

A New Species of *Anatoma* (Vetigastropoda: Anatomidae) from a Hydrothermal Vent Field in Myojin Knoll Caldera, Izu-Ogasawara Arc, Japan

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Abstract. *Anatoma fujikurai* sp. nov. is described from the hydrothermal-vent environment at Myojin Knoll, southern Japan. The shell of the species is characterized by the predominant axial sculpture on the shoulder and base and by the undulating selenizone. The animal lacks eyes and shows a radular structure not seen in any other anatomid species examined to date. Hypotheses about its radular structure related to habitat depth, chemosynthetic environment, and geography (Tethys Sea) are rejected; the most plausible explanation is simple interspecific variation. The species is compared with all Japanese anatomid species, as well as to conchologically similar ones, i.e., those with stepped shell profiles from throughout the Indo-Pacific region. Comments on several misidentifications of anatomid species in the literature are provided along with SEM images of the type material of *Thielella sagamiana* (Okutani, 1964) and *Anatoma soyae* (Habe, 1951) for comparison.

INTRODUCTION

The hydrothermal vent environment (see Van Dover, 2000, for a general review) has yielded many new species, most of which are restricted geographically, as well as in terms of habitat preference, to this unique setting. Many species continue to be described from chemosynthetic environments (e.g., Warén & Bouchet, 2001; Sasaki et al., 2005). The species of small size are less well known in general (for a review of Japanese species, see Sasaki, 2008), which is also the case for deep-sea species. The family Anatomidae contains many undescribed species worldwide (Geiger, 2008). Here, we introduce a new taxon from the Myojin Knoll submarine volcano off southern Japan. The examination of the anatomy of this species, and particularly the radula, has yielded surprising results.

MATERIALS AND METHODS

Two specimens of the new species were collected from the Myojin Knoll, south off Izu Islands, Japan, 32°06.20'N, 139°52.17'E, at 1224 m (see Sasaki et al.,

2003: fig. 1 for map) on June 24, 2003, on dive HD#185 of ROV *Hyper-dolphin* during cruise NT03-06 of R/V *Natsushima*. The anterior parts of the animals were removed from the shells by pulling the head-foot complexes, and the visceral masses remained inside the shells. The isolated animals were photographed under a binocular microscope and dissected to remove the radulae. The shells, opercula, radulae, and animals were examined with a scanning electron microscope (SEM) after being mounted on metal stubs and coated with platinum-palladium. The shells and radulae were cleaned in diluted commercial bleach, and the animals were freeze-dried for SEM examination. Uncoated type specimens of *Thielella sagamiana* were examined using variable-pressure SEM. The holotype and paratype of the new species were deposited in the Department of Historical Geology and Paleontology, The University Museum, The University of Tokyo (UMUT).

Abbreviations for repositories of specimens and descriptions are as follows: BMNH (The Natural History Museum, London, UK), NSMT (National Museum of Nature and Science, Tokyo, Japan

[formerly National Science Museum, Tokyo]; SBMNH (Santa Barbara Museum of Natural History, California, USA); SH (shell height); SW (shell width); UMUT (The University Museum, The University of Tokyo, Japan).

SYSTEMATICS

Class GASTROPODA

Clade VETIGASTROPODA

Family ANATOMIDAE McLean, 1989

Remarks: See Geiger (2003) for the differentiation of the family from Scissurellidae and Zelaya & Geiger (2007:395) for a diagnosis of the family. The elevation to family rank is based on the molecular phylogeny of Geiger & Thacker (2005, 2006).

Genus *Anatoma* Woodward, 1859

Type species: *Scissurella crispata* Fleming, 1828 (original designation).

Anatoma s.l. *fujikurai* Sasaki, Geiger & Okutani, sp. nov.

(Figures 1–4)

Type material: Holotype: 3.2 (SW) × 3.1 (SH) mm (UMUT RM29549), paratype: 3.1 (SW) × 2.7 (SH) mm (UMUT RM29550).

Shell: Shell turbiniform, medium size for genus (Figure 1A, C). Protoconch unknown (corroded). Teleoconch I, nine axial ribs on last quarter whorl, no spirals; earlier portion unknown (eroded or broken off). Teleoconch II of 1.75 whorls. Shoulder rounded; approximately 29 comarginal fine, equally spaced axial ribs on first whorl; approximately 10 fine, equally spaced spiral threads running over axial ribs; interstices with fine irregular growth lines. Suture (s, Figure 1A, C) deeply impressed, below selenizone (sz, Figure 1A, C), separated by space equal to width of selenizone. Base rounded, axial ribs (ar, Figure 2A) similar in number and strength on first 1.5 teleoconch I whorls, subsequently becoming less distinct; axial ribs on base slightly more blunt than those on shoulder; approximately 20 fine spiral lines, more or less equally spaced, between selenizone and umbilicus, lines running over axials. Umbilicus (u, Figure 1A) open, deep, moderately wide, no funiculus. Aperture rounded, basal adumbilical portion flared (ir, Figure 1A), roof overhanging. Selenizone slit at periphery (sl, Figure 1A, C), keels (ks, Figure 1C) quite strong, height equal to width of selenizone, undulating, mostly broken off; growth lunules weak; slit open, with parallel margins.

Operculum: Operculum (Figure 2B) thin, round, covering aperture, multispiral, nucleus central; margin (om, Figure 2B) is slightly thinner, undulating when dried.

Radula: Radula rhipidoglossate (Figure 3), slightly asymmetrical. Rachidian tooth (R, Figure 3B–C, E) taller than wide, with V-shaped cusp, denticle at tip largest, approximately 5 denticles on each side, gradually decreasing in size. Lateral teeth 1–3 (L1–3: Figure 3B–C, E) similar, inner edge of cusp smooth, outer edge with 3–4 strong denticles. Lateral tooth 4 (L4: Figure 3E) two-thirds the size of lateral teeth 1–3, cusp triangular, with approximately 10 denticles on inner edge, 4 denticles on outer edge. Lateral tooth 5 (L5: Figure 3C) enlarged by broadening, cusp triangular, denticle at tip largest, approximately 8 on each side, decreasing in size towards base. Inner marginal teeth similar in shape to lateral tooth 5, shaft half the size, cusps decreasing in size towards periphery (Figure 3F). Outer marginal teeth spoon shaped, cusp with many fine denticles. Radular interlock of central field moderate.

Animal: Animal's anterior portion entirely pale in fixed condition except for dark food matter in intestine (i, Figure 2C, D). Head with papillate cephalic tentacles (Figure 4A–C); papillae all around circumference of tentacle; no eyestalks or eyes (Figure 2C, D); suboptic tentacle (st, Figure 4A, B) short, simple. Epipodial tentacles consisting of four pairs (Figure 4A), tapering toward tips, biserially papillate along anterior and posterior edges (Figure 4E). Epipodial sense organ (ESO, Figure 4A, D) located between second and third epipodial tentacles, stalked, nonpapillate, with blunt tip. Opercular attachment (op, Figure 4A) drop-shaped, with scaly appearance of muscle fibers (Figure 4A, F). Intestine of 1.5 loops visible on surface (Figure 2C, D). Pallial cavity deep; one pair of monopectinate ctenidia attached to pallial roof; hypobranchial gland (hg, Figure 2C) surrounded by loops of intestine in pallial cavity between ctenidia. Anus (a, Figure 2C) opening at anterior central part of pallial cavity.

