Anatomy of *Zetela alphonsi* Vilvens, 2002 (Mollusca: Solariellidae) casts doubt on its original placement based on conchological characters

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Running head: ANATOMY OF *ZETELA ALPHONSI* VILVENS, 2002.

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Abstract

Zetela is a genus of marine gastropods belonging to the family Solariellidae (Vetigastropoda, Trochoidea). The species *Zetela alphonsi* Vilvens, 2002 was originally described using classical conchological characters from samples obtained from deep water off Chiloé, Chile, but no other features were recorded in the original description. In the present paper, taxonomically relevant characters such as the operculum, radula, and soft part anatomy are illustrated and described for the first time from a specimen of *Zetela alphonsi* from a new locality, a methane seep area off the coast of central Chile. We find that many features differ substantially from other members of the genus, including several which deviate from characters that are diagnostic for *Zetela*. *Zetela alphonsi* also lacks retinal screening pigment, giving the appearance of eyelessness from gross examination. Although pigmentation loss has been reported in other deep sea genera, this feature has not been reported in any other members of *Zetela.* We reconstructed a tomographic model of the eye and eyestalk, and demonstrate that a vestigial eye is still present but externally invisible due to the loss of pigmentation. Based on these new morphological characters, particularly observations of the radula, we suggest that the current placement of this species in the genus *Zetela* should be reconsidered.

Introduction

Trochoidean gastropods are found in a huge range of habitats across the world, from the intertidal to abyssal depths, and are one of the most diverse clades of marine gastropods (Hickman 1996), as well as exhibiting high morphological and ecological diversity (Williams et al. 2007). They form a significant component of the molluscan fauna in the fascinating deep-sea habitats off the West coast of South America, and they merit greater attention from the scientific community. Few studies have addressed the biology, taxonomy or ecology of trochoideans along the Chilean coast, and even reported geographic distributions are patchy. *Calliostoma fonki* (Philippi, 1860), a moderately shallow water species found as far north as Peru and the Galápagos Islands, was the first recorded species initially reported by Keen (1971). Among the deeper water species, McLean and Andrade (1982) reported two species of the genus *Calliostoma* (*C. chilena* [= *Maurea chilena* (Rehder, 1971)] and *C. delli* [= *Maurea delli* (McLean & Andrade, 1982)]) and two species of *Bathybembix* (*B. macdonaldi* (Dall, 1890) and *B. humboldti* Rehder, 1971) as accompanying fauna of bathyal crustacean fisheries in central Chile. In a detailed survey, Forcelli (2000) cited 27 species from the Magellanic province, most of them also being deep-water taxa occurring mainly on the Atlantic side. In turn, Véliz and Vásquez (2000) studied the latitudinal and bathymetric distribution of eleven trochoidean species for the northern coast of Chile (18-31°S), also covering the neritic and intertidal areas.

The location of a methane seep 40 miles north-west off the Bay of Concepción has been reported by Sellanes et al. (2004). At methane seeps and in other chemically reducing marine environments, chemically reduced fluids are utilised as a source of energy for carbon fixation by free-living and endosymbiotic chemosynthetic bacteria (Paull et al. 1984), and carbonates

are produced as a by-product of the anaerobic oxidation of methane within the sediment (Boetius et al. 2000). The abundant fauna found at these sites benefits from both the chemosynthetically-derived food sources and the shelter and substrate provided by the reefs formed by carbonate-cemented mud (Sibuet and Olu 1988). About 30 species of molluscs (Sellanes et al. 2008) have been recorded in the Concepción methane seep area (CMSA) and part of this assemblage comprises many new species of chemosymbiotic bivalves (Holmes et al., 2005; Oliver and Sellanes, 2005; Sellanes and Krylova, 2005). Among the non-chemosymbiotic species present, five species of trochoids have been recorded (Vilvens & Sellanes 2006, 2010). One of the latest species to be added to the list of Chilean trochoideans is *Zetela alphonsi* Vilvens 2002, described from off Chiloé (~41°S) at 800 metres depth (Vilvens 2002). This species has now also been found further north (~36°S), at the Concepción methane seep area, located 40 miles northwest off the Bay of Concepción (Sellanes et al. 2004; Warén et al. 2011). However, the original description of this species focused on shell morphology only, despite live-collected specimens having been available, and in spite of the doubts expressed by some authors on the reliability of using shell features to distinguish solariellid taxa (e.g. Herbert 1987, Hickman & McLean 1990, Dornellas & Simone 2015). Radular features in particular may provide more useful characters for identification and placement (Herbert 1987), but these have not been described in *Z. alphonsi*. Recent studies have demonstrated that Solariellidae in particular could become a key model group for examining evolution in deep water, particularly the loss and reduction of eyes and retinal pigmentation (Williams et al. 2013, Sumner-Rooney et al. 2016). Reduction of eye structures in the deep-sea is a well-known phenomenon reported also in other taxa like cephalopods, crustaceans or teleosts (see e.g. Warrant and Locket 2004), but it is found repeatedly in Solariellidae (Williams et al. 2013, Sumner-Rooney et al. 2016). In the present study, it was also shown that *Z. alphonsi* exhibits certain reduced characters of the eye in line

