricle.

The skeneid hypoathroid and the streptoneuran central nervous system with pedal cords are plesiomorphic conditions in gastropods.

Both *Lodderena* species investigated have eyes with closed vesicles filled by a vitreous body (*sensu* Sasaki, 1998) and a pigmented retina, as is found in several other vetigastropod taxa. Haliotidae and Trochidae show open ocelli (i.e. the plesiomorphic condition). Thus, the condition in *Lodderena* is a derived one, and is clearly paralleled by many cases elsewhere in gastropods (Haszprunar, 1988c; Ponder & Lindberg, 1997; Sasaki, 1998). The condition of the statocysts with several statoconia again shows the vetigastropod condition, whereas the relatively large size of the osphradium is unusual among vetigastropods.

### Systematics

The vetigastropod nature of *Lodderena* is beyond doubt and is well supported by a range of molecular and morphological data. These include the papillate condition of the tentacles and mantle rim; the ctenidium with skeletal rods and bursicles; two different kidneys, the right one ramifying between the viscera and forming an urinogenital opening; eggs with a vitelline layer; a rhipidoglossate radula; an intestine with a longitudinal furrow; a hypoathroid and streptoneuran nervous system; and statocysts with several statoconia.

Molecular systematic studies have placed *Lodderena* within the Trochoidea. Morphologically, this is supported by the epipodial conditions with attached ESOs (as in *L. minima*; see discussion earlier); the Seguenzioidea (*sensu* Kano, 2008; Kano, Chikyu & Warén, 2009), Scissurellidae, Clypeosectidae and Lepetodrilidae all have separated ESOs (Haszprunar *et al.*, 2016, 2017; Kunze, Heß & Haszprunar, 2016).

To overcome the ‘catch-all’ concept of ‘skeneiform’ gastropods, an alternative concept based on the monophyly of the Skeneidae has recently been proposed (Haszprunar *et al.*, 2016). This concept is supported by the synapomorphic conditions of the genital apparatus, namely a hermaphroditic genital system with the ovary/oviduct separated from the testis/vas deferens, a large receptaculum in the mantle roof and a unique penis formed by the right propodium.

The data currently available for *Lodderena* reveal significant differences in the genital system between it and Skeneidae. Whereas in *Lodderena* a true ovotestis is present, and both a propodeal penis and receptaculum are absent, in skeneids there are a separate testis and ovary, and both a propodeal penis and receptaculum are

present. The report of a propodial penis in ‘*Lodderena catenoides*’ by Warén (1992) is not relevant here, this species now classified as *Skeneia catenoides* (MolluscaBase, 2019). Accordingly, *Lodderena* cannot be included in Skeneidae, as currently defined.

There are numerous other genera assigned to Skeneidae that are currently diagnosed by hard-part characters alone; such characters are obviously insufficient for clarifying the systematics of this group (e.g. Chen *et al.*, 2015). There is a great need for further studies on the soft anatomy or molecular systematics of skeneimorph microgastropods, and ideally both these aspects should be considered. This combined with research on traditional morphological characters, such as the teleoconch, protoconch and radula, will advance our understanding of the phylogenetics and evolution of the many small species that constitute the Skeneidae. It seems wisest at present to treat *Lodderena*, as well as many other skeneimorph genera, as ‘Trochoidea *incertae sedis*’.

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