Type locality: Myojin Knoll, south off Izu Islands, Japan, 32°06.20'N, 139°52.17'E, 1224 m.

Distribution and type of habitat: Known only from the type locality; hydrothermal-vent field.

Etymology: The new specific name is given in honor of Dr. Katsunori Fujikura (Japan Agency for Marine-Earth Science and Technology) for his substantial contribution in biological studies of chemosynthesis-based communities.

Remarks: *Anatoma fujikurai* is distinguished from Japanese species as follows.

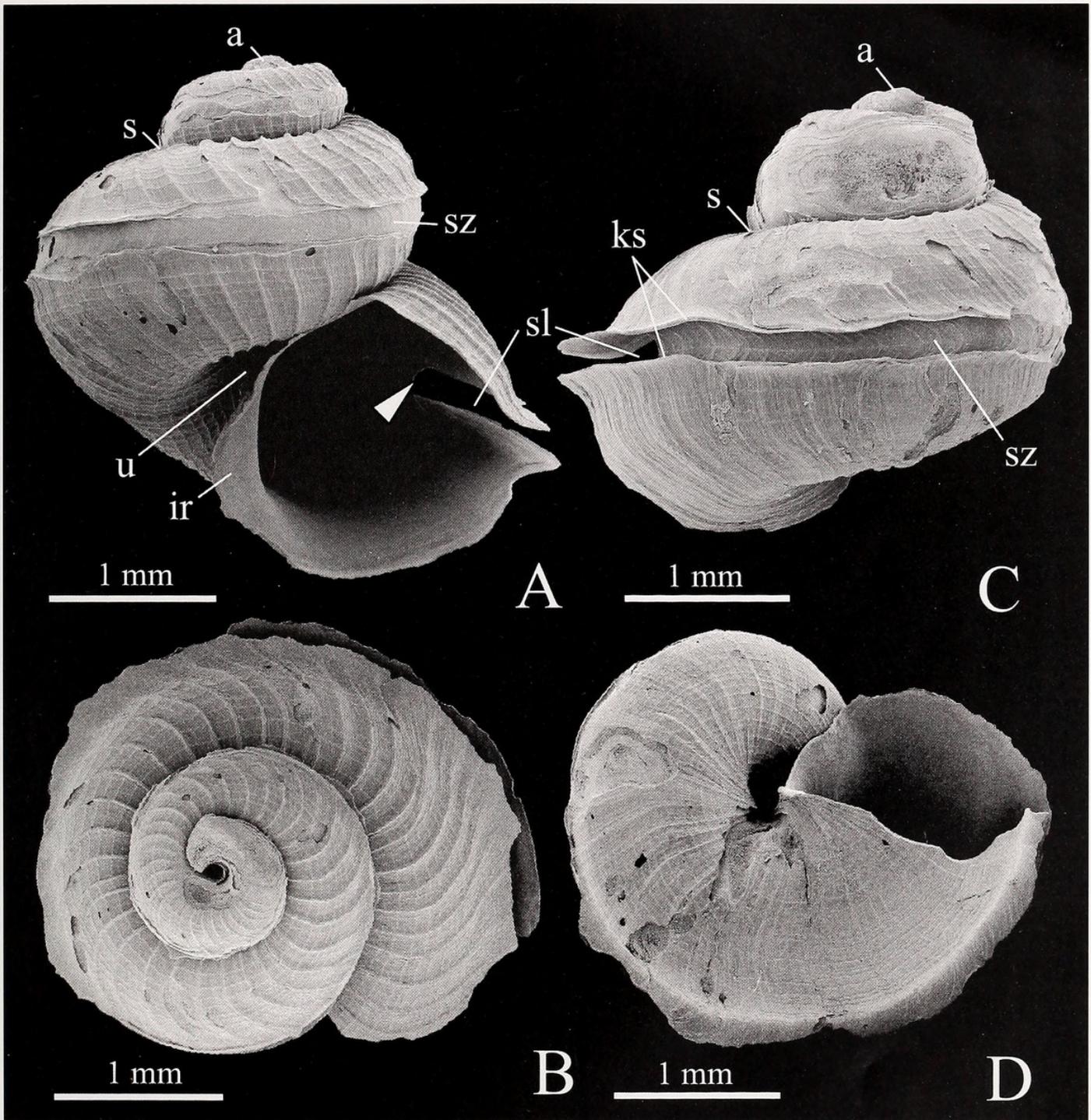


Figure 1. *Anatoma fujikurai* n. sp. Shell. A, Frontal view. Arrowhead indicates end of slit. B, Apical view. C, Back view. D, Basal view. Abbreviations: a = apex; ir = reflected part of inner lip; ks = keels along selenizone; s = suture; sl = slit; sz = selenizone; u = umbilicus. A–B, Holotype, UMUT RM29549. C–D, Paratype, UMUT RM29550.

Anatoma lamellata (A. Adams, 1862) from Japan has a similar overall shape and similar density of axial lamellae. However, on teleoconch I, it has a distinct spiral cord in the position of the selenizone (absent in *A. fujikurai*), teleoconch I is of less than 0.5 whorls (>0.75 in *A. fujikurai*), the spiral cords are approxi-

mately one-third the strength of the axial lamellae ($<$ one-fifth in *A. fujikurai*), the suture is 1.5 times the width of the selenizone below the selenizone (space equal to width of selenizone in *A. fujikurai*), and a distinct funiculus is present in the umbilical cavity (absent in *A. fujikurai*). The differentiation is based on