with its deep-sea habitat. Other aspects of the soft body anatomy of *Z. alphonsi* remain unknown, but could be of vital importance, both to future evolutionary studies in Solariellidae and its taxonomic placement in the absence of molecular data (Sumner-Rooney et al. 2016). In the present work we describe the soft part anatomy, operculum, jaw and radula of *Z. alphonsi* for the first time from material collected at the CMSA, and we use these characteristics to assess the validity of the generic status originally proposed for the species, namely its placement in *Zetela*.

Material and methods

Morphological examination

Specimens were collected off the coast of Chiloé, Chile, from depths between 600-1000 metres using an Agassiz trawl (see Table 1) and fixed in 2.5% glutaraldehyde in phosphate buffer (0.1M, pH 7.4). Dissection and maceration procedures for the examination of the soft body and extraction of the radula and operculum followed those described by Hickman and McLean (1990). The preparation, scanning electron microscopy, and illustration of the radula, operculum, and jaw follow the method described in Schwabe and Barclay (2003). For histology and electron microscopy, eye stalks were excised, washed in buffer and serially dehydrated before embedding, sectioning and tomographic model reconstruction using AMIRA 3D software (FEI) after Ruthensteiner (2008). Semithin sections (655 slices at 1 µm) were stained after Richardson (1960) and photographed with an Olympus DP25 camera mounted on an Olympus CX41 light microscope (objectives Plan CN 20x and Plan CN 40x). Thin sections (13 slices at 80 nm) were cut intermittently from embedded tissues, mounted on copper grids and visualised on a Zeiss EM 900 at 80 kV. In addition, semithin and ultrathin sections of the eyestalk of *Phorcus lineatus* (da Costa, 1778), another trochoid, collected in the intertidal near Roscoff (Bretagne, France), were investigated for comparison.

Systematics

Class Gastropoda Cuvier, 1795

Subclass Vetigastropoda Salvini-Plawen, 1980

Order Trochoidea Rafinesque, 1815

Family Solariellidae Powell, 1951

Genus *Zetela* Finlay, 1926 (: 359)

Type species: *Minolia textilis* Murdoch & Suter, 1906, by original designation.

Zetela alphonsi Vilvens, 2002 (: 61)

(Figs 1-3)

Holotype: MNHN 2000-30362 (not seen)

Type locality: Chile, Región de los Lagos, off Chiloé, at 800 m depth on muddy bottoms.

Results

Shell. The shells of the newly collected specimens are identical to those reported in the original description of this species (Figure 1A, B).

Head. The elongated snout has short tentaculiform processes (Figure 1C-E) on the dorsal margin of the oral disc. The mouth lacks oral lappets, and there is no visible pseudoproboscis. The epipodium bears three pairs of micropapillate epipodial tentacles (Figure 1C-F) with a fringe of four smaller tentacles between the anteriormost two (epipodial lobes *sensu* Marshall 1999). The epipodial sense organ is situated anteriorly at the base of the first epipodial tentacle. A pair of flat neck lobes extends from either side of the eye stalks to the epipodial sense organ. The cephalic tentacles are smooth (lacking any papillae), and rather long,

reaching at least 3 mm in the illustrated specimen, tapering to an obtuse point (Figure 1C-F). Very short eye stalks (approximately 300 μm in length, Figure 1C-F), without any traces of visual pigmentation, are present at the base of the cephalic tentacles (see below). A single, tan ctenidium is found posterior to the head.

Foot. The foot is hammer-shaped at the anterior end, terminating in two long, pointed, and laterally-expanded tips, the so-called propodia (Figure 1F). The anterior edge is bent downwards. The foot extends posteriorly, beyond the operculum.

Operculum. The operculum is horny, tan, and multispiral (about 12 revolutions), with the side attaching to the dorsal part of the foot being strongly convex (Figure 2A, B). In profile the operculum (diameter 3 mm) has a height of 970 μm, with an angle of divergence of 155 ° (Figure 2B). In accordance with Hickman and McLean (1990), the growing edge of the operculum is long (Figure 2A).

