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Four new species of Anatomidae (Mollusca: Vetigastropoda) from the Indian Ocean (Reunion, Mayotte) and Australia, with notes on a novel radular type for the family

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Abstract

Four new species of Anatomidae are described: *Anatoma herberti* n. sp. with strong axial sculpture on the shoulder and base; *A. austrolissa* n. sp. with almost smooth sculpture except for axial cords in the adumbilical half of the base; *A. boucheti* n. sp. with sunken protoconch and selenizone that starts after more than one teleoconch I whorl; and *A. flexidentata* n. sp. with a highly modified radula, shared only with *A. austrolissa,* among known anatomid species. Three of the species are only known from the Indian Ocean, while the more deep-water *A. austrolissa* is known from Reunion Island and New South Wales, Australia. The radula of *A. flexidentata* and *A. austrolissa* is strikingly different from that of other Anatomidae and Vetigastropoda in that it has flexible equally-shaped teeth in the central field and filamentous teeth in the marginal field. Similar radular morphologies are known from Calliostomatidae.

Key words: new species, Indian Ocean, Reunion Island, Mayotte, Australia, radula

Introduction

The family Anatomidae contains small, slit-bearing vetigastropods and is distributed in all fully marine environments (Bandel 1998; Geiger 2003; Geiger *et al.* 2008), including several dozen undescribed species (Geiger 2008). The taxon was elevated to full family rank based on a comprehensive molecular phylogeny of Vetigastropoda (Geiger & Thacker 2005, unpubl. data; see also Kano 2008).

The Mascarene Islands (Reunion Island and Mauritius) are located 700–900 km to the east of Madagascar and the marine fauna shows a general east African affinity (Sharabati 1984; Drivas & Jay 1988). Yaron (1983) and Herbert (1986) treated the Scissurellidae and Anatomidae of the Red Sea and South Africa, respectively, with Bandel (1998) and Geiger (2006a) adding further taxa. Specimens housed in the Muséum national d'Histoire naturelle, Paris, from the Mascarene Islands could not be identified under existing names and are herein described.

The radulae of Anatomidae have been rarely illustrated, with place-holding taxa such as *Anatoma crispata* (Fleming, 1828) being the most commonly figured (*e.g.*, Hickman 1998). Notable exceptions include Herbert (1986), Sasaki (1998) and Geiger (2006c). The radula of the family was presumed to show little interspecific variability, which has shown to be the case with the more extensively

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examined Scissurellidae (*e.g.*, Marshall 2002; Geiger 2003, 2006a; Geiger & Jansen 2004b). First indications of appreciable variability of the radula came to light with *A. janetae* Geiger, 2006, which showed a different fine structure of the inner marginal teeth (Geiger 2006c). Additional species with thus far unrecorded radular structures are to be described elsewhere (Sasaki *et al*. unpubl. data).

Here we report on four new species of Anatomidae, two of which show a novel radular structure for Scissurellidae s.l. and Anatomidae, so different that one might consider it significant at the family level. We also provide some details on preparation and imaging details that will prove to be useful in any study of micromolluscs.

Material and methods

Standard methods for scanning electron microscopy (SEM) were employed as detailed in Geiger (2006a,b,c) and Geiger *et al.* (2007). A brief summary is provided here. Shells of specimens were cleaned by sonication as much as the specimens permitted. Shells were mounted using a moist brush on double-sided carbon tabs. They were first mounted so that the base was at an angle of less than 90° to provide apertural, apical and protoconch views. Subsequently they were detached from the carbon tab with a brush moistened with 100% ethanol and remounted with the shell shoulder making contact with the carbon tab to provide the umbilical view. The specimens were sputter coated with gold after each mounting on a Cressington 108auto sputter coater with rotary-planetary stage (Watford, Great Britain). The stage was set at maximum inclination and rotation to lowest speed.

Soft parts were removed from the water soaked specimens with tungsten needles (Fine Science Tools, Foster City, CA: FST 10130-05) and emery-paper-sharpened forceps. The soft parts were dissolved in fresh KOH (1 pellet in approximately 2.5 ml distilled water), heated to approximately 50°C in a dry bath incubator for several hours. The radula was washed twice in distilled water and mounted on double-sided carbon tabs or directly on pieces of a microscopy covers slip in a drop of distilled water using tungsten needles for manipulation. The radula was sputter coated with gold. One unsuccessfully prepared radula (Fig. 6B), that was very dirty and insufficiently spread, was released from the glass support with water, dipped in bleach for a few seconds, washed in water several times, and re-mounted (Fig. 6A).

Most SEM images were taken on a Zeiss EVO40 XVP (Zeiss, Cambridge, Great Britain) at the Santa Barbara Museum of Natural History, with a few images on a LEO 1435VP (LEO/Zeiss, Cambridge, Great Britain) at the Australian Museum, Sydney. Usually, shells were imaged at variable pressure (30 Pa chamber pressure), using the Variable Pressure Secondary Electron Detector, at 20 kV accelerating voltage, a probe current of 50–100 pA and a target working distance of 10 ±1 mm. Occasionally longer working distances had to be used due to constraints of specimen orientation and possible stage movements. Radulae were imaged by SEM in high vacuum; usually at 15–20 kV, a probe current of 20–100 pA, at 10 mm working distance, using the secondary electron detector.

Images were digitally processed in *Adobe Photoshop CS2* (Adobe Systems, Inc.). Shells were cut out from the background and assembled to multilayer plates. Some highlights were mitigated using the *Image-Adjust-Shadow/Highlight* function, with *Amount* usually set to 100%, while *Tonal Width* (usually 15–50%) and *Radius* (usually 5–30 pixels) were selected to produce a pleasing result. Shell defects and dirt were not mended, *i.e.,* tools such as cloning stamp and healing brush were not applied to maintain the scientific integrity of the images.

With the material examined, the repository institution, registration number (if used by institution), and the number of specimens are given. Numbers of specimens refers to dry empty shells, otherwise the preservational state is given. With some material abbreviations for cruise and station numbers are provided as on original label.

Descriptive terms of shell sculpture used are defined as follows. Teleoconch I: Shell from apertural lip of protoconch to onset of selenizone. Teleoconch II: Shell from onset of selenizone onwards. These terms [apparently introduced by Geiger (2003) *fide* A. Warén pers. comm.] are the logical extensions of the well-known terminology for protoconch I and II (*e.g.,* Gustafson & Lutz 1994), *i.e.*, differentiating portions of the protoconch with discrete morphological features. The teleoconch I/II distinction is not restricted to Scissurellidae s.l., but may also be applied for instance to *Tibia* spp. (Strombidae).

Rib: A sculptural element that is higher than wide. Cord: Distinct sculptural elements, about as high as wide, easily seen under the light microscope, wider than lines, lower than ribs. Line: Sculptural element that may be seen under the light microscope only with great difficulty and are approximately as wide as high. Lines are wider than threads, and narrower than cords. Thread: Thin sculptural element, most likely not visible with the light microscope, weaker than lines.

Institutional abbreviations

AMS	Australian Museum Sydney, Australia.
BMNH	The Natural History Museum, London, Great Britain.
NMW	National Museums and Galleries of Wales, Cardiff, Great Britain.
NMSZ	National Museum of Scotland, Edingburgh, Great Britain.
MNHN	Muséum National d'Histoire Naturelle, Paris, France.
USNM	United States National Museum, Smithsonian Institution, Washington (DC), USA.

Systematics

Anatomidae McLean, 1989

Anatoma Woodward, 1859

Type species: *Scissurella crispata* Fleming, 1828 (by monotypy).

Anatoma herberti new species (Figs 1–2)

Type material. Holotype (MNHN 20632: Fig. 1). Paratypes: 630–710 m, Reunion Island, MD32, DR62, 21.150°S, 55.200°E (MNHN 20634, 3: Fig. 2). 825–890 m, Reunion Island, MD32, DR63, 21.167°S, 55.150°E (MNHN 20633).

Type locality. 280–340 m, Reunion Island, MD32, DC128, 20.850°S, 55.600°E.

Additional material. 825–890 m, Reunion Island, 21.167°S, 55.150°E (MNHN, 1).

Etymology. The name honors Dai Herbert of the Natal Museum, Republic of South Africa, for his detailed works on the South African scissurellid fauna.