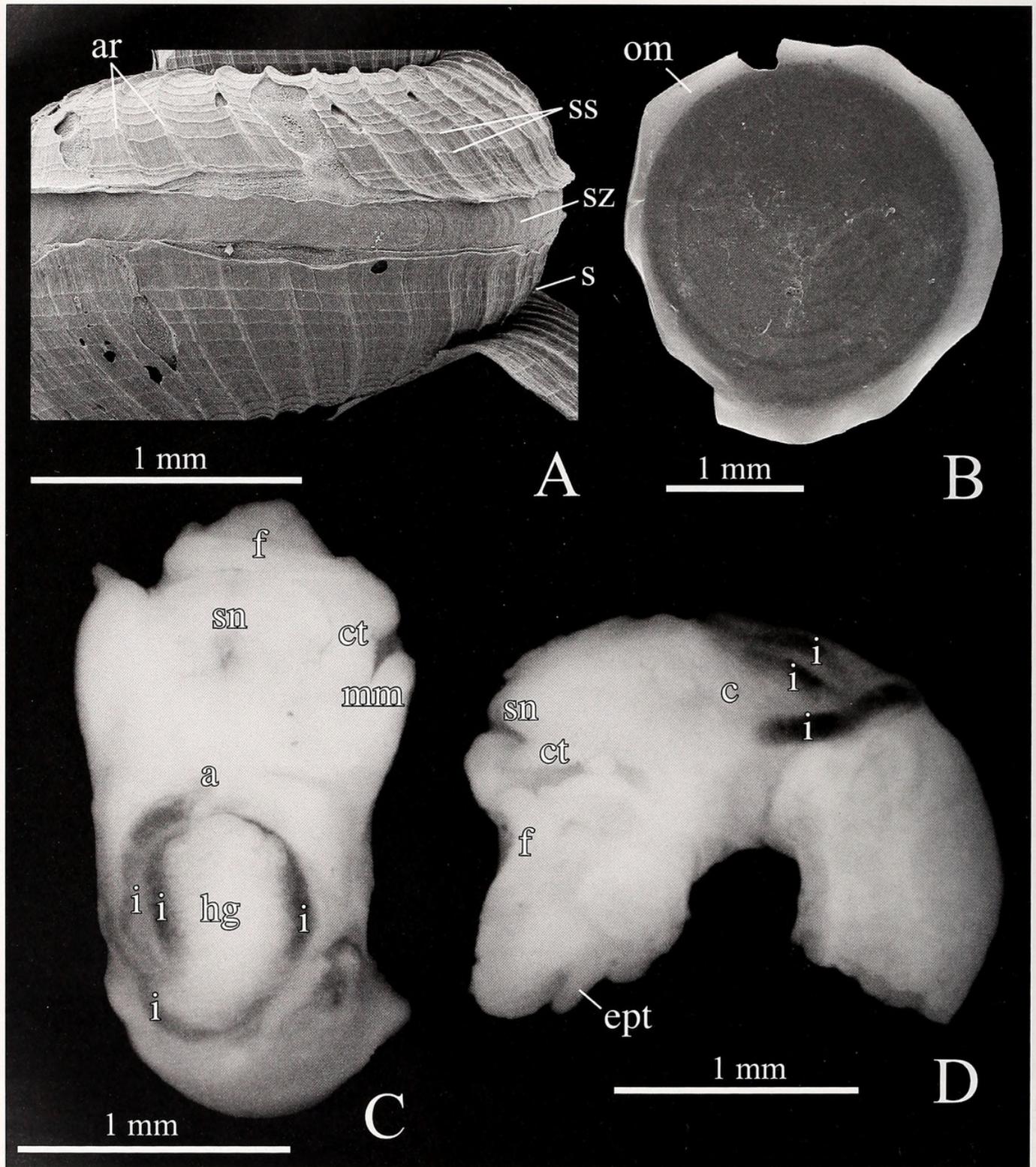


Figure 2. *Ananoma fujikurai* n. sp. A, Enlargement of sulature of body whorl. B, Exterior view of operculum. C, Dorsal view of anterior part of the animal. D, Lateral view of same part. Abbreviations: a = anus; ar = axial ribs; c = ctenidium; ct = cephalic tentacle; ept = epipodial tentacle; f = foot; hg = hypobranchial gland; i = intestine; mm = mantle margin; om = thin margin of operculum; s = suture; sn = snout; ss = spiral streaks; sz = selenizone. A, Holotype, UMUT RM29549. B-D, Paratype, UMUT RM29550.

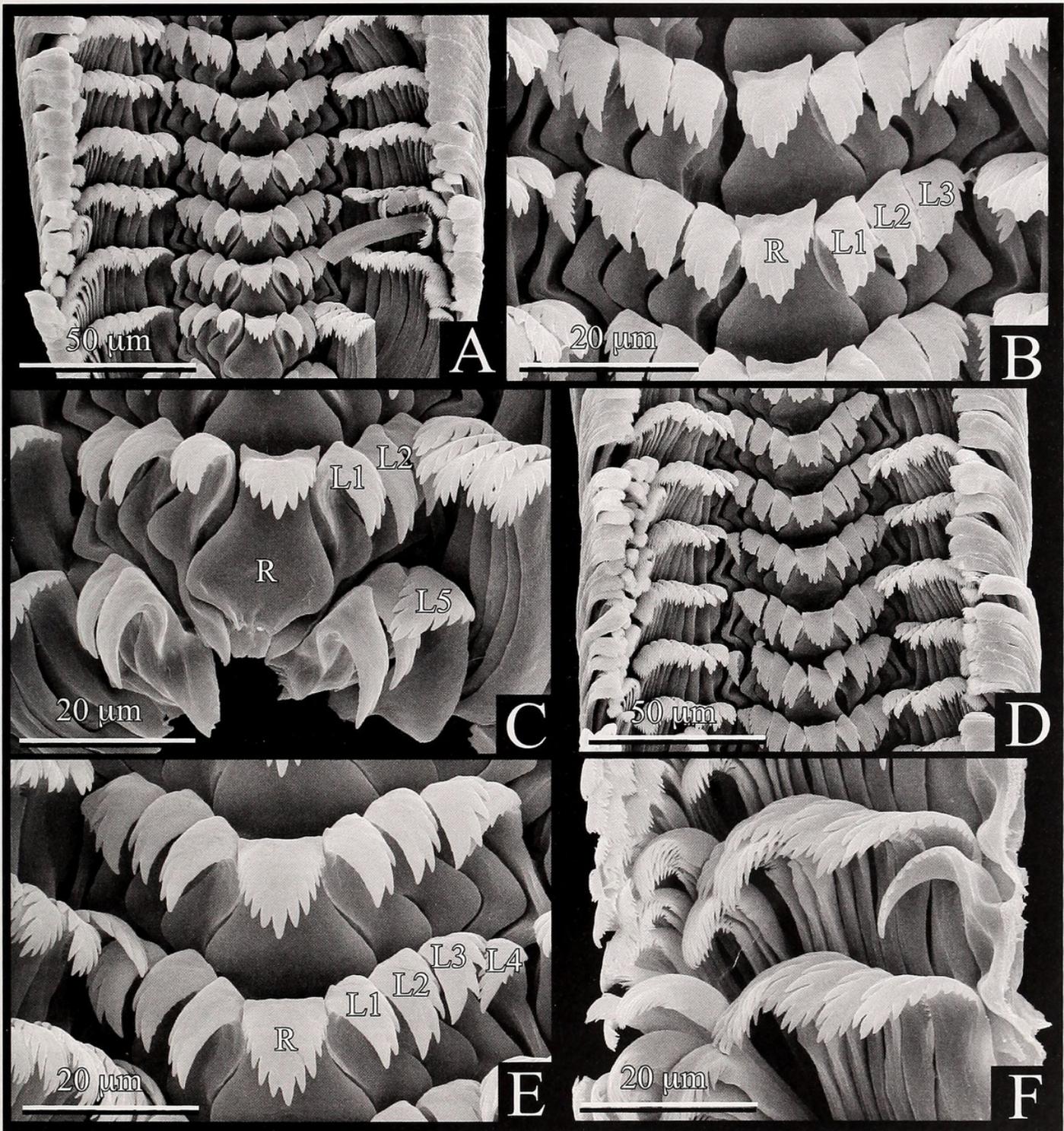


Figure 3. *Anatoma fujikurai* n. sp. Radula. A, D, Six rows of whole radular teeth. B, E, Rachidian (R) and lateral teeth (L1–L4). C, Entire view of rachidian and part of lateral teeth, showing bases of teeth, F, Enlargement of left rows of marginal teeth. A–C, Holotype, UMUT RM29549. D–F, Paratype, UMUT RM29550.

