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REDISCOVERY OF *MARGINELLONA GIGAS* (MARTENS, 1904), WITH NOTES ON THE ANATOMY AND SYSTEMATIC POSITION OF THE SUBFAMILY MARGINELLONINAE (GASTROPODA: MARGINELLIDAE)

M. G. Harasewych¹ and Yuri I. Kantor²

ABSTRACT. Based on anatomical data, the genus *Sigaluta* Rehder, 1967, and its type species *S. pratasensis* Rehder, 1967, originally described in the Volutidae, are synonymized with the genus *Marginellona* Martens, 1904, and its type species *M. gigas* (Martens, 1904), of the family Marginellidae. The originally questionable inclusion of this species in Marginellidae is supported by additional anatomical characters. The subfamily Marginelloninae, type genus *Marginellona*, differs from other marginellids not only in its much larger size and distinctive radular morphology, but also in having a relatively unmodified neogastropod alimentary system with a large valve of Leiblein, and a large gland of Leiblein that lacks a separate duct to the buccal cavity.

Key words: Marginellidae; *Marginellona*; *Sigaluta*; South China Sea; anatomy.

INTRODUCTION

The genus *Sigaluta* and its type species *S. pratasensis* were described from two shells and provisionally assigned to the volutid subfamily Cymbiinae on the basis of general conchological similarities (Rehder, 1967). An additional, larger specimen, also without preserved animal, was reported by Rehder (1970). Weaver and duPont (1970: 99) followed Rehder's subfamilial assignment, but remarked that *Sigaluta pratasensis* ". . . does not resemble any other species in the family Volutidae."

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Rokop (1972) assigned a second species, from abyssal depths off Baja California, to this genus, also on the basis of shell characters.

During our recent visit to the Zoological Institute in Leningrad, Dr. Boris Sirenko brought to our attention several specimens of *Sigaluta pratasensis*, three with preserved animal. Preliminary dissections revealed this species to have a marginellid radula. A survey of the literature on Marginellidae disclosed that *Sigaluta pratasensis* is a synonym of *Marginellona gigas* (Martens, 1904).

As *Marginellona gigas* is the type species of the type genus of the small and poorly known subfamily Marginelloninae Coan, 1965, we take this opportunity to describe the anatomy of this unusual marginellid, to compare it with that of other marginellids, and to discuss its relationship within the family Marginellidae. The systematics of *Sigaluta cukri* Rokop, 1972, is discussed in Harasewych & Kantor (1991).

MATERIALS AND METHODS

In addition to the holotype and paratype of *Sigaluta pratasensis* in the collections of the National Museum of Natural History, Smithsonian Institution (USNM), we examined six specimens in the collections of the Zoological Institute, Leningrad (ZIN). Anatomical data is based on gross dissections of three of these specimens, a large, mature male (fig. 3), a small female (fig. 4), and an immature male (fig. 5). The terminology for shell ultrastructure follows Hedegaard (1990).

SYSTEMATICS

Family MARGINELLIDAE Fleming, 1828

Subfamily MARGINELLONINAE Coan, 1965

The subfamily was proposed by Coan (1965: 186) to include the monotypic genera *Marginellona* Martens, 1904, and *Afrivoluta* Tomlin, 1947, and was characterized by having unusually large (>4 cm) shells and short radulae consisting of extremely broad rachidian teeth with numerous (60-90) cusps. The unique radular morphology has been termed "Type 7 radula" by Covert (1989: 33). The two species comprising this subfamily have a Type 1 animal in the terminology of Covert (1987: 19).

Genus *Marginellona* Martens, 1904.

Marginella (*Marginellona*) Martens, 1904: 108-109, pl. 5, fig. 16; Thiele, 1904: 170, pl. 9, fig. 64; Tomlin, 1917: 268 [type species: *Marginella* (*Marginellona*) *gigas* Martens, 1904, by monotypy].

Marginellona Martens, 1903 [sic], Thiele, 1929: 355-356, fig. 431; Wenz, 1943: 1380, fig. 3903.

Marginelloma Cossmann, 1906: 225 [error in spelling].

Sigaluta Rehder, 1967: 182-183, text-figs. 1-4 (type species: *Sigaluta pratasensis* Rehder, 1967, by original designation).

Martens (1904) observed that his taxon had affinities to the Volutidae, but included it in the Marginellidae on the basis of radular and shell morphology. Although *Marginellona* was originally described as a subgenus of *Marginella*, Thiele (1929: 355-356) considered it to be one of but three genera within Marginellidae.

Marginellona gigas (Martens, 1904)

Figures 1-19, Table 1

Marginella (*Marginellona*) *gigas* Martens, 1904: 108-109, pl. 5, fig. 16; Thiele, 1904: 170, pl. 9, fig. 64; Tomlin, 1917: 268.

Marginellona gigas Martens, Thiele, 1929: 356; Wenz, 1943: 1380, fig. 3903.

Sigaluta pratasensis Rehder, 1967: 182-183, text-figs. 1-4.

Description: Shell (Figs. 2-5, Table 1) to 157 mm, thin, translucent, porcellaneous, narrowly ovate. Protoconch of 2-2½ rapidly expanding (diameter 0.5 mm to 11.5 mm in 2 whorls), smooth, conical, glassy whorls, deflected from coiling axis of teleoconch by up to 15°. Transition to teleoconch abrupt, marked by growth line (Fig. 6, t), and accompanied by formation of thin parietal callus (Fig. 6, c). Teleoconch with up to 3 smooth, inflated, convex, rapidly descending whorls. Suture with abutting whorls. Shell surface smooth, glazed, lacking spiral and axial sculpture. Aperture ovate, narrow posteriorly, broad anteriorly. Outer lip smooth. Inner lip smooth, with thin, whitish inductural overglaze in some specimens. Columella with single sharp, axially oriented columellar fold (Fig. 3, cf) and sharp siphonal fold (Fig. 3, sf) of nearly equal magnitude. Outer shell surface uniformly tan to greenish-tan; aperture darker brown.

Ultrastructure: Shell composed of five crystalline layers (Fig. 7). Innermost layer (Figs. 7, 9, i), thin (to 65 µm), of simple prismatic crystals. Subsequent layer (Figs. 7, 9, t) thickest (to 300 µm), composed of linear simple crossed lamellar crystals oriented perpendicular to growing edge. Next outer layer (Figs. 7, 8, c) nearly as thick (to 250 µm), orthogonally oriented, with faces of linear simple crossed lamellar crystals parallel to growing edge. Next outer layer (Figs. 7, 8, p) thin (to 20 µm), with intersected crossed platy structure. Outermost layer (Fig. 8, o) thin (to 70 µm), again of simple prismatic crystals.