Description. Shell medium sized (to 2.03 mm: holotype), trochiform, tabulated. Protoconch of 0.75 whorls, sculpture flocculent, apertural varix not connected to embryonic cap, apertural margin slightly sinusoidal. Teleoconch I of 0.6–0.75 whorls, 14–26 axial cords, usually with spiral cord in position of selenizone forming distinct knobs at intersection with axials. Teleoconch II of up to 2.25 whorls. Suture impressed, slightly more than width of selenizone below selenizone; shoulder arched, 27–29 axial ribs on last whorl, quite evenly spaced, increasing in strength, elevation with growth; fine axial cords on apical surface of keels of selenizone, approximately 3–5 between each pair of strong axial ribs; very fine spiral lines running over axial cords, first spiral line starting after 0.25–0.33 teleoconch II whorls in middle of shoulder, approximately a dozen fine spiral lines evenly spaced over shoulder at apertural margin of 2 mm specimen. Base with moderately distinct constric-

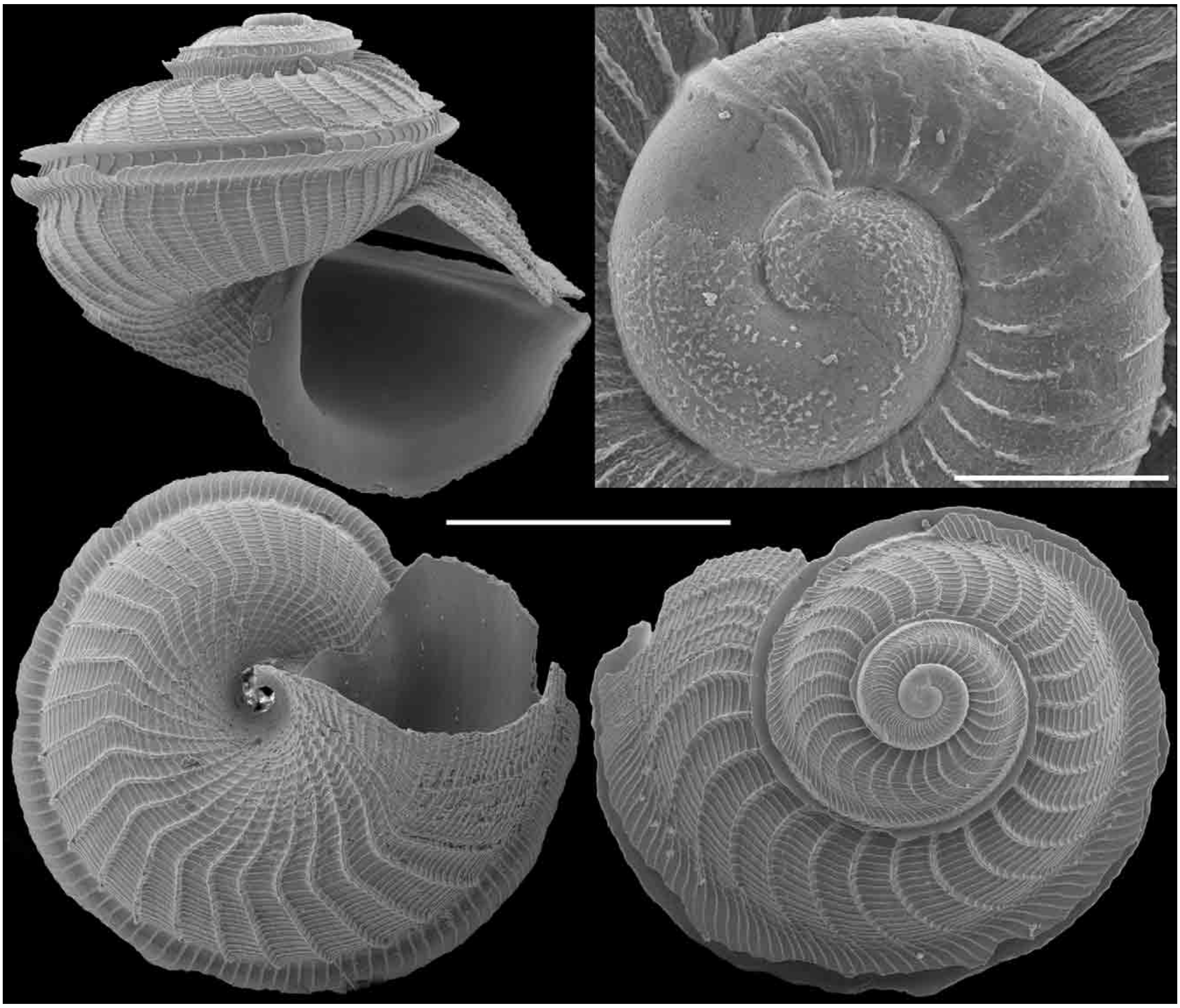

Figure 1. Holotype of *Anatoma herberti* new species (MNHN 20632). 280–340 m, Reunion Island, 20.850°S, 55.600°E. Scale bar shell = 1 mm. Scale bar protoconch = 100 µm.

tion below selenizone, sloping continuously into open umbilicus, sculpture similar to that on shoulder; spiral lines more or less equally spaced, approximately 25 from selenizone into umbilicus; axials increasing in strength from cords to raised ribs on last whorl; exterior of basal keel of selenizone with supernumerary axial lines compared to base. Selenizone at periphery; keels strongly elevated, average strength for family, smooth on inside, fine axial lines on outside; lunules fine, evenly spaced; slit open, with parallel margins. Aperture rounded, roof overhanging. Soft parts unknown.

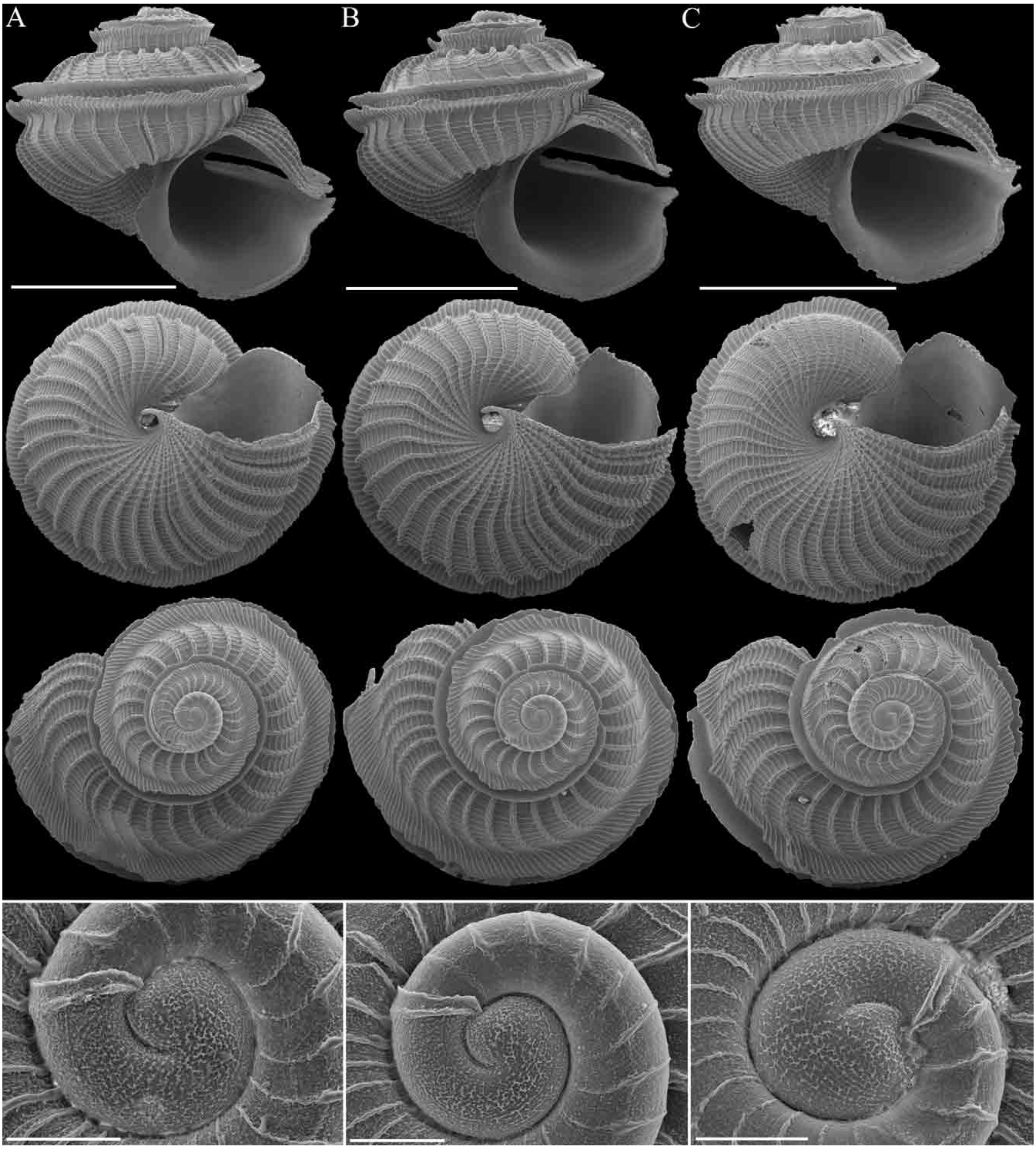

Figure 2. Paratypes of *Anatoma herberti* new species (MNHN 20634). 630–710 m, Reunion Island, 21.150°S, 55.200°E. Scale bars shell = 1 mm. Scale bars protoconch = 100 µm.