the examination of type material in the BMNH by SEM (Geiger, pers. obs.). The species has usually been misidentified, e.g., Habe (1951) and Izawa & Matsuoka (1999) illustrated an anomalous species with a distinct absence of spiral cords just below the

selenizone, characters not found in *A. lamellata*, but quite typical for *T. reticulata*; McLean's (1967: pl. 56, fig. 8) illustrated specimen is an *A. lyra* (Berry, 1947); Kuroda et al. (1971) showed an unidentified anatomid species lacking the lamellae typical for *A. lamellata*;

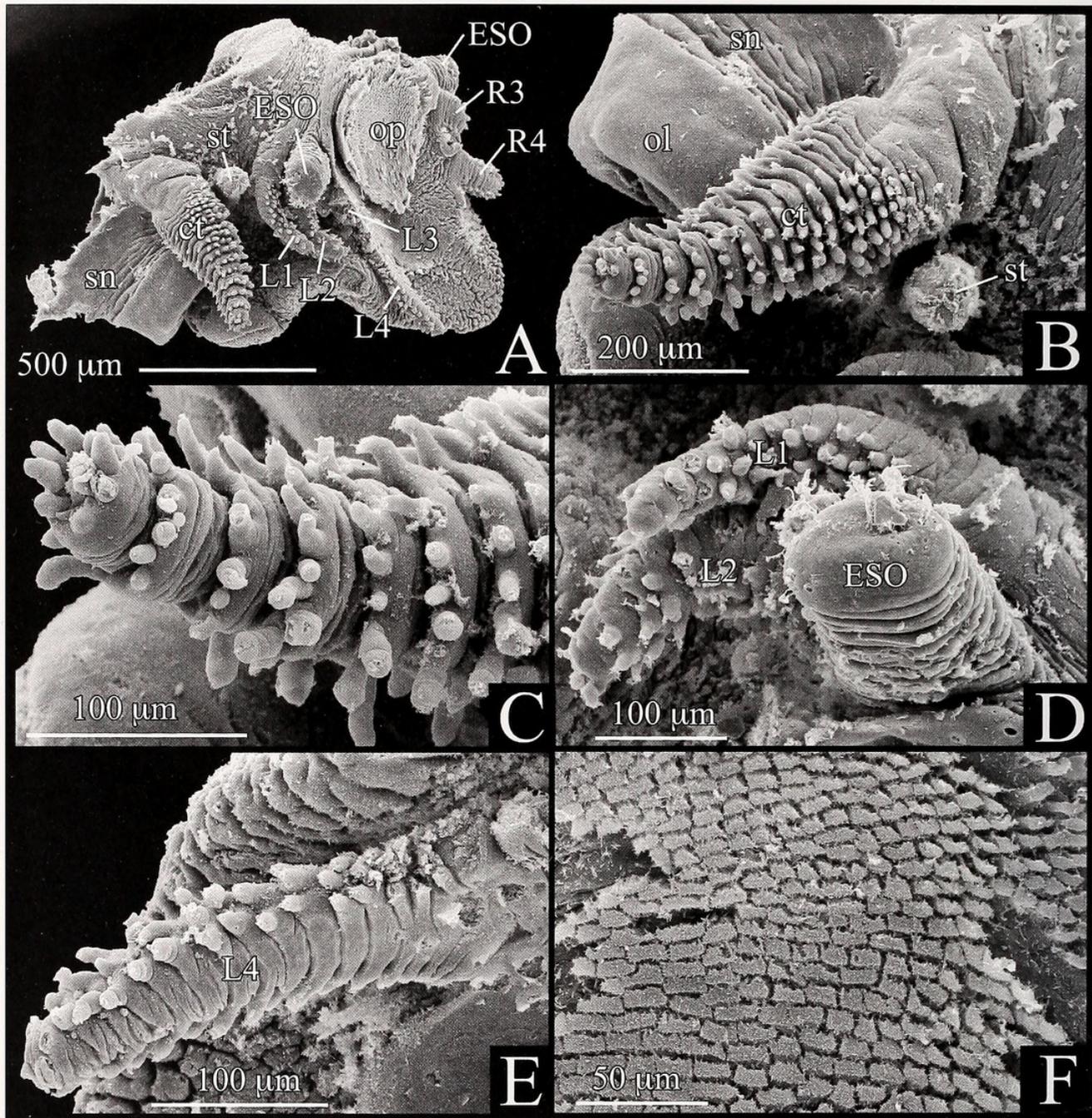


Figure 4. *Anatoma fujikurai* n. sp. Head-foot of animal. Paratype UMUT RM29550. A, Left lateral view of head-foot with buccal mass removed. B, Enlargement of head. C, Papillate tip of left cephalic tentacle. D, First to second left epipodial tentacles with epipodial sense organ. E, Fourth left epipodial tentacle. F, Surface of opercular attachment. Abbreviations: ct = cephalic tentacles; ESO = epipodial sense organ; L1–L4 = first to fourth left epipodial tentacles; ol = outer lip of mouth; op = opercular lobe; R3–R4 = third and fourth right epipodial tentacles; sn = snout; st = suboptic tentacle.

Numanami & Okutani (1990) showed an unidentified species not conspecific with *A. lamellata*; Okutani & Hasegawa (2000: pl. 18, figs. 1a, 1b) figured *Thielelea reticulata* Bandel, 1998. Other published illustrations (e.g., Habe, 1961) are so small as to make positive identification impossible. Only Tsuchida et al. (1991) and Tsuchida & Hori (1996) illustrated the true *A. lamellata*, and Thiele's (1912) line drawing agrees

exceptionally well with the SEM images of the type material.