External anatomy: Soft parts of largest and only complete specimen (Figs. 3, 14) comprising 2 ½ whorls, excluding foot. Mantle cavity spanning

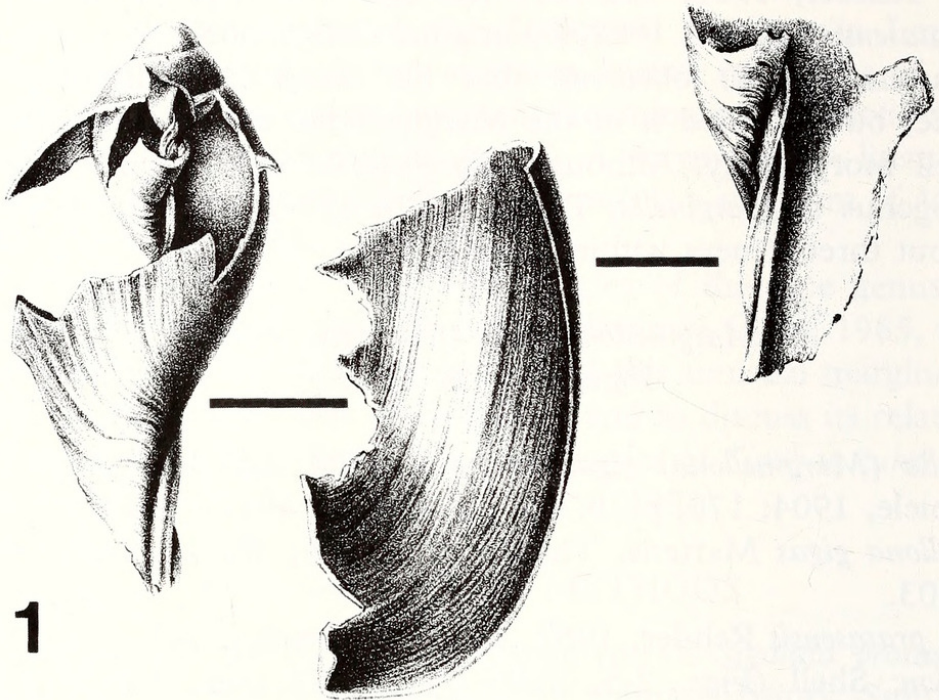


Figure 1. *Marginellona gigas* (Martens). Original illustration of holotype, reproduced at 0.9 X.