Radula. Immediately behind the mouth opening there is a pair of trapezoid jaws. These are anteriorly (i.e. behind the mouth opening) thickened, and reach a shallow point at their posterior end, with a fringe of short, elongated, and obtusely pointed scale-like processes that reach a size of 13.5 μm x 6 μm (Figure 2C, D). The rhipidoglossate radula (Figure 2E, F) contains 32 teeth rows, and has a formula of: 8 + lmp (lateromarginal plate) + 4 + 1 + 4 + lmp + 8 (Figure 2E, F). The rachidian (Figure 2F) is quadrangular at the base and about 50 μm in width, with a triangular, sharply pointed cutting edge, which is approximately 31 μm in width and 45 μm in length. The cutting edges of the lateral margins are strongly and irregularly serrated, with up to six denticles per side. The first lateral tooth (Figure 2F) has a curved shaft, and measures 28 μm in width and 31 μm in length. Its cutting edge is triangular and sharply pointed, with the inner margin smooth, straight and steep, and the outer margin shallower, with about eight denticles. The second lateral tooth (Figure 2E) has a quadrangular

shaft, which is about 50 μm in width and length and narrower toward the anterior. Its cutting edge is triangular and inwardly directed, similar to the first lateral tooth but with a longer and shallower outer margin. The shaft of the third lateral tooth is similar in size to that of the second lateral tooth, but appears more thickset due to its smaller, sharply pointed cutting edge. The fourth lateral tooth, about 145 μm in total length, is slender, sharp-pointed, and strongly inwardly curved. The cutting edges of the marginal teeth are serrated. The marginal teeth are similar; slender, with a hook-like curve at the upper end, with a distinct serration in the distal quarter. The rectangular lateromarginal plates (Figure 2E) are short and wide, measuring 44 μm x 56 μm. Some of them show a rudimentary cusp (or its remains) on the inner margin.

Eyes. The eye stalk splits near the base to give another fine accessory tentacle (Figure 3A, C, D). Superficially, *Zetela alphonsi* appears to be eyeless, but histological sections show there is a vestigial eye structure present beneath the surface (Figure 3B-D), rendered invisible to gross examination by the loss of retinal pigmentation. The retina itself is intact and well organised (Figure 3B, D), innervated by the optic nerve (Figure 3A, B, C) and with microvilli extending from the distal retina into the eye lumen (Figure 3B, 4B, C. The vitreous body, which in vetigastropods characteristically forms a discrete globular shape at the centre of the lumen and acts as a lens, is also present (Figure 3B). However, the eyes of *Z. alphonsi* display several indicators of a regressive state when compared to an eyed trochoid, *Phorcus lineatus* (Figure 4A). Retinal pigment cells in *Zetela alphonsi* lack their characterising pigmentation (Figure 4B, C), and the aperture of the pit eye has become enveloped by the surrounding epithelium (Figure 3B).

Discussion

Zetela alphonsi was originally described from a sample collected off the coast of Chiloé (41°85´S at 800 m depth) and also reported from off Taltal (25°40´S in 900-1000 m). Here we report it from an intermediate point within this range at the Concepción methane seep area (CMSA), and from depths of 600 to 1000 m. Although estimations of abundance are not possible due to the non-quantitative nature of the sampling gear used in all these studies, *Z. alphonsi* is more frequently collected at the CMSA than elsewhere, which however could be an effect of the sampling bias at this particular site, rather than true abundance. Further relationships between this species and methane seep habitats are at this point precluded. Warén et al. (2011) followed Sellanes et al. (2008) and considered the species an occasional intruder to seep areas.

Crucially, the recovery of living specimens of *Zetela alphonsi* at this site greatly enhances our knowledge of the species, and the new characters described here throw significant doubt on its placement in this genus. The diagnostic features of Solariellidae (under the now synonymised name Solariellinae) were summarized by Hickman and McLean (1990, p. 113), who characterized the group by: 1) the absence of cephalic lappets, 2) unusually long cephalic tentacles, 3) presence of tentaculiform processes around the oral disc, which are longer at the dorsal margin, 4) foot with lateral projections anteriorly, 5) radula with a reduced number of rows (fewer than 30), and 6) differentiation in shape and size of the lateral teeth. The examined material fulfils characters 1-4 and 6, supporting the placement of *Zetela alphonsi* within the Solariellidae, although the number of radular teeth rows (32) is slightly higher than diagnosed by Hickman and McLean (1990).

Herbert (1987) also pointed out the taxonomic importance of lateromarginal plates in the solariellid radula, describing the new genus *Ilanga* as being characterized by the absence of this feature. Furthermore, he explicitly excluded the genus *Zetela* Finlay, 1927 from the Solariellidae (Solariellinae) with lateromarginal plates. Marshall (1999, p. 33) also reported

the lack of a lateromarginal plate for *Minolia textilis* Murdoch and Suter, 1906, the type species of *Zetela*. However, a lateromarginal plate is present in *Zetela alphonsi* (Figure 2E). If this radular character is of such relevance that its presence or absence justified the creation of a new genus by Herbert (1987), these new data cast doubt on the likelihood that *Zetela alphonsi* is placed in the correct genus. In addition, the examined material shows differences in the number of marginal teeth: about six pairs per row were described for the type species of *Zetela* by Marshall (1999), while *Zetela alphonsi* has eight pairs of marginal teeth and resembles more closely the radula condition presented by Marshall (1999, fig. 131) for the genus *Bathymophila* Dall, 1881. However, *Zetela alphonsi* certainly differs from *Bathymophila* conchologically, and attempts to resolve its phylogenetic position using molecular data have so far been unsuccessful (Sumner-Rooney et al. 2016). Marshall (1999) additionally demonstrated that species of *Zetela* have four epipodial tentacles on each side, a character we did not observe in the present material. *Z. alphonsi* has three epipodial tentacles with four additional small tentacles between the two anterior epipodial tentacles. All the species Marshall examined had broad neck lobes, while in *Z. alphonsi* they are flat.