Anatoma japonica (A. Adams, 1862) from Japan has an overall biconical shape (stepped in *A. fujikurai*); the density of the axials is at least twice as high as in *A. fujikurai*, while the spirals are almost as strong as the axials (< one-fifth in *A. fujikurai*), and the keels of the open slit converge towards the apertural margin (they

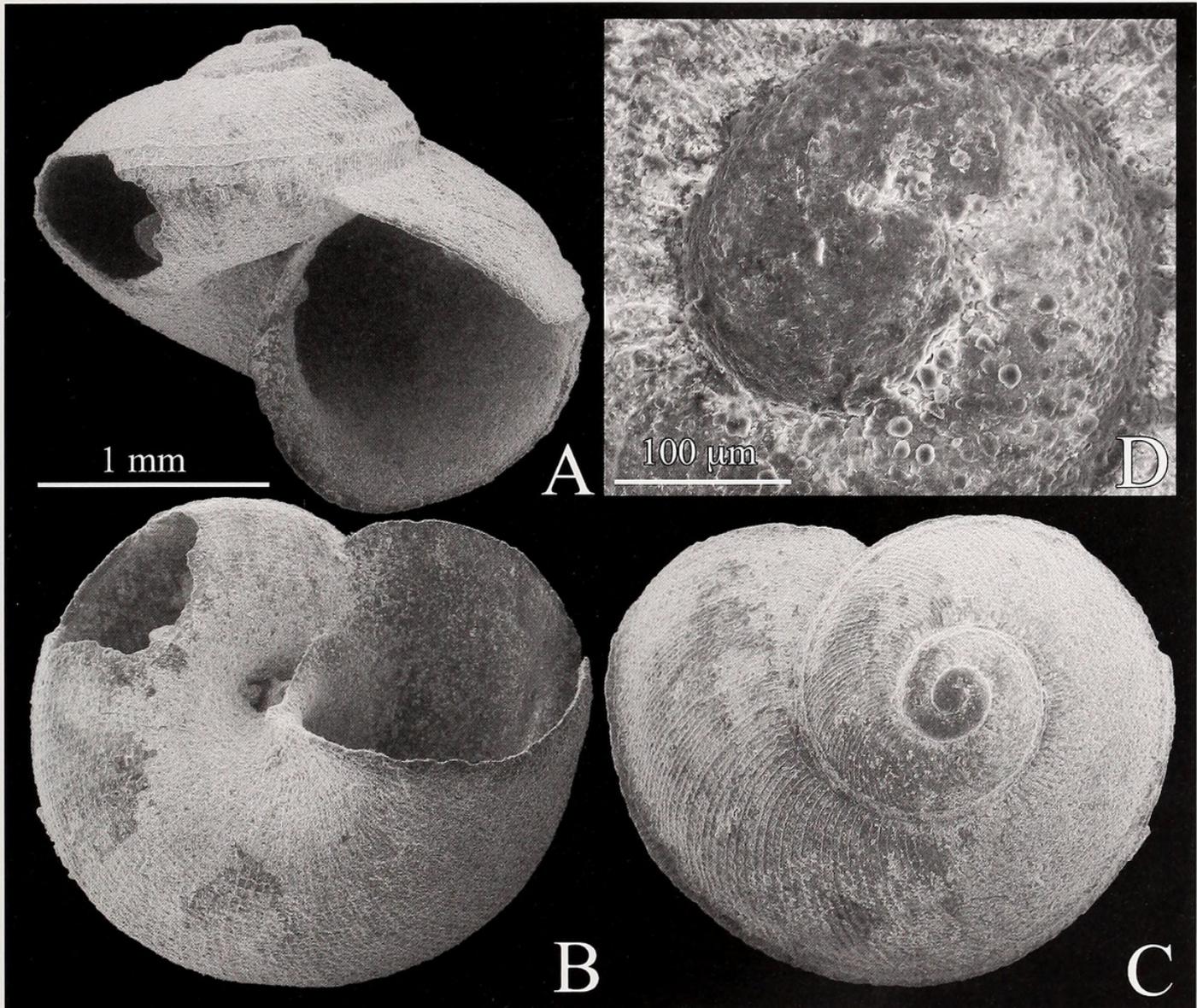


Figure 5. Holotype of *Anatoma soyae* (Habe, 1951), NSMT Mo-38615. A, Frontal view. B, Basal view. C, Apical view. D, Protoconch.

maintain same width in *A. fujikurai*). The differentiation is based on the examination of type material in the BMNH by SEM (D. L. Geiger, personal observation).

Anatoma soyae (Habe, 1951) from Japan has an overall biconical shape (stepped in *A. fujikurai*), has denser axial sculpture (17 vs. 9 on the last quarter of teleoconch I), and the suture inserts immediately below the selenizone on early whorls (space equal to width of selenizone in *A. fujikurai*), and the keels of the selenizone are low [eroded?] (as high as selenizone width in *A. fujikurai*). The differentiation is based on SEM images of the holotype (NSMT Mo-38615: Figure 5).

Thielella sagamiana (Okutani, 1964) has a protoconch with reticulate sculpture, slightly shorter teleoconch I (0.66 vs. >0.75 whorls) with slightly more

axial cords (11 vs. 9 on last quarter whorl). On teleoconch II, the axials are not elevated to low lamellae as in *A. fujikurai*, and *T. sagamiana* is anomphalous, while *A. fujikurai* shows a distinct umbilicus. The comparison is based on SEM examination of the holotype (UMUT RM8808: Figure 6, unfigured in the original description), the paratype (NSMT Mo-69582: Figure 7, Okutani, 1964: pl. 5, fig. 2), and conspecific material collected from southeast off Kamogawa, Chiba Prefecture, 922–959 m (R/V *Tansei-Mar*, cruise KT-99-6, station 14, 34°48.820'N, 140°37.620'E to 34°48.854'N, 140°39.661'E), Hyuga Basin, 779–803 m (cruise KT-93-9, station HY-4, 31°53'22"N, 131°52'16"E to 31°54'16"N, 131°53'23"E), and Kumano Basin, 2029–2045 m (cruise KT-86-6,