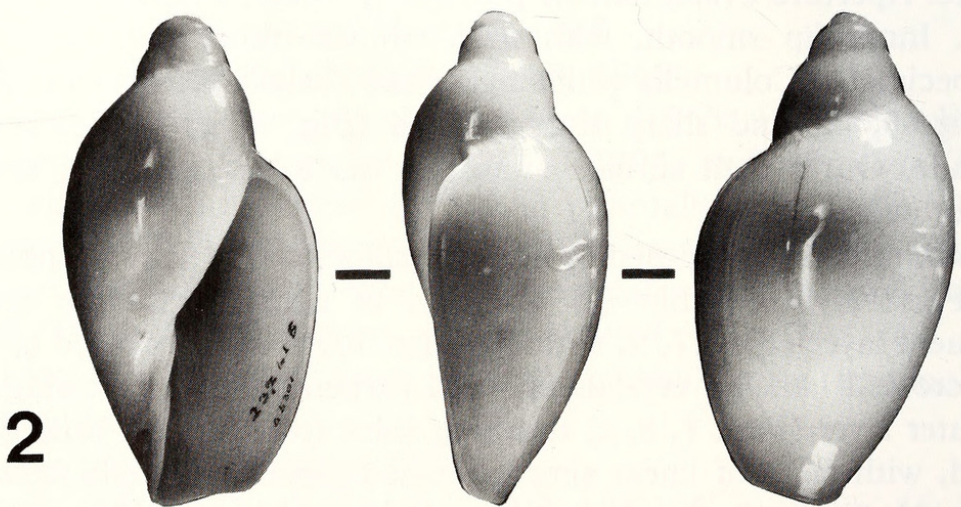
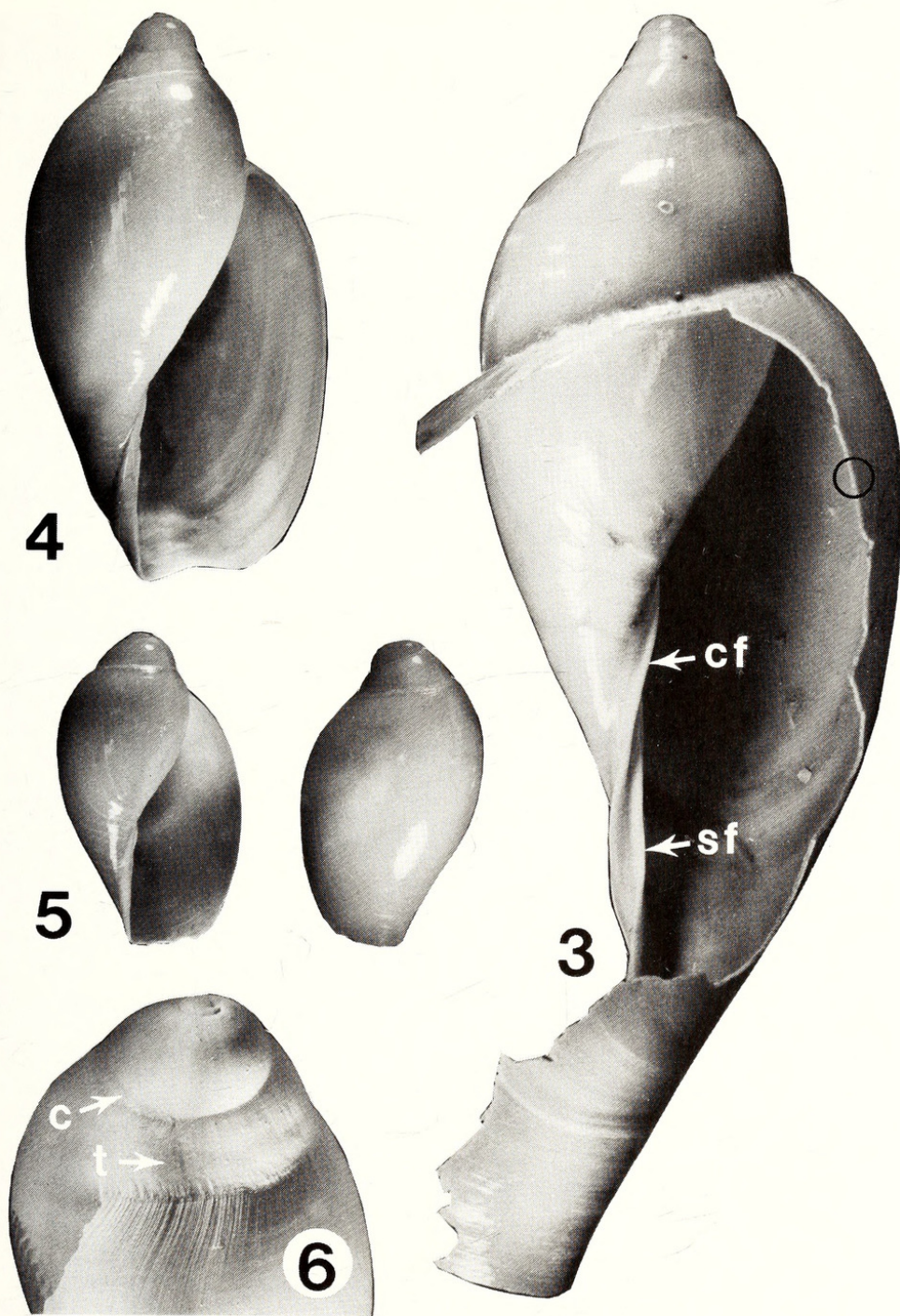
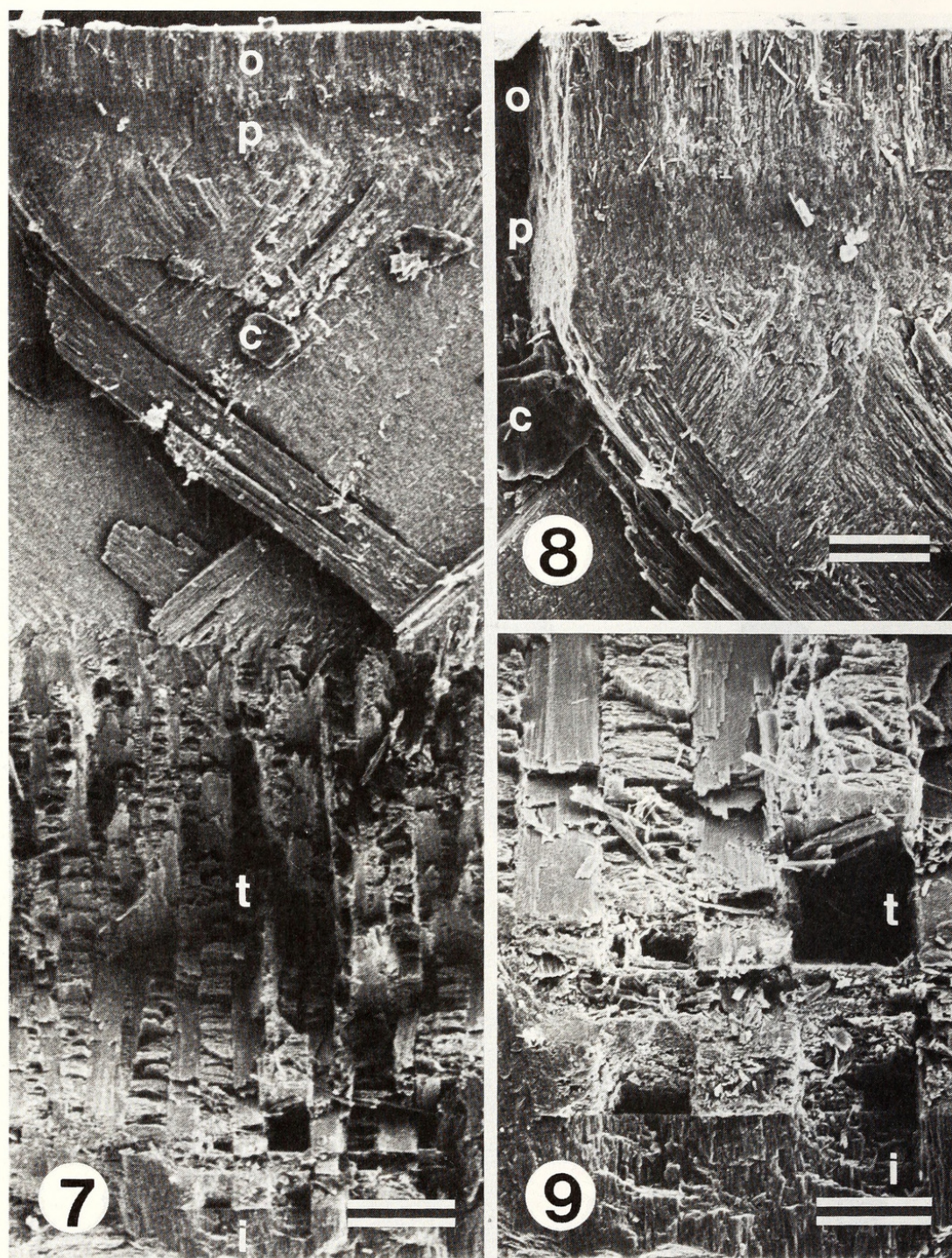


Figure 2. Holotype of *Sigaluta pratasensis* Rehder, 1967, apertural, lateral and dorsal views. W. of Pratas Reef, South China Sea, 20°37'N, 115°43'E, in 380 m, gray mud and sand bottom, 0.9 X.