Differential diagnosis. *Anatoma herberti* is characterized by the strong axial ribs on shoulder *and* base, and the fine axial lines on the outer surface of the keels of the selenizone. *Anatoma finlayi* (Powell, 1937) from New Zealand (see Geiger & Jansen 2004) has similar sculpture on the shoulder consisting of strongly raised axial ribs, but the sculpture on the base lacks those ribs. *Thieleella gunteri* (Cotton & Godfrey, 1933) from SE Australia (see Geiger & Jansen 2004) has a protoconch with honeycomb pattern diagnostic for *Thieleella*. It shares the elevated ribs on the shoulder, but has much reduced sculpture on the base. *Anatoma agulhasensis* (Thiele, 1925) from South Africa (see Herbert 1986; Geiger & Jansen 2004) has an overall more rounded shell lacking the strong axial ribs. In addition, it has less elevated keels of the selenizone and the protoconch lacks an apertural varix. *Anatoma munieri* (Fischer, 1862) [= *A. turbinata* (A. Adams, 1862) = *A. jacksoni* (Melvill, 1904): Geiger 2006, unpubl. data] with broad Indo-Pacific distribution lacks an apertural varix on the protoconch. It has an overall more turreted shell and lacks the strong axial ribs as well as the supernumerary axial lines on the outer surface of the selenizone keels of *A. herberti*. *Anatoma lamellata* (A. Adams, 1862) from Japan (BMNH syntypes examined by SEM: Geiger unpubl. data) lacks an apertural varix on the protoconch, has less raised axial cords and lacks the supernumerary axial lines on the outer surface of the keels of the selenizone. *Anatoma yaroni* Herbert, 1986, has an overall biconical shell morphology, lacks the raised axial ribs, and has smooth external surfaces of the selenizone keels.

Anatoma boucheti new species (Fig. 3)

Type material. Holotype (MNHN 20635: Fig. 3).

Type locality. 1,150–1,180 m, Reunion Island, MD32, DC64, 21.2°S, 55.067°E.

Etymology. Honoring Philippe Bouchet (MNHN) for his accomplishments with respect to advancing our knowledge of micromolluscs.

Description. Shell medium sized (2.85 mm), trochiform tabulated. Protoconch sunken, 0.75 whorls, sculpture flocculent; apertural varix weak, not connected to embryonic cap, apertural margin convex. Teleoconch I of 1.1 whorls, 39 distinct axial cords, spiral cord in position of selenizone, very fine spiral lines below periphery. Teleoconch II of two whorls, suture moderately impressed, separated from selenizone above by width of selenizone in early whorls, by approximately three widths of selenizone at apertural margin. Shoulder convex, same density of axial cords as on teleoconch I (67 on first teleoconch II whorl), crossed by fine spiral lines forming minute thickenings at intersection with axials, first spiral line starting at onset of selenizone on outer half of shoulder, approximately 12 fine lines after one teleoconch II whorl, approximately 15 at apertural margin, spiral lines becoming weaker near selenizone keels. Base slightly constricted below selenizone, continuously sloping to open umbilicus; sculpture similar to that on shoulder, approximately 35 fine spiral lines, additional finer lines towards keels of selenizone. Selenizone at periphery, keels distinctly elevated, rather weak for family; lunules regularly spaced; slit open, margins converging but not touching. Aperture round, roof overhanging, peristome flaring, no funiculus. Soft parts unknown.

Differential diagnosis. *Anatoma boucheti* can be recognized by the sunken protoconch, the teleoconch I with more than one whorl, the tabulated (*i.e.*, non-biconical) shell shape and the fine reticulate sculpture with predominant axial cords. *Anatoma agulhasensis* from South Africa (see Geiger & Jansen 2004) has a teleoconch I of 0.75 whorls and an overall more globular shell shape with protruding protoconch. *Anatoma yaroni* from East Africa (see Herbert 1986) has an overall biconical shell shape with the suture less than one width of the selenizone below the selenizone of the previous whorl and 0.75 teleoconch I whorls. *Anatoma aetheria* (Melvill & Standen, 1903) from the Indian Ocean (types in NMW and NMSZ examined by SEM: Geiger unpubl. data) has an overall biconical shell shape with the suture's position less than the width of the selenizone below the selenizone of the previous whorl and 0.5 teleoconch I whorls. *Anatoma munieri* (see above) has a teleoconch of 0.5–0.75 whorls, is overall more turreted, has proportionally stronger and less dense sculpture and has a much more prominent constriction below the selenizone.

Remarks. This species is currently only known from the holotype. It is sufficiently distinct to be recognized as a distinct species as noted in the differential diagnosis above.

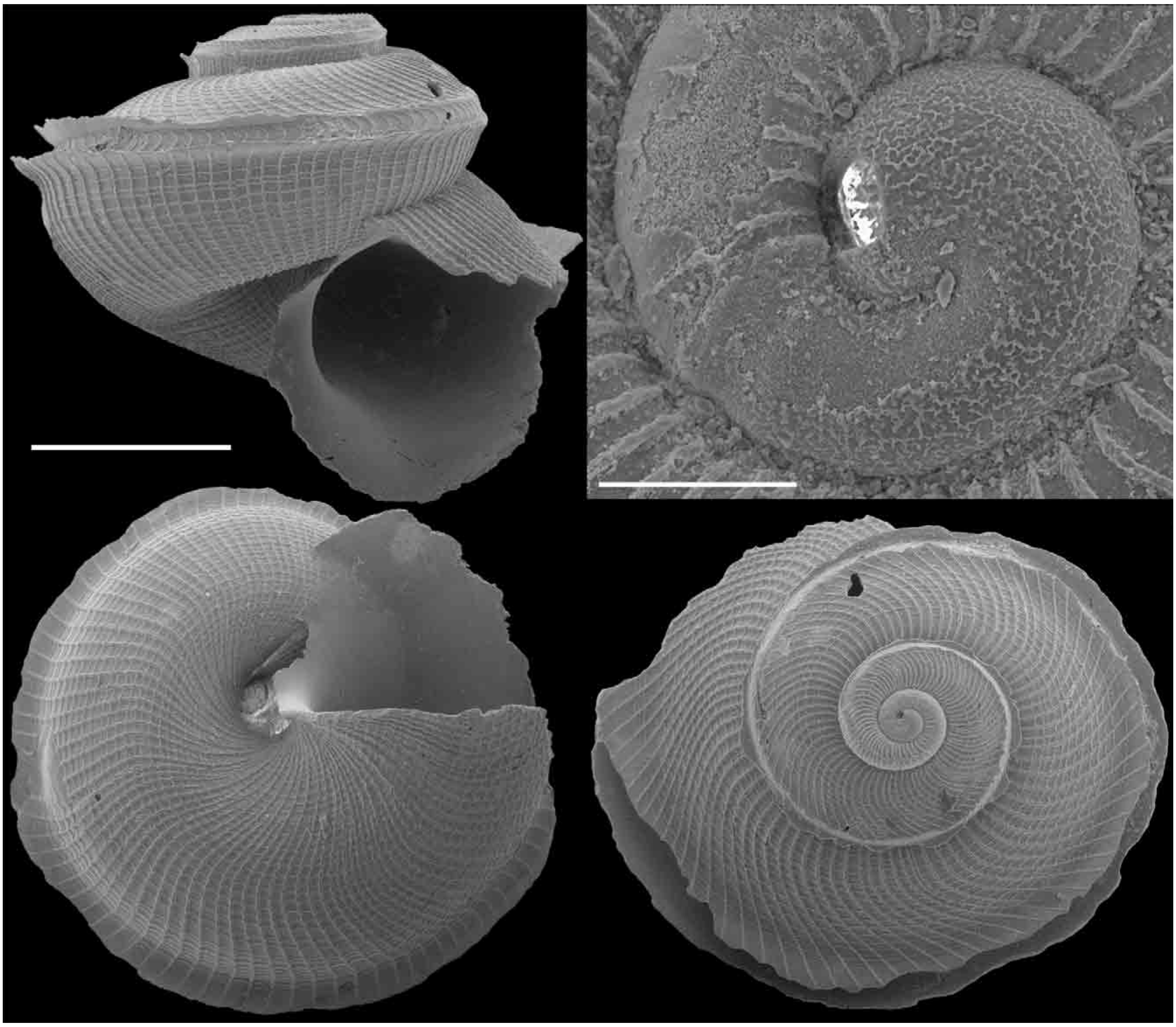

Figure 3. Holotype of *Anatoma boucheti* new species (MNHN 20635). 1,150–1,180 m, Reunion Island, 21.200°S, 55.067°E. Scale bar shell = 1 mm. Scale bar protoconch = 100 µm.