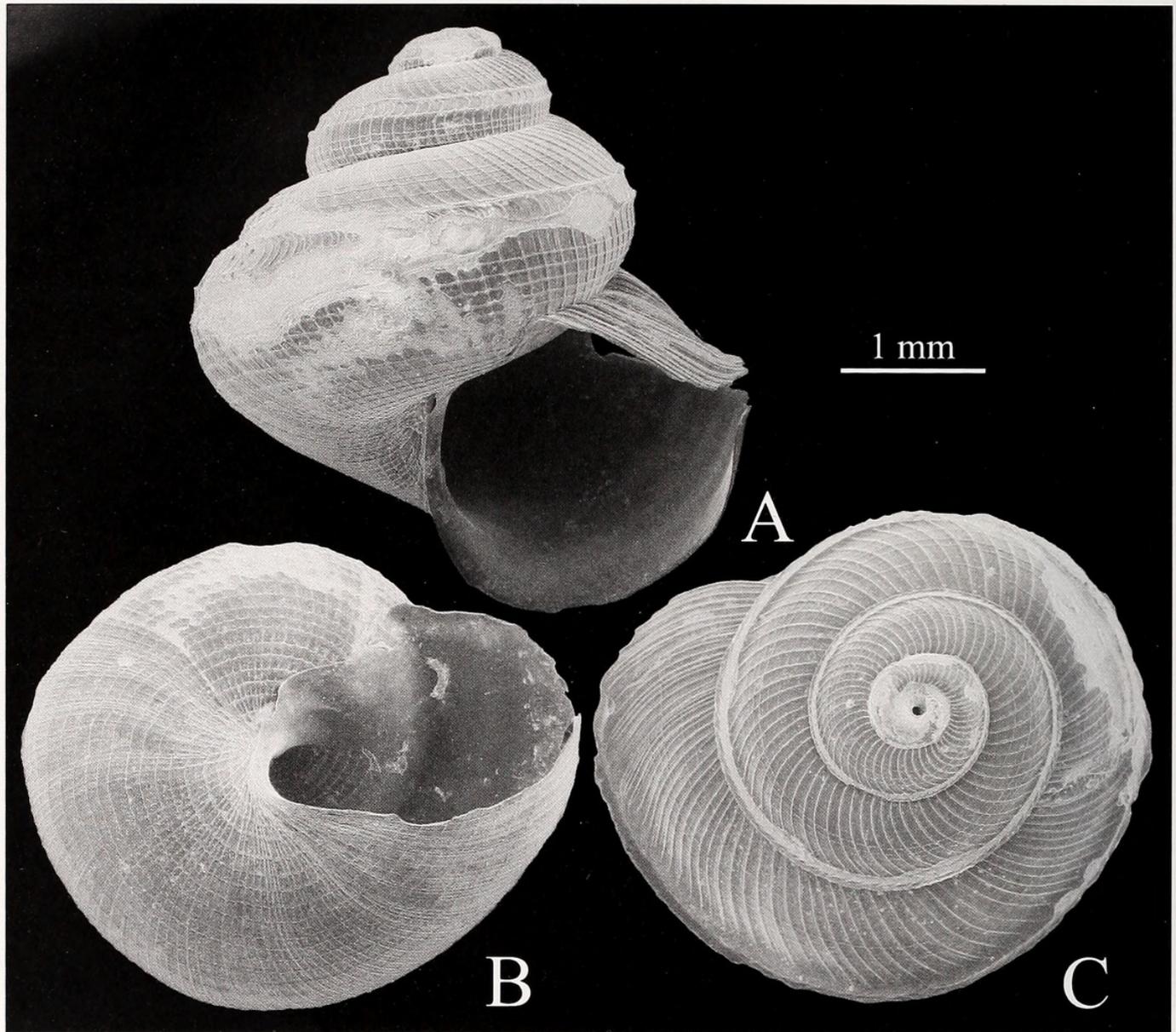


Figure 6. Holotype of *Thielella sagamiana* (Okutani, 1964), UMUT RM-8808. A, Frontal view. B, Basal view. C, Apical view.

station KN6, 33°46'6"N 136°40'0"E to 33°46'6"N, 136°37'6"E) (Figure 8).

Among Indo-Pacific species with overall stepped shell shape, *A. fujikurai* is distinguished as follows.

Anatoma indonesica Bandel, 1998, has on teleoconch I a spiral cord in the position of the selenizone (absent in *A. fujikurai*), has more strongly elevated spiral lamellae on the shoulder, crossed by approximately 4–8 fine spiral lines concentrated in the middle of the shoulder (equally distributed in *A. fujikurai*), and has fine cancellate sculpture on the base (strong axials and fine spirals in *A. fujikurai*).

Anatoma boucheti Geiger & Sasaki, 2008, from Reunion Island, Indian Ocean, has a teleoconch of 1.125 whorls, shows fine reticulate sculpture of axials

and spiral lines of approximately equal strength, and has the keels of the selenizone distinctly elevated.

Anatoma herberti Geiger & Sasaki, 2008, from Reunion Island, Indian Ocean, has more strongly elevated axial lamellae and a distinct constriction of the base below the selenizone (absent in *A. fujikurai*), which bears strongly elevated keels (low/eroded in *A. fujikurai*) bearing three to four fine axial striae between each axial cord (none in *A. fujikurai*).

Anatoma lamellata nanshaensis Feng, 1996, has on teleoconch I a spiral cord in the position of the selenizone (absent in *A. fujikurai*), the shoulder is at an angle of approximately 10° (45° in *A. fujikurai*), the selenizone is in the upper third of the whorl (below the midline in *A. fujikurai*), and has fine reticulate sculpture