Vilvens (2002) described this new taxon as "*Solariella*-like" and underlined its conchological similarity to the genus *Calliotropis* Seguenza, 1903 despite its placement among *Zetela*. Marshall (1999) also considered *Zetela* very similar to *Calliotropis* generally, the latter is currently classified under the Seguenzioidea, Calliotropidae (according to Kano et al. 2009), although this is not yet subject to full consensus (e.g., Bandel 2010, Ferrari et al. 2014). However, there are several important differences between *Z. alphonsi* and *Calliotropis*, too. *Calliotropis* has a fine axial ornamentation of the protoconch (e.g., Marshall 1979, Bandel 2010), whereas in *Z. alphonsi* it is granulated with a thick abapical spiral cord (Vilvens 2002). Other shell characters are difficult to interpret (e.g., Marshall 1979) and should be handled with care. Radulae have only been described from a limited number of species in

225 *Calliotropis* (e.g. Marshall 1979, Vilvens & Sellanes 2010) and are not yet sufficient for a
226 conclusive interpretation: while Vilvens & Sellanes (2010) demonstrated the presence of a
227 lateromarginal plate in *Calliotropis ceciliae*, such modified inner marginal teeth were not
228 observed in Marshall's study. Also common is the presence of three (*vs*. four in *Z. alphonsi*)
229 lateral teeth. Finally, Quinn (1983) demonstrated that Seguenzioidea (as "Seguenziacea")
230 have a varying number of epipodial tentacles, but an epipodial sense organ seems to be
231 lacking. In *Z. alphonsi* we observed this organ at the first epipodial tentacle. Taking these
232 differences into account, we prefer to exclude a closer affinity of *Z. alphonsi* with
233 *Calliotropis*. Instead, the characters investigated in our material i.e., three pairs of epipodial
234 tentacles, the presence of an epipodial lobe between the first epipodial tentacles, the presence
235 of a lateromarginal plate, the short at the base widened, sharply pointed rachidian, Vilven's
236 (2002) characterization of the protoconch, are more in line with the characteristics Warén
237 (1993) provided for *Solariella*, especially *S. amabilis* (Jeffreys, 1865). We suggest that the
238 placement of *'Zetela' alphonsi* be revisited thoroughly and revised if necessary, but until
239 sufficient evidence is available to resolve its position, care should be taken to highlight its
240 precarious assignment to the current genus.

241 The state of the eyes in *'Zetela' alphonsi* is intriguing. The characters we find here suggest an
242 intermediate state of eye reduction in this deep-water species. The penetration of biologically
243 relevant light is negligible below around 700 metres (by day), where most of the current
244 specimens were recovered, and the loss or degeneration of eyes and visual structures is very
245 common in dark environments (Fong et al. 1995). Additionally, it is commonly true that even
246 reduced eyes are not completely eliminated in deep-sea, troglobitic or fossorial taxa, and this
247 appears to also be the case in *'Z.' alphonsi*. As found by Sumner-Rooney et al. (2016)
248 following observations made by Williams et al. (2013), the loss of eyes in deep water has
249 appeared several times within Solariellidae, but *'Z.' alphonsi* is the only putative

representative of the genus known to exhibit eye reduction. This is unusual in the context of the genus, given that many species of *Zetela sensu stricto* inhabit deep water (700 m or greater) but display no apparent signs of eye reduction (Sumner-Rooney et al. 2016). Although the ecological and evolutionary drivers for eye loss are not known in this case, it is possible that the eyes of *'Z.' alphonsi* indicate another distinction from the rest of their proposed congeners. The analyses of Williams et al. (2013) support an expansion into deep water more than 30 million years ago, before the divergence of *Zetela*, and so a simple extension of the depth range of *'Z.' alphonsi* is unlikely to explain the striking difference in eye structure to other species.