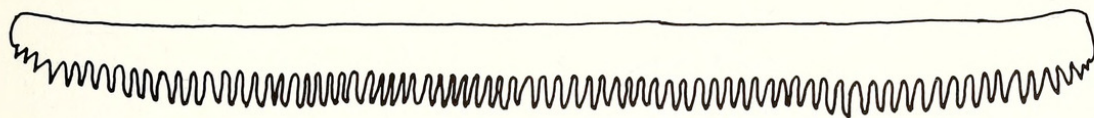
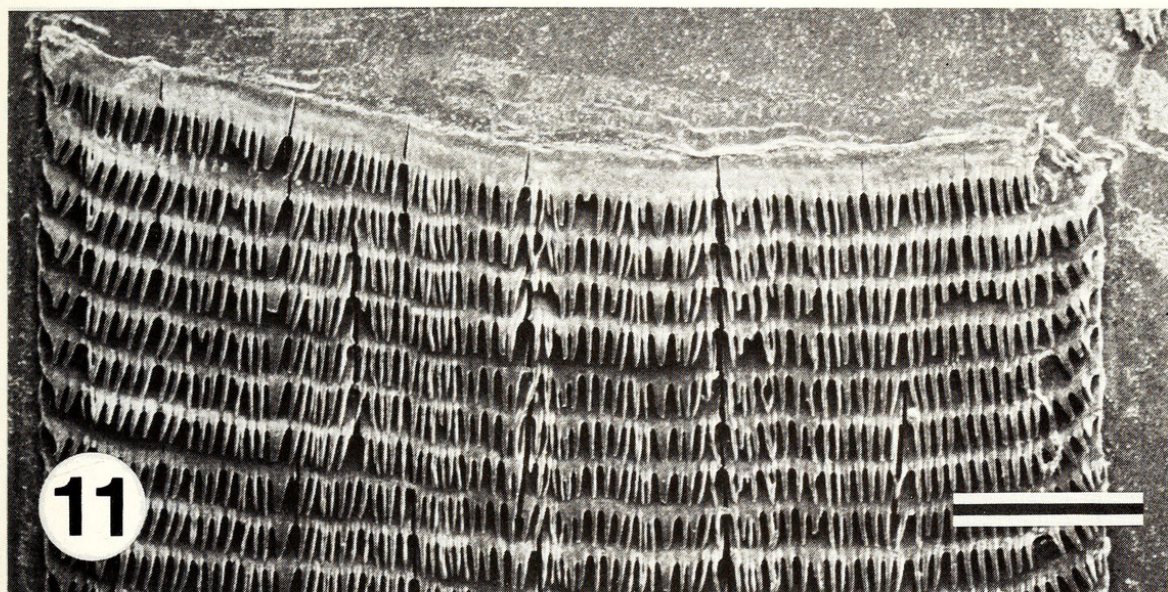
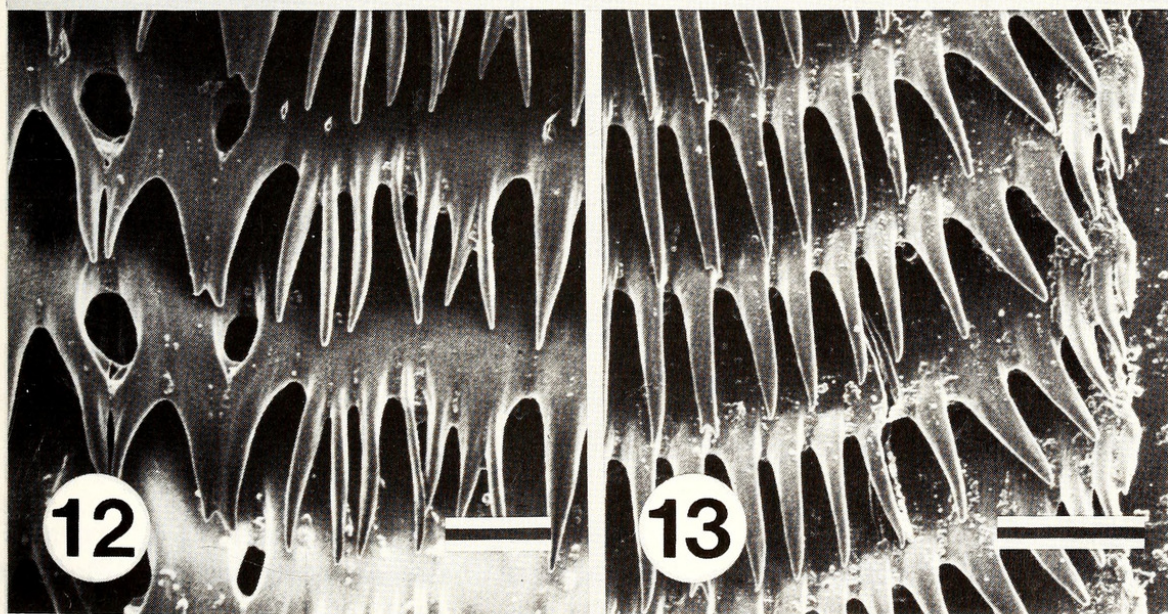
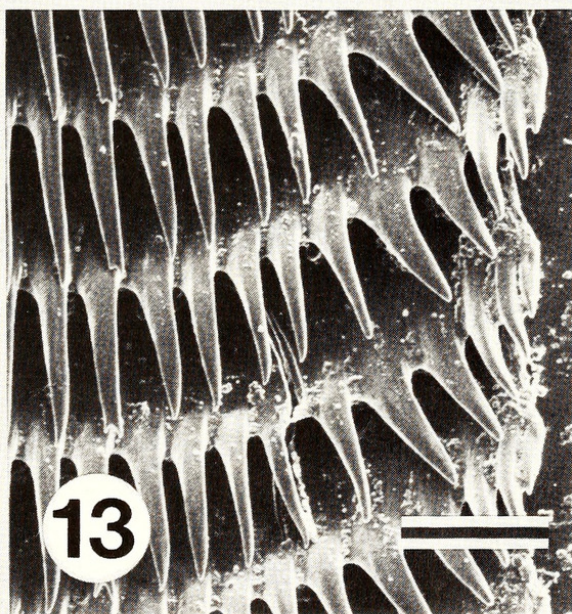
Figures 3-6. *Marginellona gigas* (Martens). 3. ZIN 44141, E. of Phan Thiet, Vietnam, South China Sea, 10°41'08"N, 109°53'08"E, in 495-500 m, ♂, 0.85 X. 4. ZIN 56353, E. of Phan Ly, Vietnam, South China Sea, 11°10'00"N, 110°10'00"E, in 1280-1000 m, mud, ♀, 0.85 X. 5. ZIN 45513, E. of Phan Ly, Vietnam, South China Sea, 11°09'06"N, 110°02'00"E, in 700 m, immature ♂, 0.85 X. 6. Protoconch of specimen in Fig. 5, 2.6 X.

c, parietal callus; cf, columellar fold; sf, siphonal fold; t, transition from protoconch to teleoconch.