Anatoma austrolissa new species (Figs 4–6)

Type material. Holotype (AMS C.212812: Fig. 4). Paratypes: 1,575–1,600 m, Reunion Island, MD32, DS139, 20.783°S, 55.633°E (MNHN 20631, 3: two shown in Fig. 5B–C, 1 wet preserved soft parts with shell). 1,200 m, off Wollongong, NSW, Australia, 34.442°S, 151.45°E (AMS 448762, 1: Fig. 5A). 768–713 m, off Coffs Harbour, NSW, Australia, 30.017°S, 153.617°E (AMS 402711, 2).
Type locality. 1,143–1,106 m, off Sydney, NSW, Australia, 33.600°S, 152.083°E.

Etymology. *Austro*- referring to the provenance of the species from the southern hemisphere; -*lissa*, Latin adjective for smooth, referring to the overall smooth shell.

Description. Shell medium sized (to 2.2 mm) trochiform biconically tabulated, thin-walled, fragile (Figs 4–5). Protoconch of 0.75 whorls, large (262, 265, 269 µm diameter), sculpture flocculent,

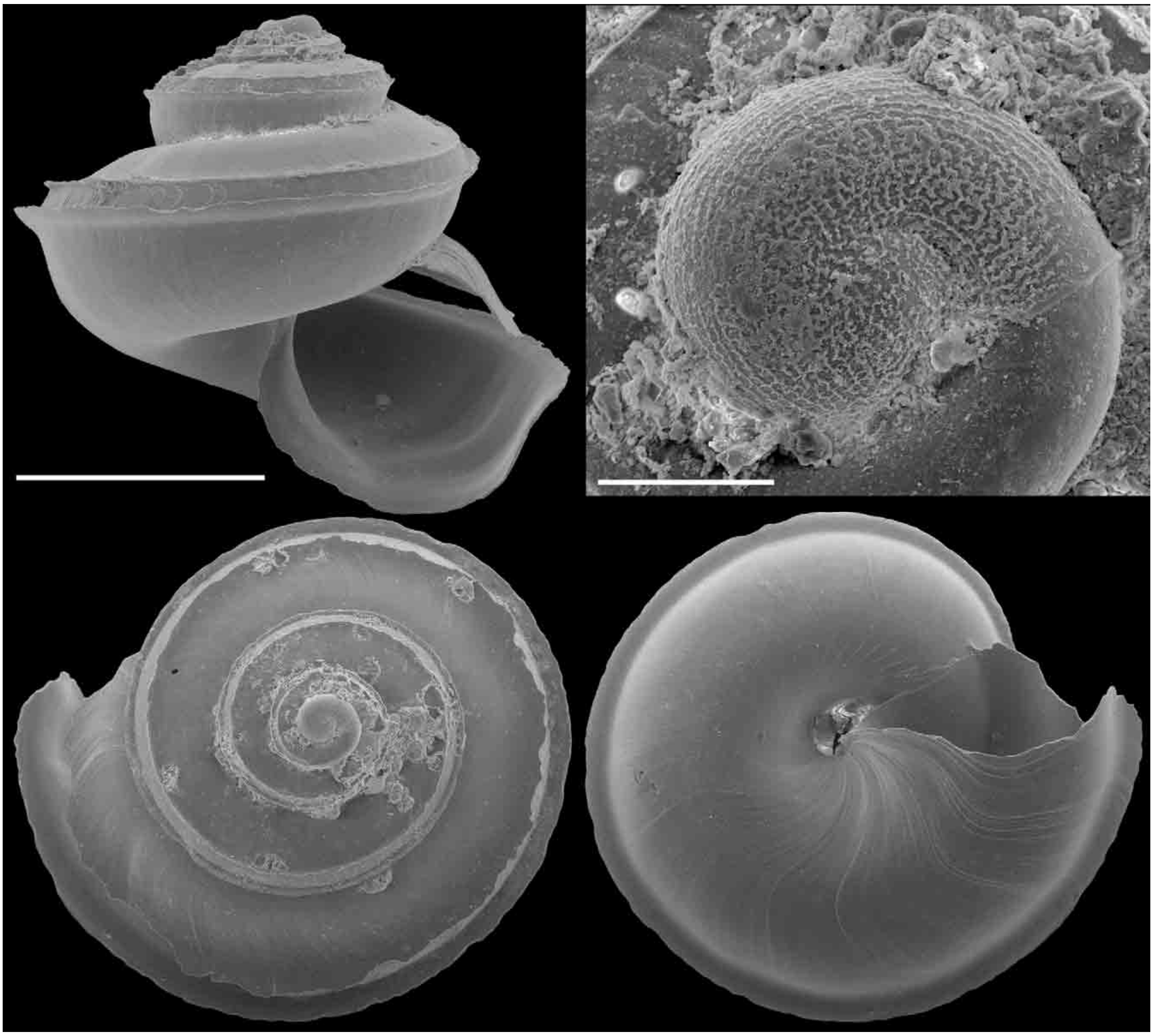

Figure 4. Holotype of *Anatoma austrolissa* new species (AMS C.212812). 1,143–1,106 m, off Sydney, NSW, Australia, 33.600°S, 152.083°E. Scale bar shell = 1 mm. Scale bar protoconch = 100 µm.

apertural varix absent, apertural margin slightly convex. Teleoconch I of 0.2 whorls, macroscopically smooth; minute pitting, round to twice as long as wide, 1–2 µm in diameter. Teleoconch II of 3.25 whorls, suture incised, descending on shell axis with growth, approximately one width of selenizone below selenizone of previous whorl at 1.4 mm, three width of selenizone below selenizone of previous at 2.2 mm. Shoulder sinusoidal in profile, macroscopically smooth, with very