It is not uncommon for newly discovered deep-water gastropod species to be described mainly or wholly from conchological characters (even if they have been live-collected) (e.g. Bouchet & Métivier, 1983; Hoare & Engl, 2007; Alf & Kreipl, 2011), which have been overwhelmingly relied upon historically for determining taxonomic placements (e.g. Thiele 1931). Our description of several important new characters from soft tissues and the radula of *'Zetela' alphonsi* throws considerable doubt on the original assignment of the species to its currently accepted genus, and by extension highlights the potential problems with our reliance on shell morphology (e.g. Hickman & McLean 1990, Warén et al. 2011 for *Margarites huloti* Vilvens & Sellanes, 2006, Dornellas & Simone 2015). But, as the conflicting radular and shell characters exemplify in this case, it is almost certain that no one set of features is sufficiently reliable for universal use in taxonomy. This emphasises the importance of collecting whole animals wherever possible and synthesising all available morphological (and where possible, molecular) data to support the classification of new species. Although this remains a challenge for the identification of deep-sea taxa, there is a considerable risk of misclassification in the many species which have been described based mainly on their conchology (see e.g. Heß et al., 2008; Haszprunar et al., 2016). As more soft

tissue samples are recovered, malacologists face increasing conflict with the current accepted assignments of a large number of species.

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Figure legends

Figure 1: *Zetela alphonsi* Vilvens, 2002, shell and external anatomy. A: dorsal view of the shell (ZSM Mol 20041458); B: ventral view of the shell (ZSM Mol 20041458); C: dorsal view of a removed specimen (ZSM Mol 20041247); D: same specimen as C, foot removed; E: same specimen as fig. C, left lateral view; F: same specimen as fig. C, right lateral view. *as* – attaching side of the operculum, *ct* – cephalic tentacle, *ept* – epipodial tentacle, *es* – eye stalk, *f* – foot, *h* – head, *p* – propodium, *tp* – tentaculiform processes. Scale bars, A, B: 2 mm, C-F: 1 mm.

Figure 2: *Zetela alphonsi* Vilvens, 2002, operculum, jaw (ZSM Mol 20041247), and radula (ZSM Mol 20041246). A: internal view of the operculum with growing edge (arrowhead); B: lateral view of the operculum with growing edge (arrowhead); C: inner view of the left jaw plate, anterior at bottom; D: detail of the jaw plate, showing the scale-like processes; E: anterior and middle portion of the radula, (lateromarginal plates indicated by an arrow); F: Rhachidian cusp (r) and first lateral teeth (l1-l3) and overhanging cusps of marginal teeth (m). Scale bars, A, B: 1 mm, C, E: 100 µm, D, F: 10 µm.

Figure 3: *Zetela alphonsi* Vilvens, 2002, eye stalk histology and 3D microanatomy. A: 3D-Reconstruction of the eyestalk and accessory tentacle of *Z. alphonsi*. Body surface transparent, outline of the eye and optic nerve yellow, c and d indicate the planes of Fig. 3 C and D; B: longitudinal section through the eyestalk; C: cross section at the level of optic nerve; D: cross section at the level of the eye. mv – microvilli, no – optic nerve (dotted line), ret – retina, v – vitreous body, * – accessory tentacle. Scale bars, A: 100 µm, B-D: 50 µm.

Figure 4: Comparative eye microanatomy in *Zetela alphonsi* and *Phorcus lineatus*. Organization of the retina in *P. lineatus* (A) and *Z. alphonsi* (B). Pigment cells in *P. lineatus* contain many dark granules of pigment (arrowhead) but do not bear any microvilli. In *Z. alphonsi* these cells contain some degenerating pigment granules (arrowhead) and form microvilli, which are typical of the photoreceptor cells in both species. The vitreous body is formed by extracellular material with slightly increased electron density; C: low magnification electron micrograph of the *Z. alphonsi* retina, somata on bottom with degenerated pigment granules (arrowheads), microvilli (mv) on top. Scale bar, B: 5 µm.

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427 **Table 1.** Material of *‘Zetela’ alphonsi* examined in this study.

Species	**Specimen number**	**Specimen size**	**Depth (m)**	**Locality**	**Expedition**	**Date collected**
‘Zetela’ alphonsi	ZSM Mol 20041458	9.5 x 8.2 mm	906-1000	Chile, Región del BioBío, off Concepción (36°12.16'S 73°39.15'W)	R/V “Vidal Gormáz”	October 2004
‘Zetela’ alphonsi	ZSM Mol 20041247	9.7 x 7.6 mm	600	Chile, Región del BioBío, off Concepción (36°24.12'S 73°36.44'W)	R/V “Kay Kay”	July 2004
‘Zetela’ alphonsi	ZSM Mol 20041246	10 x 8 mm	600	Chile, Región del BioBío, off Concepción (36°24.12'S 73°36.44'W)	R/V “Kay Kay”	July 2004