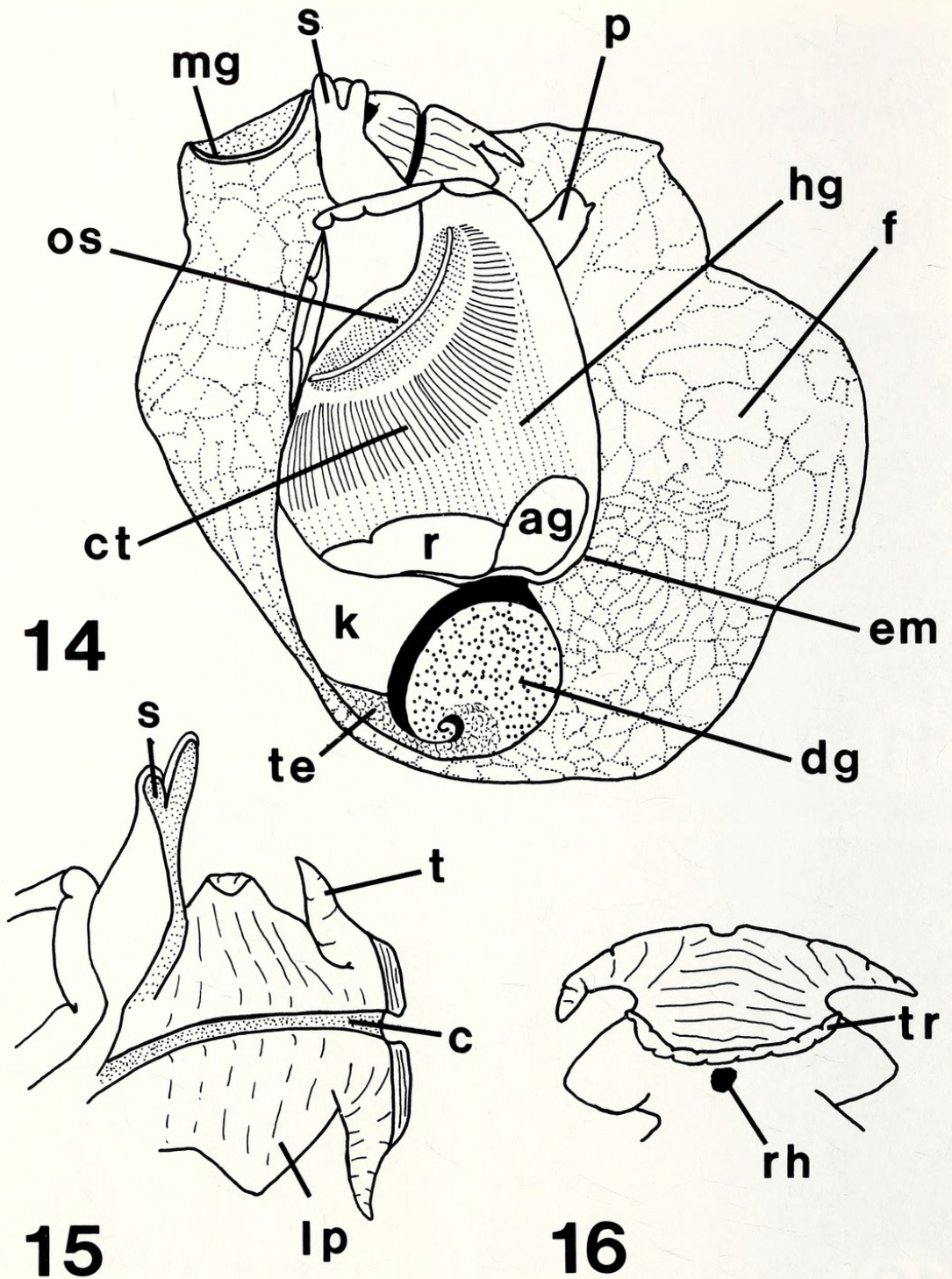


Figures 7-9. Shell ultrastructure of *Marginellona gigas*. 7. Fracture surface parallel to growing edge, $\frac{1}{4}$ whorl behind aperture, circled region in Fig. 3. Scale bar = 50 μm . 8. Enlargement, showing outer surface of shell. Scale bar = 20 μm . 9. Enlargement, showing inner surface of shell. Scale bar = 20 μm .

c, colabrally oriented crossed lamellar crystals; i, innermost layer of simple prismatic crystals; o, outermost layer of simple prismatic crystals; p, layer with crossed platy structure; t, transversely oriented crossed lamellar crystals.

**10****11****12****13**

Figures 10-13. Radular morphology. **10.** Radular tooth of holotype of *Marginellona gigas*, redrawn from Thiele (1904: pl. 9, fig. 64). Scale bar = 500 μm . **11-13.** Radula of specimen in Fig. 3. **11.** Distal end of radula. Scale bar = 500 μm . **12.** Region along central portion of tooth. Scale bar = 50 μm . **13.** Region along right margin of tooth. Scale bar = 100 μm .



Figures 14-16. External anatomical features of *Marginellona gigas*. 14. Shell-less animal from specimen in Fig. 3, dorsal view, 0.65 X. 15. Dorsal view of head, 1.0 X. 16. Ventral view of head, 1.0 X.

ag, anal gland; c, channel along mid-line of head; ct, ctenidium; dg, digestive gland; em, efferent margin of mantle cavity; f, foot; hg, hypobranchial gland; k, kidney; lp, lateral lappets; mg, anterior mucus gland; os, osphradium; p, penis; r, rectum; rh, rhynchostome; s, siphon; t, tentacle; te, testis; tr, transverse ridge.