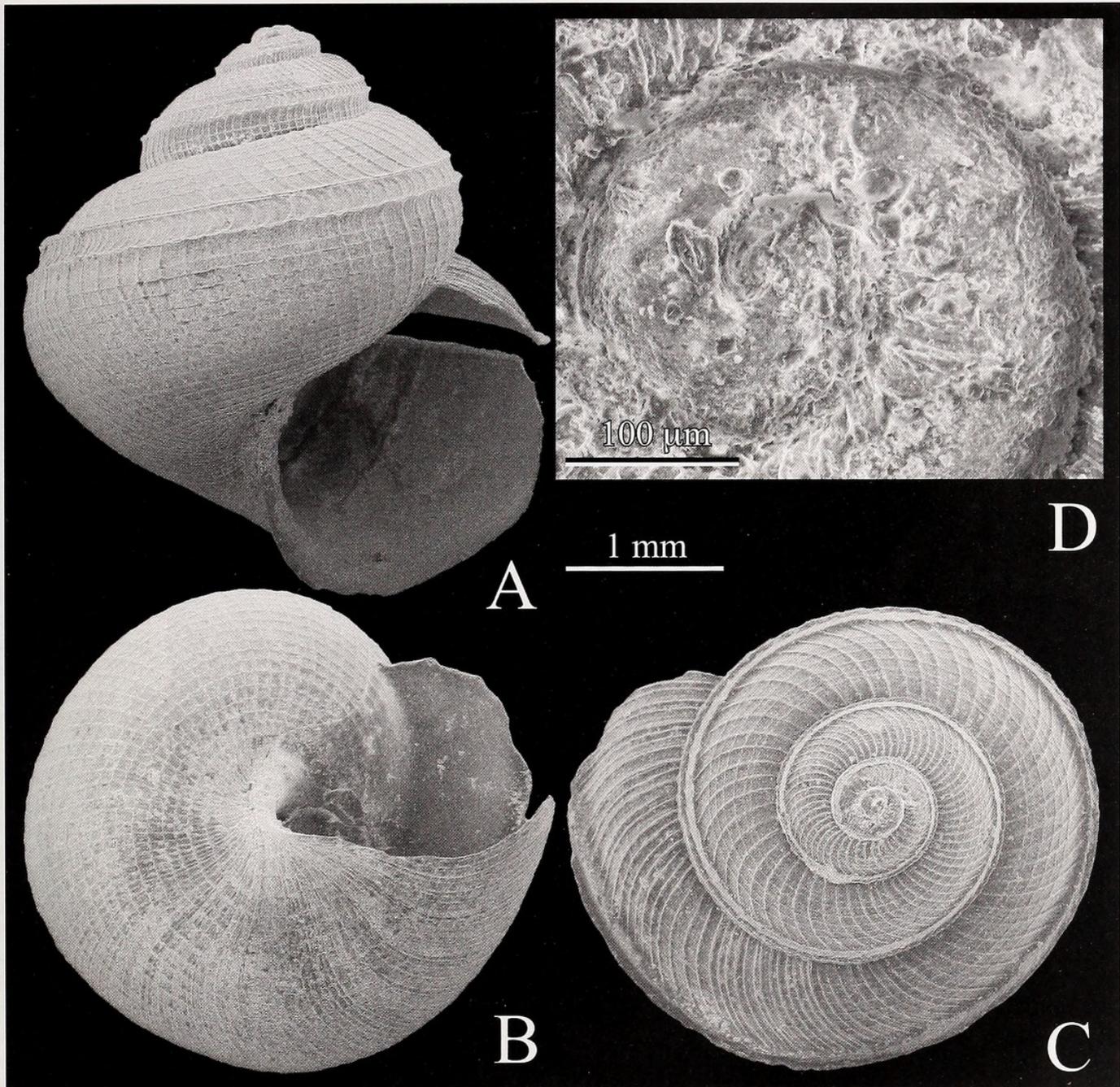


Figure 7. Paratype of *Thielella sagamiana* (Okutani, 1964), NSMT Mo-69582. A, Frontal view. B, Basal view. C, Apical view. D, Protoconch.

on the base (more prominent axials in *A. fujikurai*). The differentiation is based on the original figures of Feng (1996).

Anatoma obtusata (Golikov & Gublin, 1978) is overall more depressed (height-to-width ratio = 0.86: 1.03 in *A. fujikurai*), seems to have reticulate sculpture with axials and spiral of similar strength (axials predominant in *A. fujikurai*) and has less distinct (eroded?) keels of the selenizone. The differentiation is based on the original line drawing and photographs of the holotype in Kantor & Sysoev (2006).

DISCUSSION

The generic placement of *Anatoma* s.l. *fujikurai* is uncertain, because the diagnostic protoconch sculpture is not preserved in either of the two known specimens. *Anatoma* s.s. has either smooth or flocculent sculpture, while *Thielella* has reticulate sculpture. Whether this character is sufficient to justify generic distinction has been discussed (Marshall, 2002; Geiger, 2003; Geiger & Jansen, 2004; Zelaya & Geiger, 2007) and is provisionally accepted (see also Geiger, 2006a, b, c).

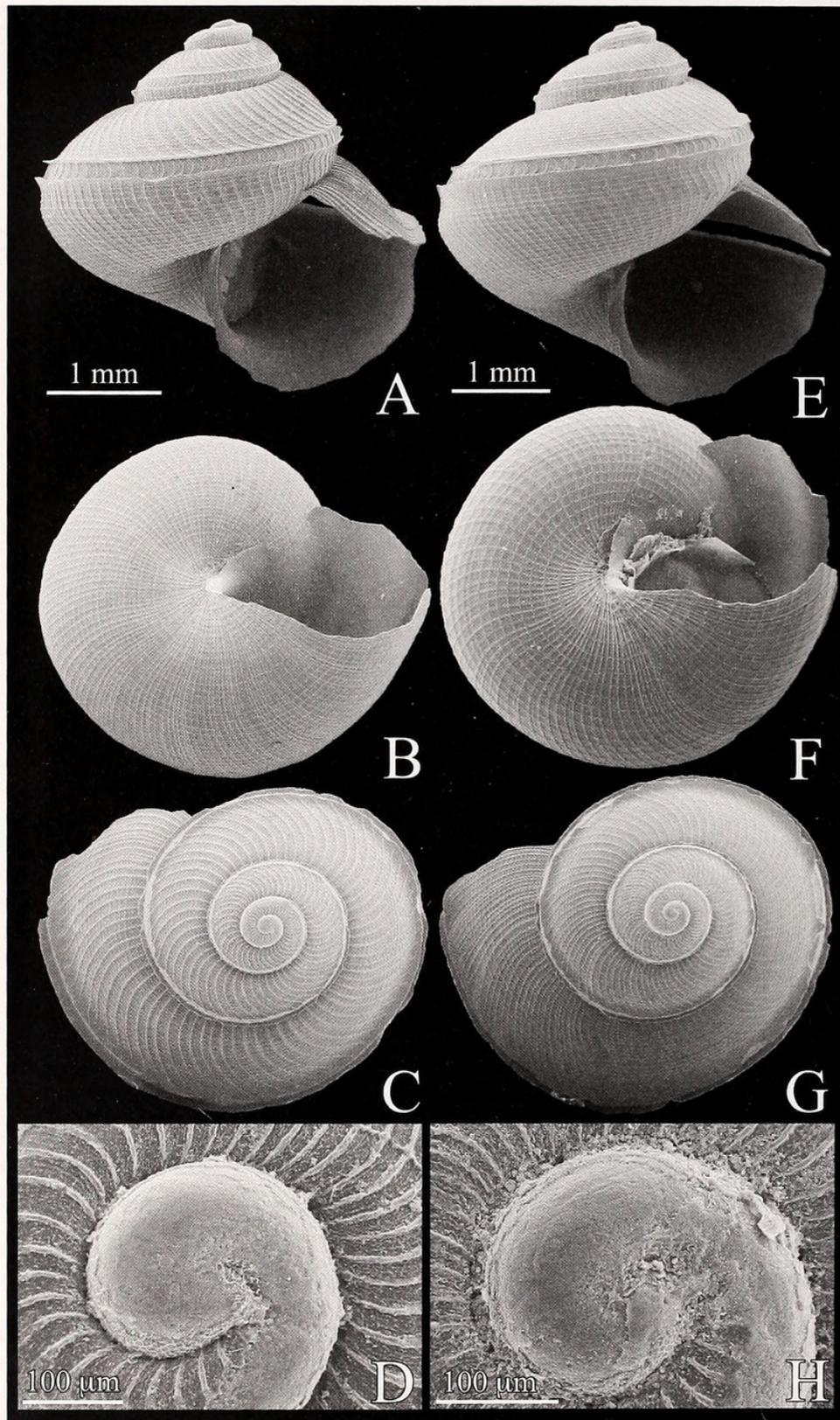


Figure 8. *Thielella sagamiana* (Okutani, 1964). A–D, Kumano Basin, 2029–2045 m (R/V *Tansei-Marui*, cruise KT-86-6, station KN6, 33°46'6"N, 136°40'0"E to 33°46'6"N, 136°37'6"E) (SBMNH 83432). E–H, Southeast off Kamogawa, Chiba Prefecture, 922–959 m (R/V *Tansei-Marui*, cruise KT-99-6, station 34°48.820'N, 140°37.620'E to 34°48.854'N, 140°39.661'E) (SBMNH 83433). A, E, Frontal view; B, F, Basal view; C, G, Apical view; D, H, Protoconch.