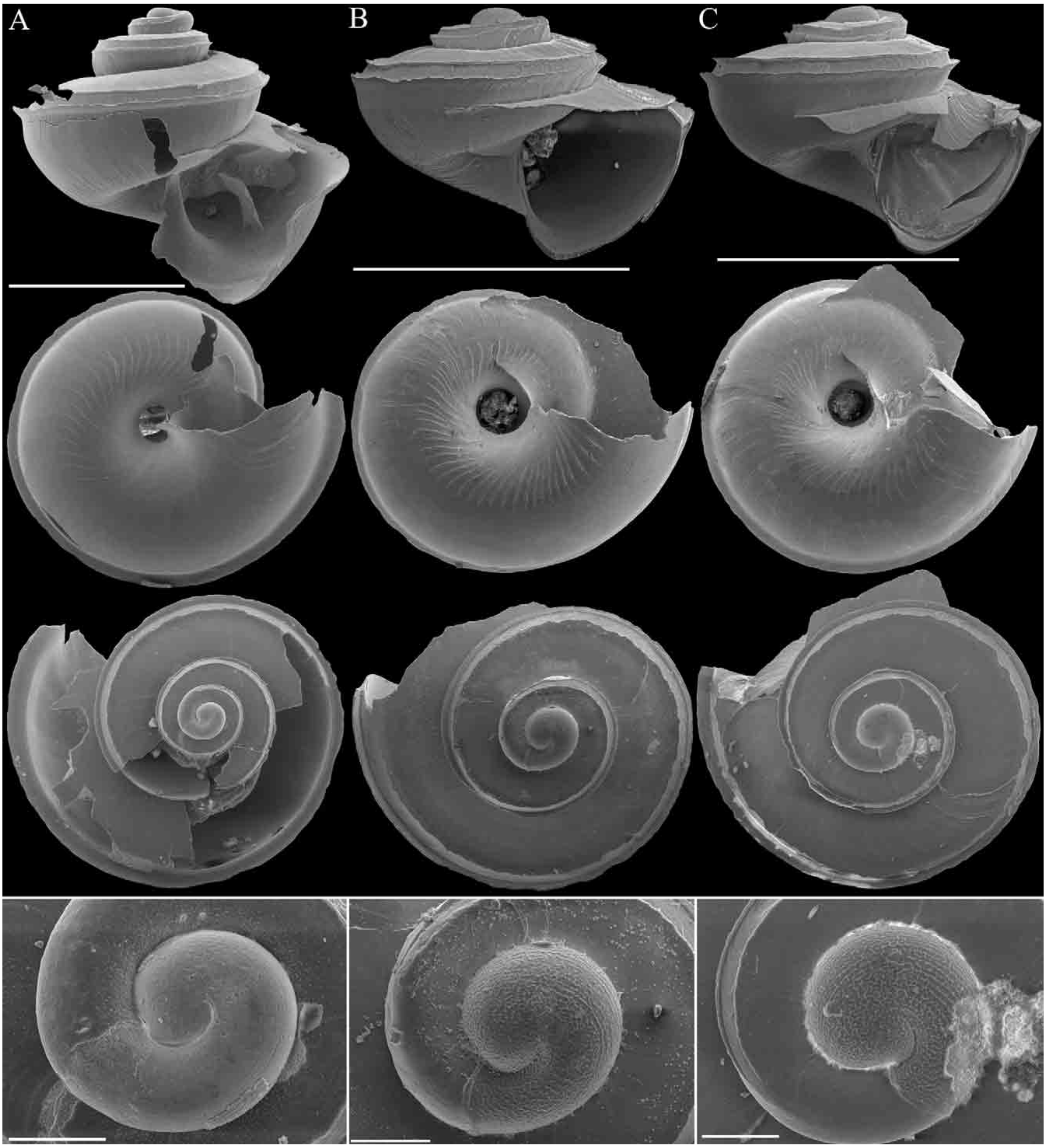

Figure 5. Paratypes of *Anatoma austrolissa* new species. **A.** 1,200 m, off Wollongong, NSW, Australia, 34.442°S, 151.45°E (AMS C.448762). **B–C.** 1,575–1,600 m, Reunion Island, 20.783°S, 55.633°E (MNHN 20631). Scale bars shell = 1 mm. Scale bars protoconch = 100 µm.

fine growth lines, minute pitting, round to twice as long (1–2 µm) as wide (Fig. 6C). Base slightly constricted below selenizone, continuously sloping into wide umbilicus, upper half of base smooth except for minute pits, adumbilical half of base with approximately 30 axial cords, starting very abruptly mid-base, remaining distinct for approximately width of umbilical cavity, diminishing into umbilicus; no funiculus. Selenizone at periphery, onset indistinct, keels with elevation and strength average for family, lunules mostly indistinct, occasionally more distinct lunules; slit open, margins parallel. Aperture subquadratic, peristome flaring. Operculum corneus, thin, multispiral, with central nucleus (Fig. 6D).

Radula with floppy teeth in central field (Fig. 6A,B). Central tooth triangular, sides concave, upper half (= cusp) with approximately nine fine denticles on each side. Lateral teeth 1–3 similar, curving towards midline of radula, decreasing in size from height equal to rachidian tooth to approximately ⅔ of it, approximately nine, six, four fine denticles on each side of respective teeth. Lateral tooth 4 reduced (30% of height of rachidian tooth) without denticles. Lateral tooth 5 enlarged by elongation, approximately 2.2 times length of rachidian tooth, sturdy, in lower portion of upper half with approximately eight fine denticles, terminal denticle almost as strong as shaft. Marginal teeth thin, elongated, approximately nine denticles on outer edge of cusp, approximately three on inner edge, terminal denticle as large as others. Radular interlock minimal.

Jaw (Fig. 6E) trapezoid, with recurved front edge, composed of rhombic elements.

Differential diagnosis. *Anatoma austrolissa* is characterized by the large protoconch, short teleoconch I, indistinct onset of the selenizone, overall smooth sculpture with microscopic pitting, and the axial sculpture restricted to the adumbilical half of the base. The floppy radula is only known from *A. flexidentata* described here, but differs in the more prominent minor denticles on lateral tooth 5, and

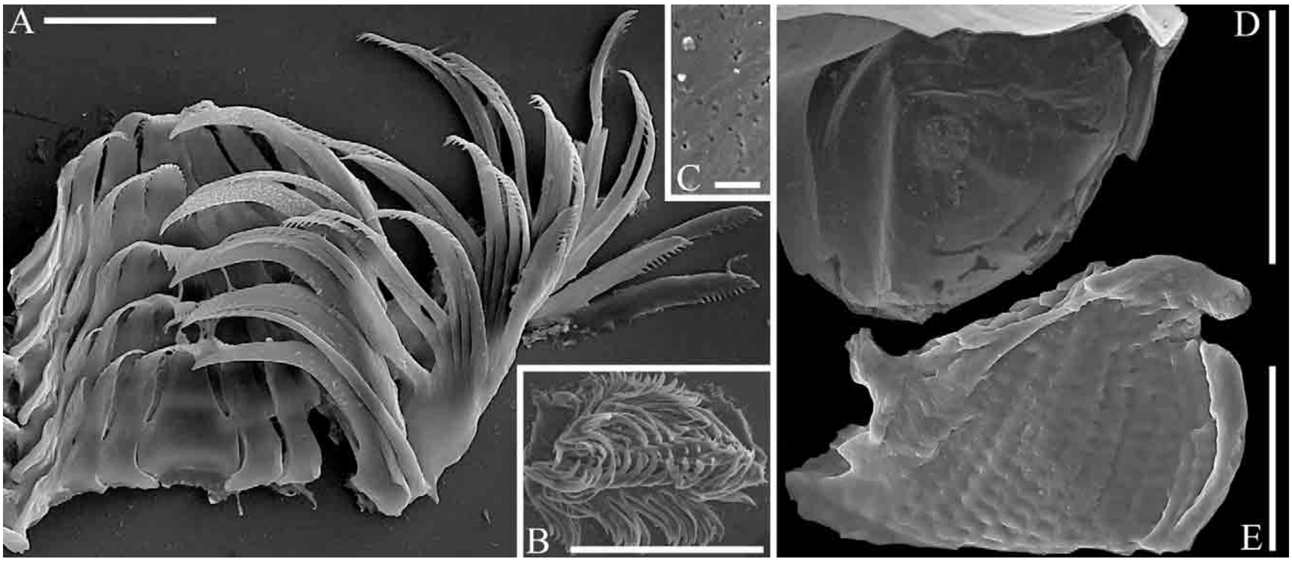

Figure 6. *Anatoma austrolissa* (AMS C.448762); see Figure 5 A for shell. **A.** Radula after bleach treatment of dirty specimen shown in Figure 6B. Scale = 20 µm. **B.** Overview of dirty radula, which was insufficiently spread to show central field. Scale bar = 100 µm. **C.** Detail of teleoconch of specimen illustrated in Figure 5B having minute pits. Scale bar = 10 µm. **D.** Operculum in aperture of specimen (MNHN 20631). Scale bar = 500 µm. **E.** Jaw. Scale bar = 50 µm.

sturdier marginal teeth with distinct denticles on cusp. *Anatoma umbilicata* (Jeffreys, 1883) from the European Atlantic and Mediterranean Seas (all syntypes in BMNH and USNM examined by SEM: Geiger unpubl. data) has a more globular overall shape with the shoulder at a steeper angle towards the coiling axis. In addition it has a teleoconch I of 0.5 whorls lacking the microscopic pitting, very faint spiral threads on the shoulder and more prominent spiral threads in the umbilical region, but lacks any axial sculpture on the base. Note that specimens labeled *A. umbilicata* in subsequent publications usually show other, misidentified species (Geiger unpubl. data), while the identity of the species discussed here is based on SEM examination of the entire available syntype material.