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Figure 1

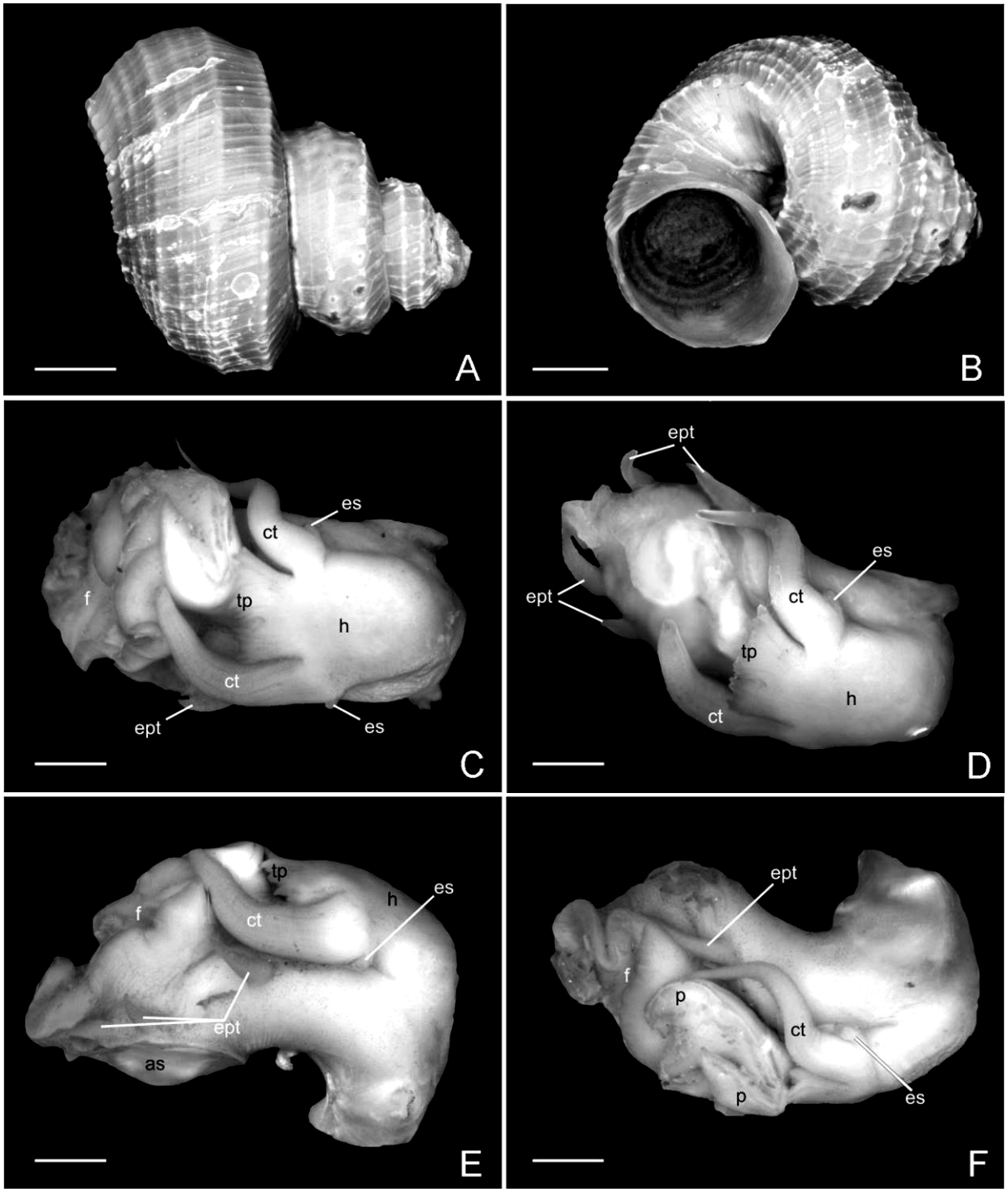
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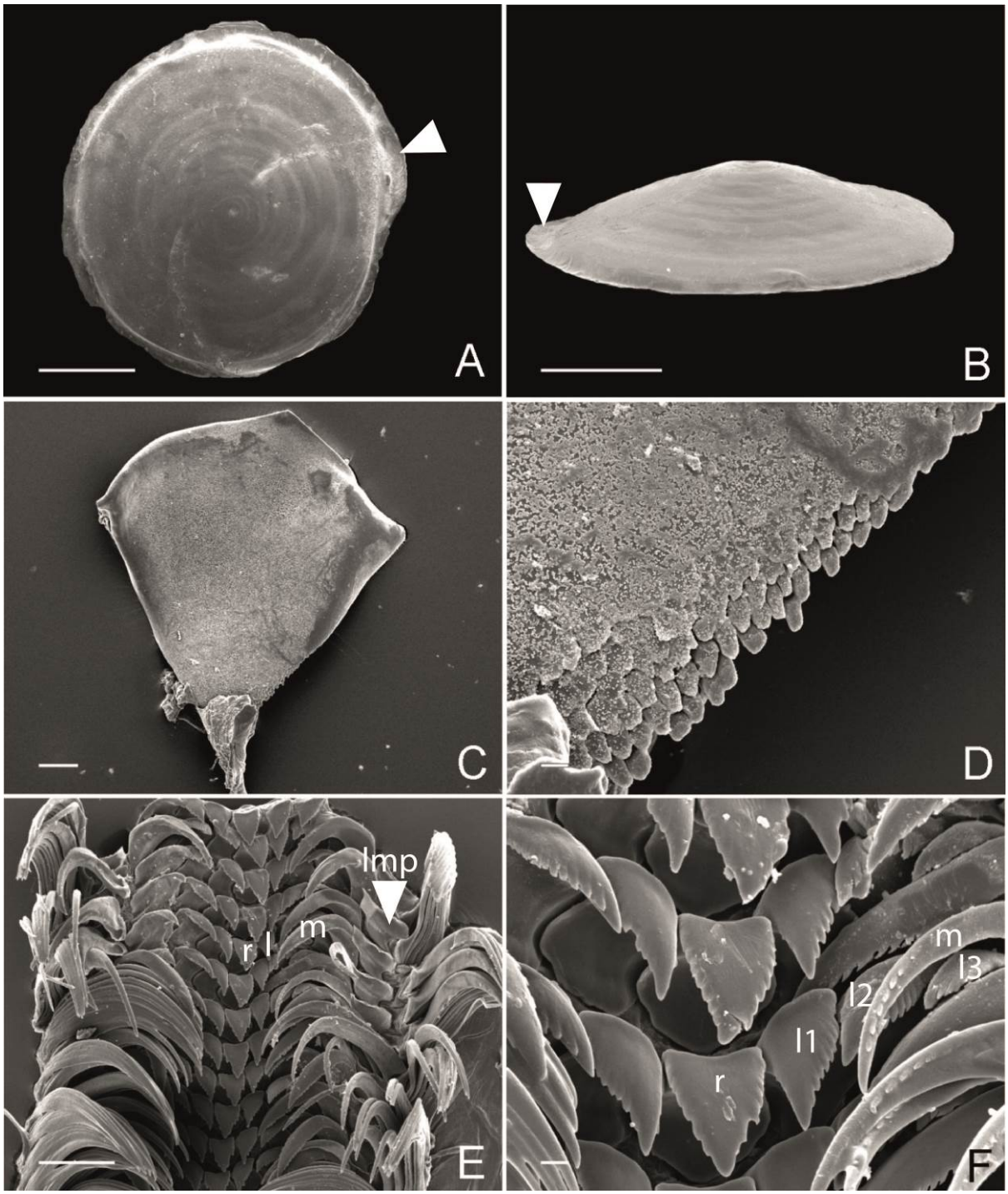
Figure 2