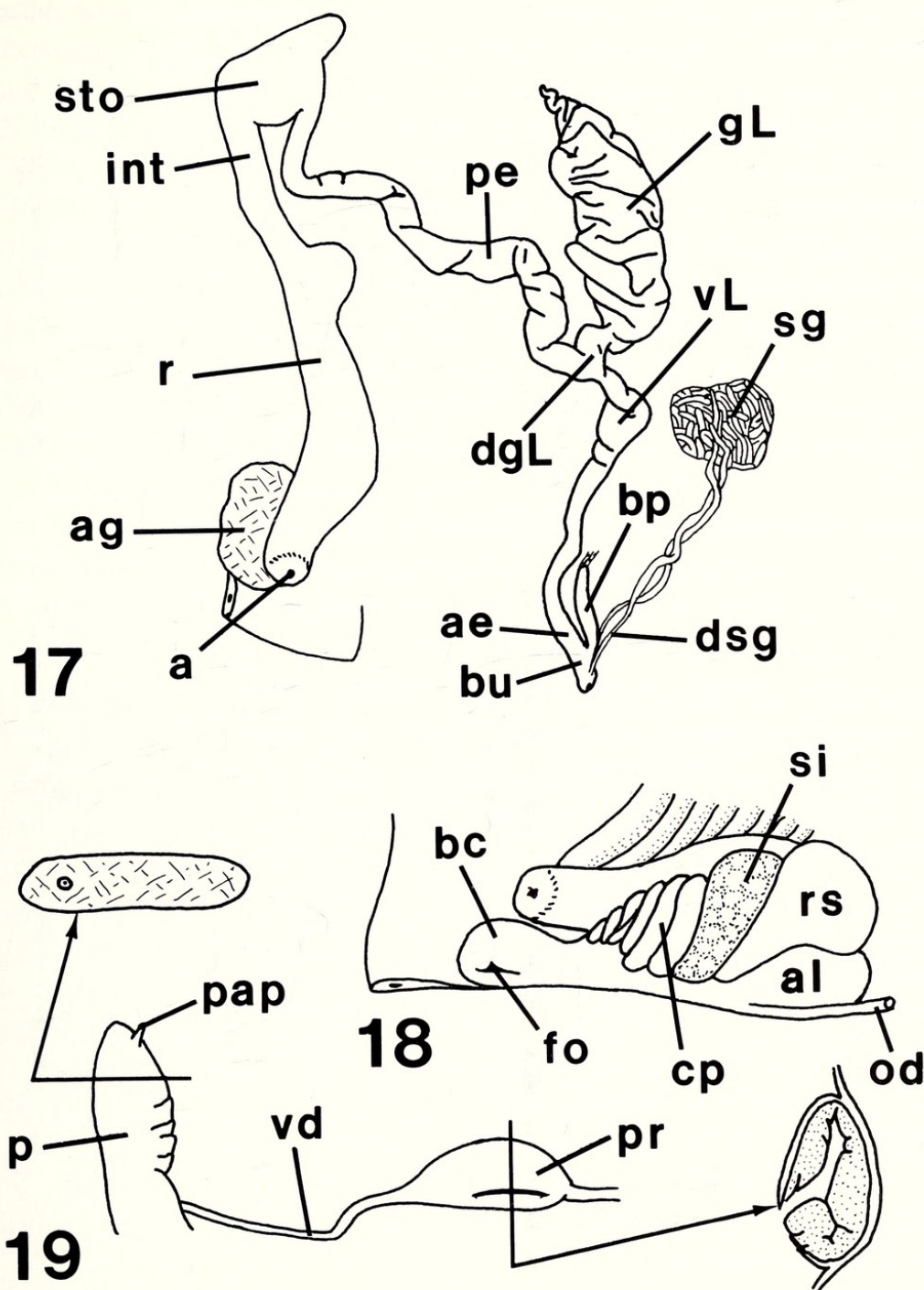


Figure 17-19. Anatomical features of *Marginellona gigas*. 17. Alimentary system, 0.66 X. 18. Female pallial oviduct, 1.1 X. 19. Male pallial gonoduct, 0.9 X.

a, anus; ae, anterior esophagus; ag, anal gland; al, albumen gland; bc, bursa copulatrix; bp, buccal pouch; bu, buccal cavity; cp, capsule gland; dgL, duct of gland of Leiblein; dsG, duct of salivary gland; fo, female opening; gL, gland of Leiblein; int, intestine; od, oviduct; p, penis; pap, penial papilla; pe, posterior esophagus; pr, prostate; r, rectum; rs, receptaculum seminis; sg, salivary glands; si, sperm ingesting gland; sto, stomach; vd, vas deferens; vL, valve of Leiblein.

Table 1. Measurements of shells and radulae of specimens of *Marginelona gigas* in Figs. 3-5. All measurements in mm.

Specimen in Figure no.	3	4	5
Shell length	157.0	68.3	37.2
Aperture length	109.9	51.6	30.7
No. protoconch whorls	2 $\frac{1}{3}$	2 $\frac{1}{4}$	2 $\frac{1}{3}$
No. teleoconch whorls	2 $\frac{3}{4}$	1 $\frac{3}{4}$	1 $\frac{1}{16}$
Radula length	10.1	5.3	3.4
Radula width	2.5	1.6	1.0
No. rows teeth	80	56	44
No. cusps/tooth*	83-85	58-59	69-71

* Number varies among teeth within the same radula.

approximately $\frac{1}{2}$ whorl; kidney (Fig. 14, k) $\frac{1}{4}$ whorl; digestive gland (Fig. 14, dg) and testis (Fig. 14, te) 1 $\frac{3}{4}$ whorl. Foot (Fig. 14, f) extremely large ($\approx 1.2 \times$ aperture length), broad ($L/W \approx 1.0$), with deep medial indentation along anterior edge, tapering posteriorly. Anterior mucus gland (Fig. 14, mg) deep. Dorsal surface of foot uniformly colored in preserved specimens, rugose in large specimen, smoother in smaller specimens. Operculum absent. Sole of foot thin, glandular. Tentacle bases fused ventrally, producing deep, tubular channel along dorsal mid-line of head (Fig. 15, c). Ventral surface of head with transverse ridge (Fig. 16, tr) anterior to rhynchostome (Fig. 16, rh). Proximal region of head with large, triangular lateral lappets (Fig. 15, lp). Eyes absent. Tentacles (Fig. 15, t) long, laterally directed. Siphon (Figs. 14, 15, s) fused to head just left of posterior margin of mid-line channel. Siphon bifurcated in largest specimen, possibly due to injury; simple, tubular in smaller two specimens.

Mantle cavity: Mantle cavity spanning approximately $\frac{1}{2}$ whorl, with right side substantially foreshortened due to posterior displacement of its efferent margin (Fig. 14, em). Arrangement of mantle cavity organs as in generalized muricacean neogastropod (Ponder, 1973: fig. 5). Mantle edge thickened, smooth, particularly broad and thick along columellar margin. Osphradium (Fig. 14, os) dark greenish-brown, half as wide and $\frac{3}{4}$ as long as ctenidium (Fig. 14, ct). Hypobranchial gland (Fig. 14, hg) of parallel, deep, pendent folds. Pallial gonoduct and rectum short. Anal gland (Figs. 14, 17, a) large.

Alimentary system: Proboscis short, broad, pleurembolic, extending through rhynchostome (Fig. 16, rh) at base of head. Proboscis retractor muscles attached to dorsal and left walls of asymmetrical cephalic hemocoel. Mouth large, leading to buccal cavity (Fig. 17, bu). Buccal cavity joined dorsally by anterior esophagus (Fig. 17, ae), ventrally by buccal pouch (Fig. 17, bp). Buccal pouch, containing buccal mass, extending nearly to rear of retracted proboscis. Radula (Figs. 11-13, Table 1) short (3-10 mm), broad (1.0-2.5 mm), uniserial, with 44-80 asymmetrical teeth. Teeth comb-like, with slightly curved basal plates that give rise to numerous (58-85) short cusps. Cusps shorter at margins (Fig. 13), irregular in thickness and occasionally fused along central portions of teeth (Fig. 12). Anterior esophagus thin, muscular, extending from buccal pouch to large, muscular valve of Leiblein (Fig. 17, vL). Posterior to valve of Leiblein, esophagus doubling in diameter and becoming sacculate, further expanding posterior to duct from gland of Leiblein before constricting to original diameter at rear of cephalic hemocoel. Gland of Leiblein (Fig. 17, gL) dark brown, extremely large, sacculate, broad anteriorly, tapering posteriorly, with large central lumen, joined to mid-esophagus posterior to nerve ring by thick, glandular stalk with narrow duct (Fig. 17, dgL). Salivary glands (Fig. 17, sg) paired, composed of extremely long, highly convoluted and intertwined tubules, situated dorsal to the gland of Leiblein in expanded right anterior portion of cephalic hemocoel. Ducts of salivary glands (Fig. 17, dsG) running anteriorly along floor of proboscis, emptying into buccal cavity laterally. Posterior esophagus reflected dorsally before joining stomach (Fig. 17, sto). Stomach simple, sack-like, with ducts from digestive gland joining to form single broad opening. Intestine (Fig. 17, int) short, narrow, running anteriorly from stomach to form rectum (Fig. 17, r). Rectum more than doubled in diameter alongside kidney, expanding further upon entering mantle cavity. Anal gland (Fig. 17, ag) extremely large, cavernous in large male, disproportionally smaller in smaller specimens, spanning the pallial portion of the rectum, entering rectum by single duct near anus.