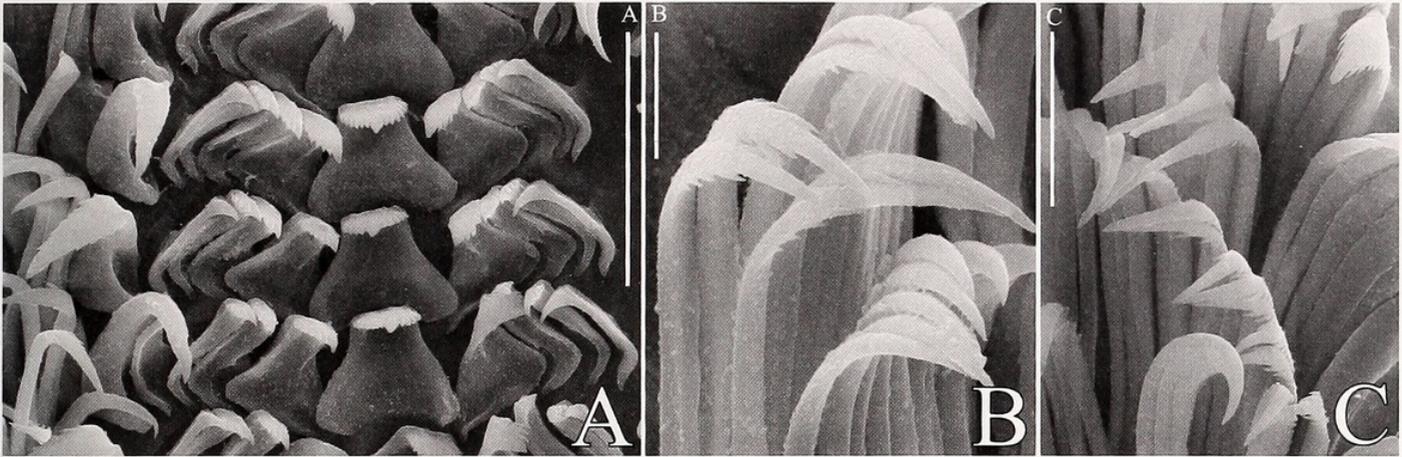


Figure 9. Radula of *Thielella sagamiana* (Okutani, 1964) from specimen shown in Figure 8 E–H. Southeast off Kamogawa, Chiba Prefecture, 922–959 m (R/V *Tansei-Maru*, cruise KT-99-6, station 34°48.820'N, 140°37.620'E to 34°48.854'N, 140°39.661'E) (SBMNH 83433). A, Central field with inner lateral teeth. Scale bar = 50 µm. B–C, Marginal teeth. Scale bar B = 10 µm. Scale bar C = 20 µm.

The shell morphological features clearly place the new species in Anatomidae, including the size, number of whorls for the size, the presence and placement of a slit and selenizone, as well as the common combination of axial and spiral sculptural elements. The presence of strong axial lamellae is unusual in Anatomidae, but it is also known from the Japanese *A. lamellata* (A. Adams, 1862) and *A. herberti* Geiger & Sasaki, 2008, from the Indian Ocean.

The radula, on the other hand, is exceptional and does not agree with the pattern thus far observed in the family. Although only a handful of species has been examined [*A. crispata*, *A. euglypta* (Pelseneer, 1903), *A. janetae* Geiger, 2006, *Anatoma* sp. from South Africa, *Thielella argentinae* Zelaya & Geiger, 2007, *T. baxteri*, *T. flemingi* Marshall, 2002, *T. kelseyi* (Dall, 1905), *T. reticulata* Bandel, 1998], in general, they have very similar features also shared with *T. sagamiana* shown here (Figure 9). These characteristics include a trapezoidal rachidian tooth with a narrowly V-shaped cusp with the central denticle distinctly larger than the remainder (not broadly V-shaped with denticles of gradually decreasing size); lateral tooth 4 strongly reduced and hook-shaped (not slightly reduced, with distinct cusp bearing multiple denticles); lateral tooth 5 with strongly elongated cusp, at least twice as large as those of the inner marginal teeth, with straight edges and acute angle (not broadened, only slightly larger than the inner marginal teeth, and with convex edges). Although previously it was thought (Sasaki, 1998; Geiger, 2003) that radular morphology will be suitable only for family-level classification—i.e., distinction between Scissurellidae s.s., Anatomidae, Larocheidae, and Temnocinclidae—examination of additional species in Anatomidae suggests otherwise. Initial indications appeared with *A. janetae*, whose innermost marginal teeth have very few denticles (Geiger, 2006c)

and *A. flexidentata* Geiger & Sasaki, 2008, and *A. austrolissa* Geiger & Sasaki, 2008, which exhibit a radula with floppy teeth.

One may hypothesize that the unusual radular form of *A. fujikurai* is caused by heterochronic process (arrested development). Generally, in other vetigastropods, the rachidian and lateral teeth are more narrowly pointed and sharply serrated in juveniles than in adults, as is found in Trochoidea (Warén, 1990) and Haliotidae (Kawamura et al., 2001), whereas in adults the rachidian often shows an unserrated cutting edge parallel with the row of teeth. Therefore, acutely serrated teeth of *A. fujikurai* may represent a state of arrested development compared with other typical *Anatoma* species. This hypothesis, however, should be tested by ontogenetic study in the future. Although we have prepared several hundred scissurellid s.l. radulae covering species over the entire size spectrum (0.6–11 mm) and including conspecific specimens of different sizes, we have not seen any ontogenetic differences. Ontogenetic variability is not mentioned in the only modern ontogenetic study of *Scissurella* by Strasoldo (1991).

It is widely acknowledged that food and feeding has a major effect on radular morphology (e.g., Hickman & McLean, 1990). Whether this is the case also in Anatomidae is uncertain as there are no data on food and feeding. Limited gut content analyses have not allowed us to identify specific food sources suggesting deposit feeding (Geiger, personal observation; Sasaki, personal observation).

Some alternative explanations for the occurrence of unusual radular morphologies have been explored, but, on the basis of available data, must be rejected.

The morphological changes are not correlated with depth, because some deep-water species, e.g., *Thielella argentinae* Zelaya & Geiger, 2007, from the abyssal

plain of the South Atlantic, has the typical anatomid radular pattern. It is tantalizing that two deep-water species from Reunion Island (*A. flexidentata*, *A. australissa*: Geiger & Sasaki, 2008) show a very similar yet untypical radular pattern of floppy teeth, but the broader significance is difficult to assess, given the sparse data available.

The hydrothermal vent environment is also unlikely as an explanatory factor, as shown by the only moderately modified radula of *A. janetae*, also collected from sites in the vicinity of hydrothermal vents.

The three species with the most aberrant radulae are from the Tethys area: Japan (*A. fujikurai*) and the Indian Ocean (*A. flexidentata*, *A. australissa*: Geiger & Sasaki, 2008). The significance of this observation is uncertain because of generally poor sampling of the deep sea owing to a lack of suitable material and the relatively few Atlantic species that have having been examined (Geiger, 2008).

The current contribution highlights the wealth of interesting new information that is obtained from small molluscan species. The examination of such understudied groups of micromollusks as Anatomidae shows significant promise for the discovery of novel characters and adaptive pathways.

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