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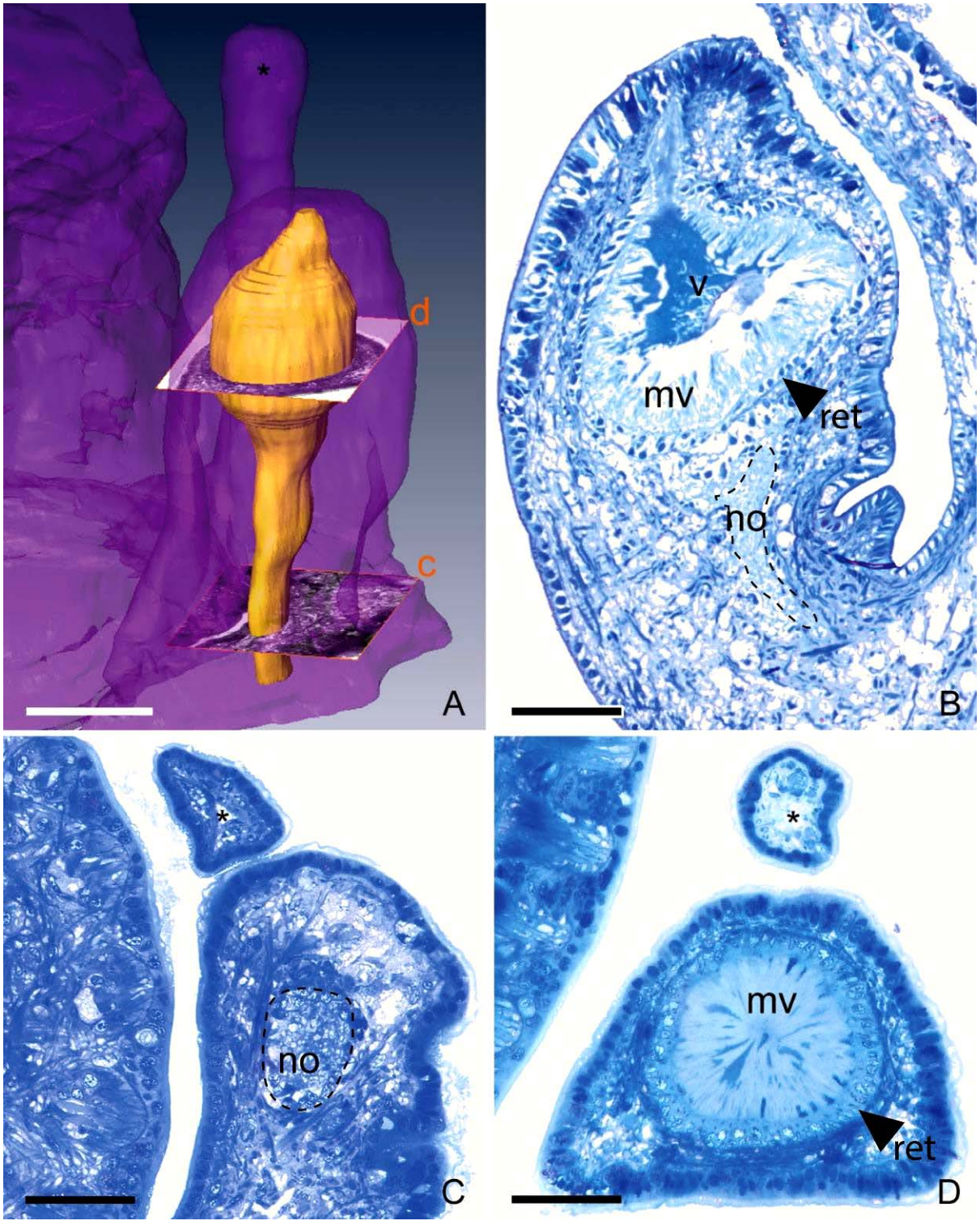
439 **Figure 3**