Remarks. The microscopic pitting is seen in all specimens examined and represents a novel character on the teleoconch in Scissurellidae s.l. Pitting is known on the protoconch of *Sutilizona* spp. (Vetigastropoda: Scissurellidae s.l./Lepetodriloidea: Sutilizonidae) from hydrothermal vent environments (McLean 1989; Warén & Bouchet 2001). In *A. austrolissa*, it does not seem to be a product of either biogenic or physical-chemical deterioration. Specimens are currently known from two localities separated by 9,500 km: Reunion Island and New South Wales. The specimens agree in several characters uncommonly seen in Anatomidae: large protoconch (262–269 µm), pitting of shell, lack of macroscopic sculpture on shoulder and upper half of base and the axial sculpture on adumbilical half of base. The onset of the selenizone is slightly more prominent in the specimens from Australia, though still not as distinct as in most other *Anatoma* spp. They also share a habitat on the upper slope (700–1,600 m), where specimens from both ends of the distributional range were collected alive. This indicates that *A. austrolissa* is a species with broad deep-water distribution in the southern Pacific.

***Anatoma flexidentata* new species (Figs 7–9)**

Type material. Holotype (MNHN 20636: Fig. 7). Paratypes: from type locality (MNHN 20637, 16: one illustrated in Fig. 8A). 280–340 m, Reunion Island, MD32, DC128, 20.850°S, 55.600°E (MNHN 20638, 2: Fig. 8B–C).

Type locality. 3,300–3,240 m, Reunion Island, MD32, DS151, 20.850°N, 56.050°E.

Additional specimens examined. 310 m, Reunion Island, MD32, DC26, 21.367°S, 55.783°E (MNHN, 2). 705 m, NE Pamanzi Island, Mayotte, France, Bethendi 1977, St. 28, 12.705°S, 45.332°E (MNHN, 1). 310 m, Reunion Island, 21.367°S, 55.783°E (MNHN, 2). 3,500–3,510 m, Reunion Island, MD32, DS149, 20.433°S, 55.667°E (MNHN, 5 dry shells, 2: wet preserved specimens with soft parts).

Etymology. *Flexi*- Latin for flexible, pliable, -*dentata*, Latin for tooth-bearing, referring to the pliable nature of the radular ribbon and its teeth.

Description. Shell medium sized (to 2.9 mm), trochiform globular. Protoconch of 0.75 whorls, sculpture flocculent, apertural varix absent, apertural margin straight. Teleoconch I of 0.25–0.33 whorls, 7–9 fine axial cords, usually with fine spiral cord in position of selenizone (occasionally eroded?). Teleoconch II of three whorls, suture moderately impressed, on first two whorls approximately half width of selenizone width below selenizone of previous whorl, at apertural margin below 1.5 time of selenizone width. Shoulder convex; approximately 42 axial cords with a few not reaching suture; first fine spiral line after 0.3–1 teleoconch II whorls, increasing to 3–6 irregularly spaced ones at apertural margin, occasionally also secondarily decreasing in number. Base slightly constricted below selenizone, continuously sloping into narrow umbilicus without funiculus (proportionally wider in small specimens), reticulate sculpture with approximately 50 axial cords of even strength from selenizone to umbilicus on last half whorl, crossed by 12–17 spiral cords forming minute points at intersections. Selenizone at periphery; keels low, average strength for family; lunules distinct, evenly spaced; slit open, with parallel margins. Aperture rounded, with overhanging roof, peristome somewhat flared.

Operculum (Fig. 9E–F) thin, corneuous, multispiral, with central nucleus.

Radula (Fig. 9A–C) very flexible. Rachidian tooth triangular, twice as high as wide, approximately eight very fine denticles on each side. Lateral teeth 1–4 similar, triangular, 3–4 times as high as wide. Lateral tooth 5 enlarged by elongation, approximately ten times as long as wide, without noticeable denticles. Marginal teeth, elongated, curved, with 2–5 small barbs. Radular interlock minimal.
Jaw triangular, composed of rhomboid plates; hole in middle an artifact (Fig. 9D).

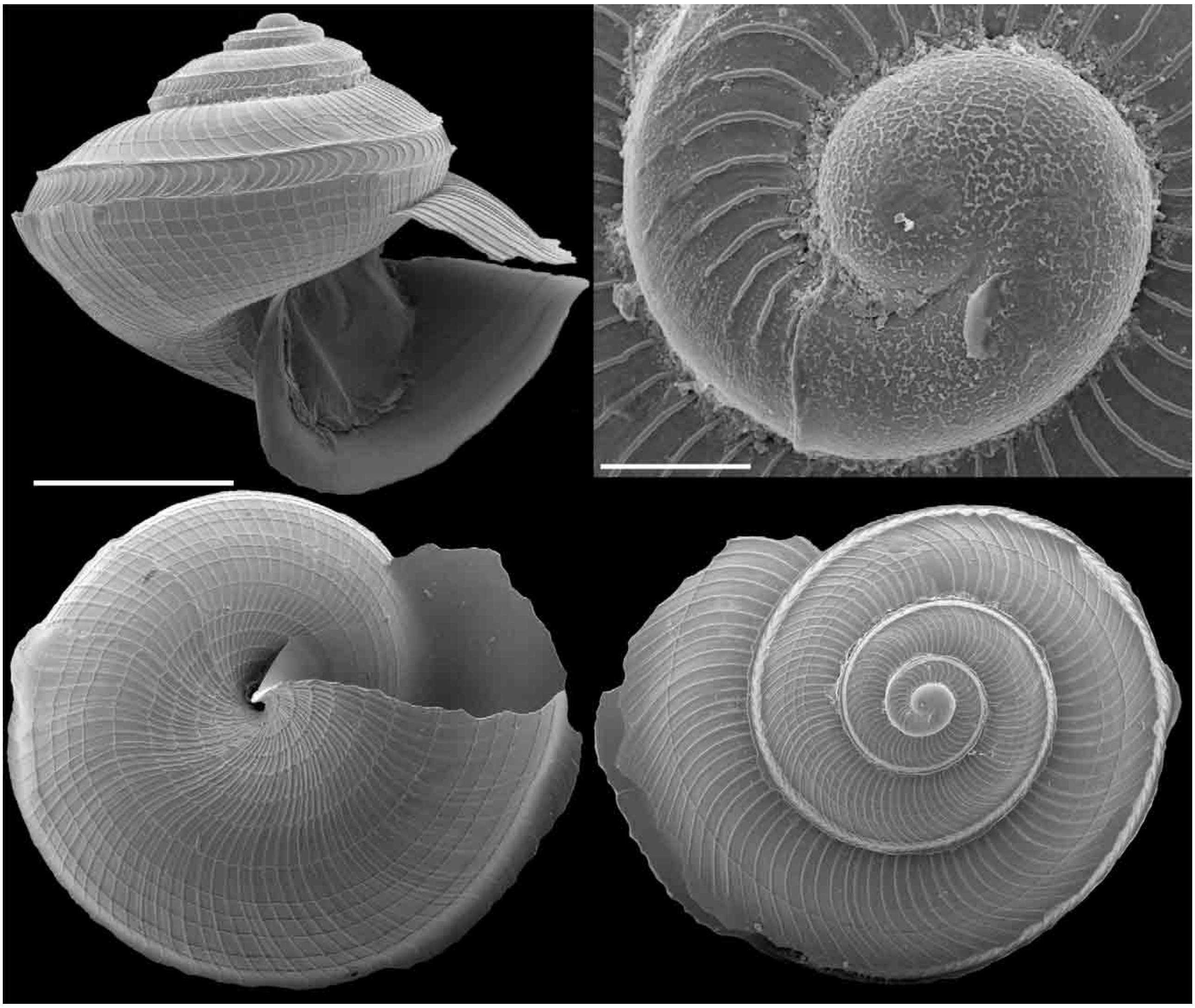

Figure 7. Holotype of *Anatoma flexidentata* new species (MNHN 20636). 3,300–3,240 m, Reunion Island, 20.850°N, 56.050°E. Scale bar shell = 1 mm. Scale bar protoconch = 100 µm.