Female reproductive system: [Only a single, poorly preserved pallial oviduct was available for examination. The functions of the two glandular structures between the capsule and albumen glands are surmised on the basis of positional homologies with the pallial oviduct of *Volvarina taeniolata* Mörch, 1860 (Fretter, 1976: fig. 2A) and will require verification when additional specimens become available.] Oviduct (Fig. 18, od) joining albumen gland (Fig. 18, al) at rear of mantle cavity. Pallial oviduct joined by sperm ingesting gland (?) (Fig. 18, si), seminal receptacle (?) (Fig. 18, rs) before expanding into broad capsule gland

(Fig. 18, cp). Bursa copulatrix (Fig. 18, bc) large, situated ventral to anus. Female opening (Fig. 18, fo) along lateral wall of bursa copulatrix.

Male reproductive system: Testis large, tan colored, lining anteriormost $\frac{1}{3}$ of digestive gland, broadest adjacent to rear wall of kidney. Testicular duct convoluted along kidney, passing adjacent to pericardium before entering mantle cavity. Prostate (Fig. 19, pr) large, glandular, not joined to rectum by connective tissue, with slit-like opening extending along posterior $\frac{3}{5}$ of length. Vas deferens (Fig. 19, vd) descending abruptly, running anteriorly to base of penis, surrounded by layer of muscle beneath mantle floor. Penis (Fig. 19, p) long, broad, dorsoventrally compressed, with terminal papilla (Fig. 19, pap) along right distal edge.

Type Locality: W. of Sombrero Channel, Nicobar Islands, Indian Ocean, 07°48'N, 92°07'E, in 805 m, coarse sand.

Material examined: USNM 237018 [holotype *Sigaluta pratasensis*], 54.1 mm, USNM 637251 [paratype *S. pratasensis*] 61.1 mm, both from W. of Pratas Reef, South China Sea, 20°37'N, 115°43'E, in 380 m, gray mud and sand bottom, U.S.B.F. Albatross I, sta. 5301; ZIN 44141, E. of Phan Thiet, Vietnam, South China Sea, 10°41'08"N, 109°53'08"E, in 495-500 m, R/V Odessey, trawl no. 55, 1 male specimen, 157.0 mm; ZIN 45513, E. of Phan Ly, Vietnam, South China Sea, 11°09'06"N, 110°02'00"E, in 700 m, R/V Odessey, trawl no. 52, 1 immature male specimen, 37.2 mm; ZIN 56351, E. of Phan Thiet, Vietnam, South China Sea, 11°01'00"N, 109°55'00"E, in 460 m, mud, R/V Odessey, 2 shells, 98.5 mm, 106.9 mm; ZIN 56352, E. of Ba Ria, Vietnam, South China Sea, 10°40'08"N, 110°03'00"E, in 760-800 m, mud, R/V Odessey, 1 shell, 108.8 mm; ZIN 56353, E. of Phan Ly, Vietnam, South China Sea, 11°10'00"N, 110°10'00"E, in 1280-1000 m, mud, R/V Odessey, trawl no. 51, 1 female specimen, 68.3 mm.

Distribution: This species has been collected in the eastern Indian Ocean (Nicobar Islands) and on the upper continental slope along the western margin of the South China Sea. The bathymetric range is 380-1000 m, with a mean station depth ($n=7$) of 661 m.

Ecology: Little is known of the ecology of this species other than it inhabits substrates ranging from coarse sand to fine mud. Gut contents of three dissected specimens were not identifiable.

Remarks: *Marginellona gigas* is the largest known marginellid. The largest specimen of *Marginellona gigas* recorded in this study measures 157 mm in length, significantly larger than the published record size of 130.9 mm for *Afrivoluta pringlei* (Wagner & Abbott, 1990: 80-039).

DISCUSSION

The genus *Marginellona* and its type species *M. gigas* were described largely on the basis of anatomical and radular characters, supplemented with a shell description reconstructed from fragments of the unique holotype. *Sigaluta* and its type species *S. pratasensis*, on the other hand, were erected exclusively on features of shell morphology. The availability of preserved specimens in which the shell morphology matches that of *S. pratasensis* (compare Figs. 2 and 4), while the unusual morphologies of the radula (compare Figs. 10 and 11), head, and external anatomy agree with published descriptions of these features in *M. gigas* (Martens, 1904: 109; Thiele, 1904: 170; 1929: 356) leaves little doubt of the synonymy of these two species and the nominal genera based upon them.

Martens (1904: 109) and Thiele (1904: 170; 1929: 356) noted the similarities of *M. gigas* to certain volutids, especially in features of the head and columellar folds, but both authors included this taxon in Marginellidae on the basis of radular morphology, absence of operculum, polished shell surface and glazed suture. Tomlin (1917: 268) disputed the inclusion of this taxon in Marginellidae, but did not offer an alternative familial placement. It is interesting to note that *Afrivoluta pringlei* (Tomlin, 1947), the only other species in the subfamily Marginelloninae, was also originally described as a volutid based on shell morphology. This genus and species were subsequently transferred to the Marginellidae when its radula was examined (Barnard, 1963).

In a survey of the literature dealing with anatomy of marginellids, we have identified a number of anatomical features of possible utility for phylogenetic inference (Table 2), and noted their distribution among the few taxa studied to date (Table 3). *Marginellona gigas* has several features that distinguish it from other marginellids, while possessing others that appear to be widespread in the family and may prove to be diagnostic of the Marginellidae.