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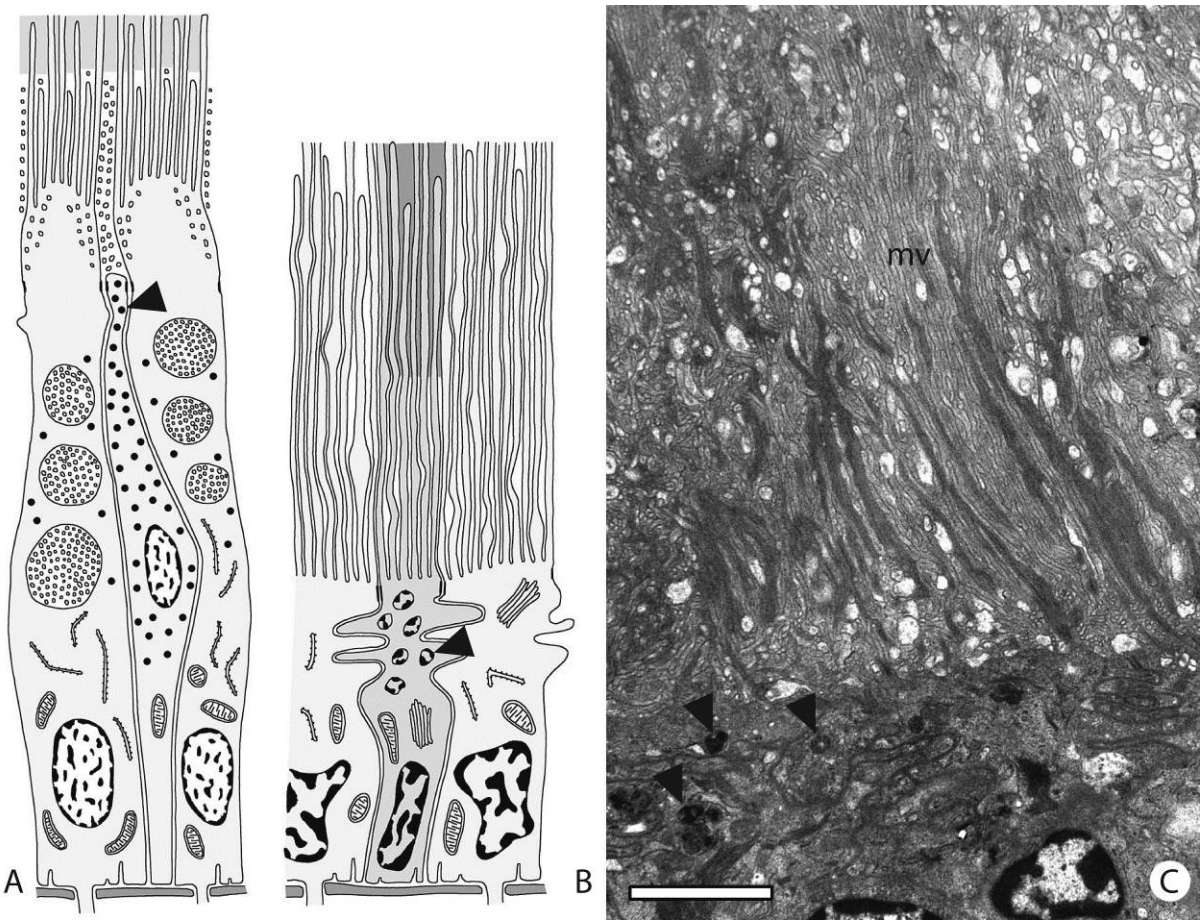
442 **Figure 4**



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