Differential diagnosis. *Anatoma flexidentata* is characterized in terms of shell morphology by the globular overall shape, the short teleoconch I (0.23–0.33) and the fine reticulate sculpture. The floppy radula is only known from *A. austrolissa* described here, but differs in the less prominent minor denticles on lateral tooth 5, and filamentous marginal teeth without distinct denticles on cusp. *Anatoma*

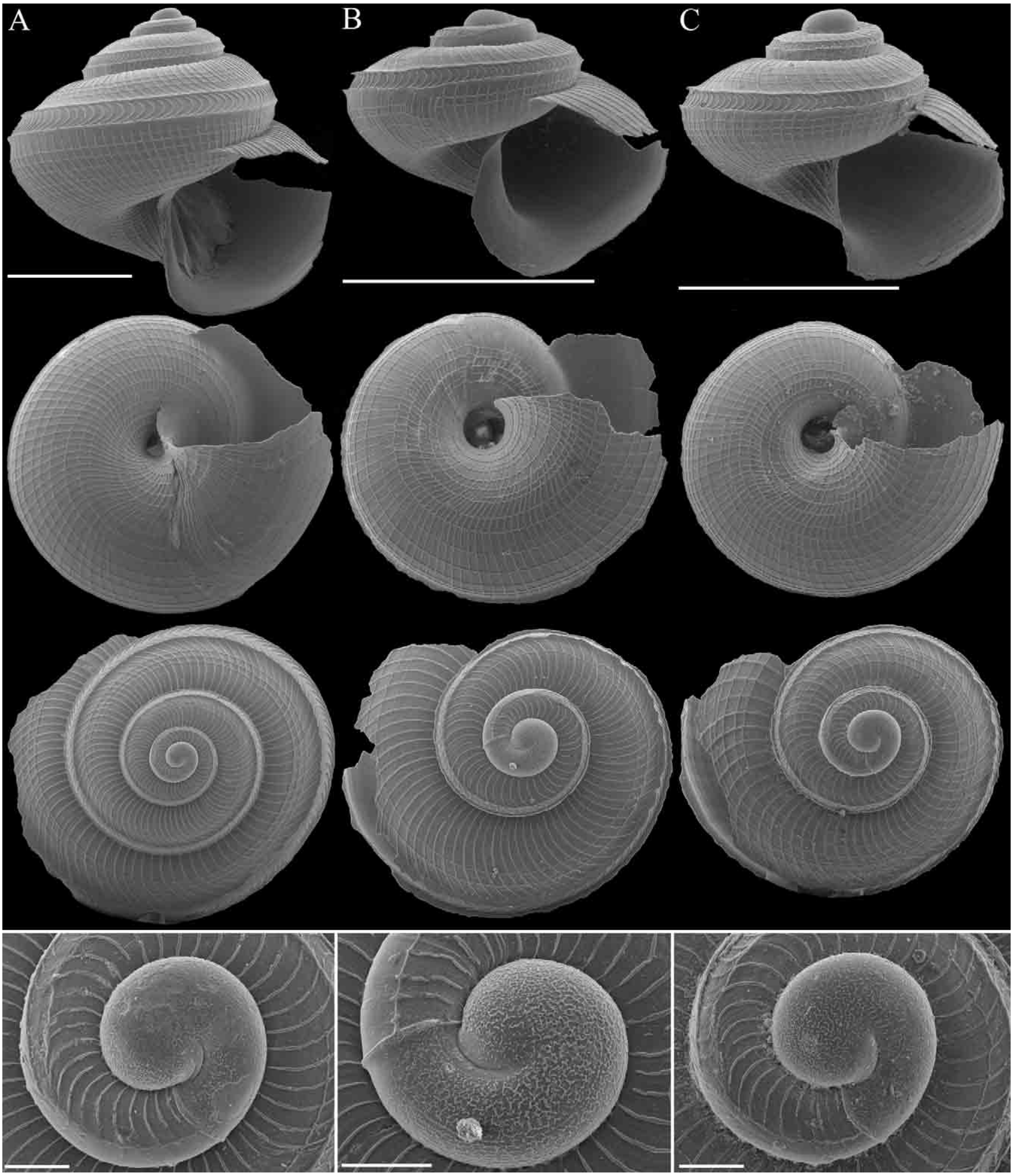

Figure 8. Paratypes of *Anatoma flexidentata* new species. **A.** 3,300–3,240 m, Reunion Island, 20.850°N, 56.050°E (MNHN 20637). **B–C.** 280–340 m, Reunion Island, 20.850°S, 55.600°E (MNHN 20638). Scale bars shell = 1 mm. Scale bars protoconch = 100 µm.

agulhasensis form South Africa has an overall more turreted shell with a distinct constriction below the selenizone, has a longer teleoconch I (0.75 whorls) and the axial cords on the shoulder are at least three times as strong as the spiral lines. *Anatoma turbinata* with broad Indo-Pacific distribution is much more turreted with a very distinct constriction below the selenizone. This species has a protoconch with an apertural varix, a teleoconch I with more than 0.5 whorls. The overall sculpture is stronger with the axial cords on the shoulder at least three times as strong as the spiral lines. *Anatoma aetheria* from the Indian Ocean (types in NMW and NMSZ examined by SEM: Geiger unpubl. data) has an overall biconical shape and the teleoconch I has more than 0.5 whorls. It has stronger sculpture, with the axial cords on the shoulder at least three times as strong as the spiral lines.

Remarks. The shell of *A. flexidentata* is unremarkable amongst other anatomids. The radula, though, is at significant variance to those known from all other species, except *A. austrolissa* also described here. The very flexible and floppy radula folded over very easily during preparation for SEM. The rachidian tooth is not trapezoidal with a distinct recurved cusp, but is triangular with fine bristles. The lateral teeth 1–4 are similar to one another as in Larocheidae, but unlike in all other Anatomidae, where lateral teeth 1–3 are similar and lateral tooth 4 is reduced, and hook-shaped. Lateral tooth 5

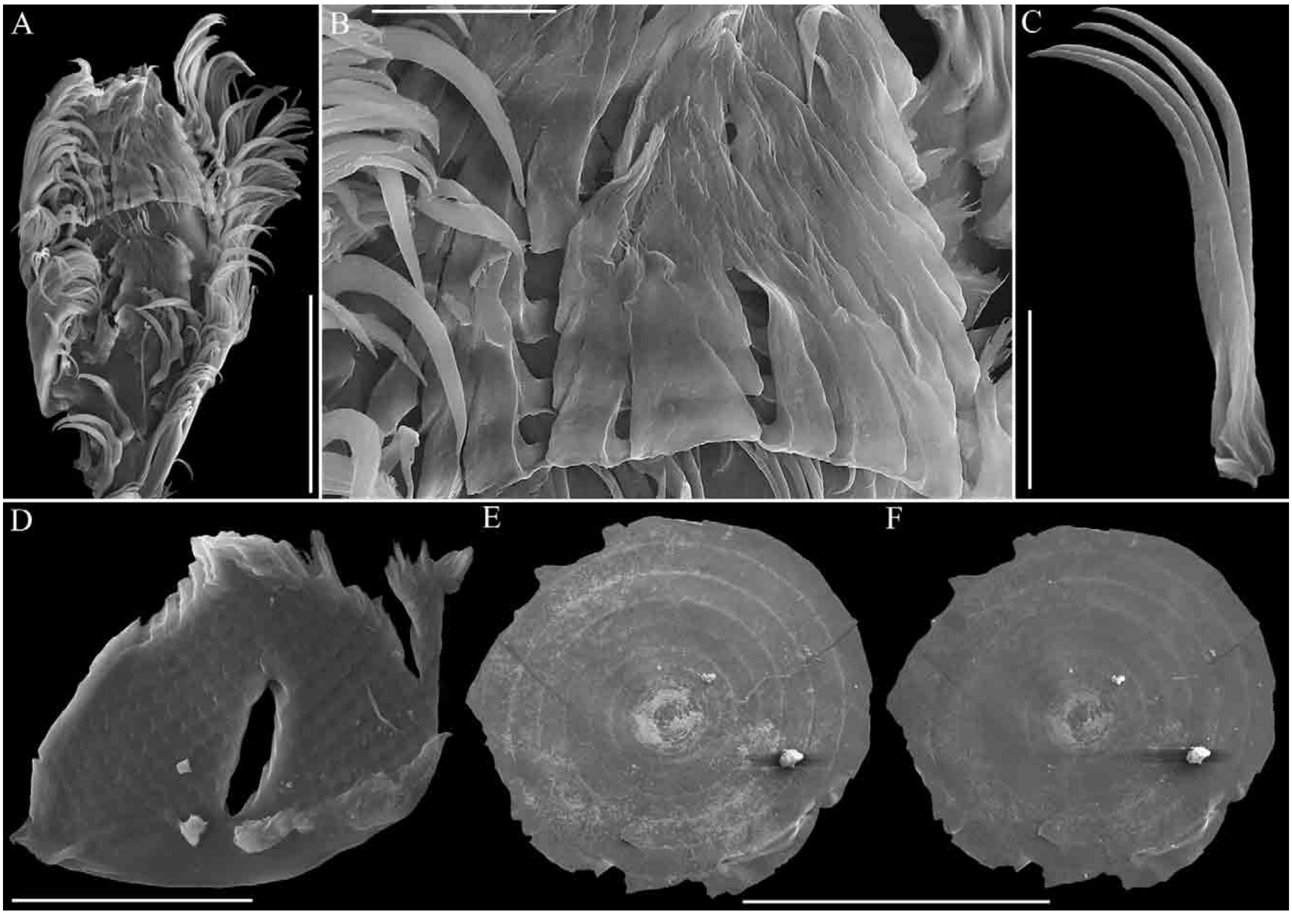

Figure 9. Radula, jaw and operculum of *Anatoma flexidentata* new species. **A.** Overview of radula. Scale bar = 100 µm. **B.** Central field of radula. Scale bar = 20 µm. **C.** Isolated marginal teeth. Scale bar = 20 µm. **D.** Jaw. Scale bar = 100 µm. **E–F.** Operculum. Scale bar = 1 mm. **E.** Operculum imaged at 10 kV. **F.** Operculum imaged at 30 kV.