As noted by Ponder (1970: 61), the fusion of the siphon to the left side of the head appears to be an adaptation for burrowing. This feature occurs in each of the three Recent marginellid subfamilies, and is likely symplesiomorphic within Marginellidae. A deep channel on the dorsal surface of the head, apparently formed by fusion of the ventral surfaces of the tentacle bases, occurs in *Marginellona*, and in several genera within Cystiscinae (Covert, 1987: 19-22). This feature has not been reported in *Afrivoluta* (Barnard, 1963; Liltved, 1985), but a similar cleft occurs in the volutid subfamilies Scaphellinae (Clench & Turner, 1964: 135), Athletinae (Woodward, 1900: 121) and Calliotectinae (Pace, 1902: 25). The lateral lappets on the proximal portion of the head of *Marginellona*

	Characters from Table 1														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Subfamily: Marginellinae Fleming, 1828															
<i>Prunum marginata</i> (Born 1778) (as <i>Marginella marginata</i>) ¹	1	0	0	0	0	0	0	1	1	2	1	?	?	?	0
<i>Marginella desjardini</i> (Marche-Marchad, 1957) ¹	0	0	0	1	1	?	1	1	0	2	1	2	?	?	0

Table 3. (continued)

Characters from Table 1

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
<i>Prunum martini</i> (Petit, 1853) (as <i>Marginella fraterculus</i>) E. A. Smith, 1915 ²	0	0	0	0	0	1	0	?	1	2	1	?	0	0	0
<i>Hyalina hyalina</i> (Thiele, 1913) ³	0	0	0	?	1	1	?	?	?	2	?	?	?	?	0
<i>Hyalina pallida</i> (Linné, 1758) ⁴	?	0	0	?	1	?	?	?	?	2	1	?	?	?	?
<i>Volvarina taeniolata</i> Mörch, 1960 ⁵	?	0	0	0	0	0	1	1	1	2	1	2	?	1	0
<i>Haloginella mustelina</i> (Angas, 1871) (as <i>Volvarina mustelina</i>) ⁶	1	0	0	0	0	1	1	0	0	2	0	2	0	1	0
<i>Dentimargo cairoma</i> (Brookes, 1924) (as <i>Volvarinella cairoma</i>) ⁶	1	0	0	1	1	1	1	1	0	2	1	3	1	0	1
<i>Mesoginella pygmaea</i> (Sowerby, 1846) ⁶	1	0	0	0	0	1	0	0	0	2	0	2	1	0	0
Subfamily: Cystiscinae Stimpson, 1865															
<i>Granula</i> sp. ⁶	1	1	0	0	0	1	1	0	0	1	1	1	1	0	0
Subfamily: Marginelloninae Coan, 1965															
<i>Marginellona gigas</i> (Martens) ⁸	1	1	1	0	0	1	0	0	0	0	0	2	0	0	0

¹Graham, 1966; ²Marcus & Marcus, 1968; ³Eales, 1923; ⁴Coan & Roth, 1976;
⁵Fretter, 1976; ⁶Ponder, 1970; ⁷Ponder, 1970, as *Diliculum* sp., see Coover, 1989: 13; ⁸herein.

and *Afrivoluta* (Barnard, 1963) appear to be restricted to the subfamily Marginelloninae within the Marginellidae, but are widespread throughout the family Volutidae.

The presence of a buccal caecum or pouch, which contains the buccal mass including odontophores and radula, with a sphincter at its opening to the buccal cavity is a feature unique to marginellids and toxoglossans (Fretter, 1976: 333). This structure may, however, be reduced or lost in aradulate species. Marginellid radular morphology has recently been reviewed by Coover (1989), who defined seven radular types. Although the loss of a radula is believed to be polyphyletic, all aradulate taxa known to date are in the subfamily Marginellinae.

Salivary glands within the family Marginellidae may be ascinous or tubular. Ascinous salivary glands appear to be uncommon and restricted to the subfamily Marginellinae. A single, medial accessory salivary gland has been reported in several marginelline and the only cystiscine taxon studied thus far.

Within the family Marginellidae, the reduction and loss of the valve of Leiblein appears to be correlated with the modification of the gland of Leiblein to form a long, tubular "poison gland" that empties, via a separate duct, into the buccal cavity. *Marginellona gigas*, which has a very large, ascinous gland of Leiblein that empties into the mid-esophagus posterior to the nerve ring, also has a very large and muscular valve of Leiblein. Progressive stages in the development of a duct from the gland of Leiblein that bypasses the valve of Leiblein have been documented by Ponder (1970; 1973: fig. 3, L-O). Those marginellid taxa that lack a valve of Leiblein all have a "poison gland" with a separate duct that empties into the buccal cavity. Two of three taxa with an esophageal caecum posterior to the nerve ring lack a valve of Leiblein. The third species, *Prunum martini*, was reported to have an "inconstant valve of Leiblein" based on a slight swelling of the esophagus observed in 3 of 5 specimens dissected (Marcus & Marcus, 1968: 65, as *Marginella fraterculus*).

The pallial oviduct of marginellids differs from that of most other neogastropods (Ponder, 1973: fig. 6) in having two glandular structures between the capsule and albumen glands. The male genital ducts agree in general respect with those of most other neogastropods, but exhibit infrafamilial variation in: position and size of prostate gland (rear of mantle cavity vs. in penis), type of opening to pallial cavity (duct or slit), and penis morphology (simple vs. bilobed).

Anatomical features of *Marginellona gigas*, including the presence of a buccal caecum, a uniserial radula with broad, comb-like rachidian teeth, a simple stomach with single, broad opening to the digestive gland,

a large rectal gland, and a pallial oviduct with separate ingesting gland and seminal receptacle, further support the original assignment of this taxon to the family Marginellidae. However, the relationship of the Marginelloninae to the Marginellinae and Cystiscinae remains unclear. Coover (1989: 30) suggested that Cystiscinae is the most primitive subfamily in Marginellidae, based on the occurrence of a triserial radula in a species tentatively ascribed to the genus *Cystiscus*. *Marginellona gigas* has an unspecialized alimentary system, containing a large gland of Leiblein without terminal bulb, as well as a large valve of Leiblein. These are primitive neogastropod features previously unrecorded in the Marginellidae. *Marginellona gigas* also lacks both the glandular duct that bypasses the valve of Leiblein, and the single accessory salivary gland that are present in Marginellinae and in the only species of Cystiscinae to be studied to date. Thus, the morphology of the anterior alimentary system suggests that Marginelloninae may be the most primitive subfamily in Marginellidae.

Although members of the Marginellidae share features with the Toxoglossa (buccal caecum, Fretter, 1976: 333), Volutomitridae (single accessory salivary gland, Ponder, 1973: 330) and Volutidae (furrowed head with lateral lappets, Martens, 1904: 109; Thiele, 1929: 356), we agree with Fretter, (1976: 335) that our knowledge of this family is, as yet, too scanty to deduce its sister group.

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FOOTNOTE

¹—Although the title page is dated 1903 and many earlier authors, including Thiele, had cited this date, the work was published in January, 1904 (see Bieler & Boss, 1989: 12).

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