shows the usual enlargement by elongation, but lacks distinct denticles on the cusp. The inner marginal teeth are more elongated, while the outer marginal teeth do not show the typical spoon shaped cusp. The possibility of radular contamination or mix-up of specimens was considered, however, two specimens showed the very same radular morphology. The unusual organization might suggest that only the incompletely developed, posterior portion of the radula was examined, which may account for the unfamiliar morphology. However, lateral tooth 5 as well as the marginal teeth shows the usual degree of sturdiness. Also, examination of early radular portions from other anatomids never showed the observed morphology of *A. flexidentata*, but rather the mature tooth morphology, with floppy teeth, across the entire radular row.

Given that further species with unexpected radular morphologies have recently come to light (*e.g.*, *A. janetae* Geiger, 2006; *Anatoma* n. sp. Sasaki *et al*., unpubl. data), we consider the radula of *A. flexidentata* one more piece of evidence of extensive within-lineage variability within Anatomidae. The alternative explanation of a freak or teratological specimen seems unlikely, particularly as two specimens with identical organizations were found, and that a similar morphology was encountered in a second species, *A. austrolissa*.

Discussion

Preparation methods. Most methodological aspects have recently been detailed by Geiger *et al.* (2007), hence, only select additional information is provided here. One of us (DLG) has experimented with different brands of tungsten needles and found the thin-base needles by Fine Science Tools (FST 10130-05) to have a by far finer tip than those available through McCrone (McCrone Microscopes & Accessories, Westmont, IL: #107-3). The FST needles are slightly more expensive but greatly facilitate work particularly with radulae.

Occasionally, radular preparations fail to produce the desired results, either because they teeth are insufficiently clean, or because the radula is insufficiently spread. Figure 6B shows such a poor preparation. As this specimen was mounted on a glass coverslip without any added adhesives, it could be released from the support after sputter coating and examination in the SEM with a drop of water. It was then post-treated in bleach for a few seconds, rinsed in water several times and remounted. Although the remounting caused some loss of teeth, sufficient radular material was retained to permit successful re-examination of a much-improved specimen (Fig. 6A).

The operculum of *A. austrolissa* proved to be extraordinarily thin; the removal of it from the specimen and mounting on double-sided carbon adhesive was disappointing. Fortunately, the operculum was imaged by SEM while still attached to the soft parts within the shell (Fig. 6C), which turned out to be the best image. It demonstrates the utility of taking multiple sets of images of structures that need to be manipulated.

Geiger *et al*. (2007) discussed many aspects of choice of SEM operating parameters on resulting images. Particularly with high-resolution radula images, contrary to general SEM operating procedures, very high accelerating voltages may actually decrease final image resolution. Here we demonstrate an advantageous effect of using very high accelerating voltage in order to mask dirt and minute surface irregularities. Figure 8E–F shows a pair of operculum images at 10 kV and 30 kV and identical probe current/spot size. Note that at 10 kV (Fig. 8E) the specimen seems to be dusted with sand, while at 30 kV (Fig. 8F) that problem has been mitigated. Despite the lowered contrast between sutures and whorls of the operculum at 30 kV, the overall structure is more apparent. This example further amplifies Geiger *et al.*'s (2007) recommendation to experiment with SEM settings for optimal result depending on each specimen. The dirt was composed of amorphous specks and some diatom frustules, and not elemental sulphur with crystals 1–2 µm in size, which can be found on the opercula of some skeneimorphs, and indicate a habitat in reducing environments (A. Warén pers. comm.).

Radular morphology. The radulae of *Anatoma austrolissa* and *A. flexidentata* are unlike that of any other scissurellid, anatomid, or other known vetigastropod in some aspects.

(1) Flexible teeth: The flexible teeth falling down in a dry condition are strikingly unusual among gastropods. Each tooth is firmly supported by a stiffened shaft in typical radulae of vetigastropods. The floppy nature of the radula suggests that *A. flexidentata* is possibly unable to rasp hard matter to digest, but may be used for ingesting bacterial films or detritus; the slightly sturdier rachidian tooth of *A. austrolissa* may facilitate food intake to a limited extent. Since the feeding habit is unknown, the functional significance of this morphology is not identified.

(2) Rachidian tooth: The rachidian tooth is highly variable in Anatomidae and, therefore, provides useful characters to differentiate species. In other species of *Anatoma* the rachidan tooth is trapezoid and wider than high. The cusp is nearly straight-lined, reflected and bears denticles, whose number may be diagnostic at the species-level. The rachidian tooth in *A. flexidentata* deviates entirely from these common features with its triangular shape without any distinct cusp. The overall organization of the rachidian tooth—triangular shape with multiple denticles on each side of the cusp—is shared by *A. austrolissa*, but its rachidian is slightly sturdier, maintaining its recurved shape.

(3) Lateral teeth: The five pairs of lateral teeth are reduced to thin flaps as in the rachidian tooth of *Anatoma flexidentata* as well as *A. austrolissa*. The tooth morphology is rather homogenous among the pairs in contrast to that of other *Anatoma* species in which teeth (especially the outer teeth) are differentiated in length, thickness and cusp morphology.

(4) Marginal teeth: The morphology of the marginals in *Anatoma flexidentata* is unlike that of any of the few Anatomidae for which the radular structure is known in that all teeth are flexible and filamentous. *Anatoma austrolissa* also has unusual tooth morphology with strongly asymmetrical distribution of denticles on the cusp, and that the cusp is not spoon-shaped. In all other species of *Anatoma*, the denticles of the cusp are mostly sharply serrated on the inner teeth, finer on middle teeth and reduced to form spoon-like cusps with marginal filaments on the outer teeth. However, in *A. flexidentata* and *A. austrolissa* these teeth are undifferentiated between inner and outer marginal teeth.

Among the above features, few taxa with a comparable state can be found in gastropods in terms of tooth flexibility; *Selastele onustum* Odhner, 1924 (Calliostomatidae: Marshall 1995: figs 138–139), is the only other species known to us to show such a degree of tooth reduction in the central field. The reduction of the teeth occurs in certain groups such as the Halistylinae and Umboniinae of Trochidae in Vetigastropoda (Hickman & McLean 1990). In these groups, the teeth are reduced into thin plates or completely loose the central field, but the marginal teeth are fully developed.

The presence of similar-looking teeth in the central field of *Anatoma flexidentata* is also notable. Although there are several vetigastropods with triangular teeth bearing fine denticles, they all differ in either the fine morphology of the individual teeth or in the central field. For example, the teeth of the central field of trochid *Falsimargarita nauduri* Warén & Bouchet, 2001, have a rather flexible, triangular-shaped rachidian tooth and lateral teeth. However, the dominant tooth (lateral tooth 6), with its short hooked shape (Warén & Bouchet 2001: fig. 11), differs significantly from the slender elongated tooth of *A. flexidentata*. *Pseudorimula midatlantica* McLean, 1992, also shares flexible, triangular teeth in the central field, although its tips are rounded (Warén & Bouchet 2001: fig. 18c), whereas those of *A. flexidentata* are acute.

Anatoma flexidentata and *A. austrolissa* clearly have a vetigastropod radula type, but we fail to find any good link of the radular morphology to other vetigastropod lineages. Instead we highlight the fact, that this shell-morphologically unquestionable *Anatoma* species has such radically different radula morphology. It demonstrates the extensive variability of organ systems within taxa, hence, highlights the continued need for detailed studies in comparative morphology based on as many taxa as can be obtained. It is particularly important in phylogenetic analyses to assess and recognize within-lineage variation, as opposed to relying on information based on a single species, let alone single specimens. As micromolluscs are the most neglected group of molluscs, the remedial need is greatest. As could be demonstrated by the present contribution, with the methodological improvements for investigating micromolluscs, the results from such work are exciting.

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