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New Philippine Cancellariidae (Gastropoda: Cancellariacea), with Notes on the Fine Structure and Function of the Nematoglossan Radula

by

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Abstract. Three new species of Cancellariidae, *Cancellaria* ***boucheti***, *C.* ***atopodonta***, and *C.* ***aqualica***, are described, all from deep water off the western Philippines. The radula of two of these, *C.* ***boucheti*** and *C.* ***atopodonta***, are figured, and a mechanism by which the cusps are interlocked is described. On the basis of mechanical considerations, we suggest that the function of the nematoglossan radula is limited to the penetration of tissues of prey organisms, in order to reach the internal fluids on which the cancellariids then feed suctorially.

INTRODUCTION

THE THREE SPECIES of *Cancellaria* described herein were brought to our attention by Dr. Philippe Bouchet, Curator of Marine Mollusca, Muséum National d'Histoire Naturelle, Paris. Specimens were collected during the MUSORSTOM-2 cruise in 1980, aboard the R/V *Coriolis*, with Dr. Bouchet as expedition malacologist. Additional specimens of one species were located in the collections of the National Museum of Natural History, Smithsonian Institution. That three rather large, undescribed species could be collected near the Philippines is indicative of our incomplete knowledge of the deeper water faunas.

In keeping with our recent work, both published and unpublished, on cancellariid anatomy, we have here adopted a conservative stand by placing these new species in the genus *Cancellaria*, even though they represent rather distinct morphological forms previously placed in different genera or subgenera. Placement of these species into more appropriate genera must await our proposed revision of cancellariid supraspecific taxa after additional study of soft parts is possible.

Abbreviations for museum collections cited are: MNHN, Muséum National d'Histoire Naturelle, Paris; USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

SYSTEMATICS

Genus *Cancellaria* Lamarck, 1799

Cancellaria ***boucheti***
Petit & Harasewych, spec. nov.

(Figures 1–4, 9–14; Table 1)

Description: Shell large, reaching 47 mm, moderately thin, elongate-oval, with conical spire and rounded anterior. Protoconch of about 1½ inflated, glassy, amber-colored whorls, deviated from shell axis by 10–15°. Transition to teleoconch marked by rapid development of spiral sculpture (Figure 3). Teleoconch with up to 6⅔ strongly convex whorls. Suture deeply impressed. Surface sculpture of both spiral and axial elements, axial dominant in majority of specimens examined. Axial sculpture of 12–14 prosocline ribs on early whorls, 16–18 on body whorl of larger specimens. Ribs strong, evenly spaced, with narrow areas of weak, numerous ribs every ½ to ⅓ whorl indicating position of internal varices. Spiral sculpture of 15–18 major cords on body whorl, 7–8 on penultimate whorl, with 3–4 fine threads between adjacent cords. Aperture large, hemi-elliptical, deflected from coiling axis by 13–18°. Outer lip with shallow indentation at juncture of body whorl and short siphonal canal, containing 19–22

weak, recessed lirae that extend backward for several millimeters. Inner lip adpressed posteriorly, with two simple columellar folds and siphonal fold. Base color white, often with ginger along crests of axial and spiral sculpture. Some young specimens with broad patches of light ginger interrupted by white spiral bands along periphery and siphonal juncture. Aperture white. No specimens fractured or sectioned, as presence of internal varices (HARASEWYCH & PETIT, 1982) at intervals of 120–180° apparent in intact shells. Critical-point dried jaw (Figure 9) 2.5 mm long (4.8% shell length), furrowed along dorsal midline. Left and right margins overlapping ventrally along anterior portion of jaw (Figure 10), forming tube (about 75 μm in diameter) leading from oral tube to buccal mass. Posterior portion of jaw broad, covering the buccal mass dorsally and laterally. Radular teeth long, ribbonlike, tricusped. Central cusp simple, smooth, with ventrally recurved rim (Figures 11–13) and laterally expanded basal areas (Figure 14). Lateral cusps each with 4 complex, anteriorly directed secondary cusps (Figures 11–14).

Holotype: MNHN, 569–595 m, SE of Batangas, Luzon, Philippines (13°31′N, 121°24′E), Musorstom-2 sta. CP 36, L = 46.3 mm.

18 Paratypes: MNHN, 299–320 m, S of Batangas, Luzon, Philippines (13°49′N, 120°50′E), Musorstom-2 sta. CP 26, L = 34.4 mm; MNHN, 416–425 m, NW of Boac, Marinduque, Philippines (13°38′N, 121°43′E), Musorstom-2 sta. CP 49, L = 24.7 mm; MNHN, 300–330 m, off northwestern Mindoro, Philippines (13°51′N, 120°30′E), Musorstom-2 sta. CP 75, L = 26.5 mm, 36.6 mm, 39.2 mm; USNM 237060, 357 m, Tayabas Bay, off San Andreas, Philippines, U.S.B. Fish. sta. 5222, L = 37.7 mm; USNM 237580, 314 m, Batangas Bay, Luzon, Philippines U.S.B. Fish. sta. 5289, L = 32.0 mm; USNM 238191, 247 m, off Destacado Island, Philippines, U.S.B. Fish. sta. 5392, L = 46.0 mm; USNM 238675, off Opol, Mindanao, Philippines, U.S.B. Fish. sta. 5505, L = 29.1 mm; USNM 238902, 567 m, SE of Pt. Tanon, Cebu, Philippines, U.S.B. Fish. sta. 5535, L = 45.2 mm; USNM 242321, 247 m, off Destacado Island, Philippines, U.S.B. Fish sta. 5392, L = 20.0 mm, 34.6 mm, 37.8 mm; USNM 242323, 247 mm, off Destacado Island, Philippines, U.S.B. Fish. sta. 5392, L = 19.5 mm; USNM 278521, 311 m, off Matocot Pt., W. Luzon, Philippines, U.S.B. Fish. sta. 5268, L = 22.4 mm; USNM 281805, 247 m, off Adyagan Island, E. Masbate, Philippines, Bur. Fish. sta. 5392, L = 20.2 mm, 28.5 mm, 30.4 mm.

Comparisons: *Cancellaria* ***boucheti*** lacks the angled, nodose shoulder of *C. spengleriana* Deshayes, 1830, to which it is most closely related. *Cancellaria jonkeri* Koperberg, 1931, from the Tertiary of Timor, is also similar to this Recent species, but has much finer spiral and axial sculpture that does not form nodules at intersections.

Remarks: Cancellariid radular teeth become highly coiled during critical-point drying, the radular ribbon taking on the appearance of a plate of spaghetti. This process aids

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Explanation of Figures 1 to 8

Figure 1. *Cancellaria* ***boucheti*** spec. nov., holotype, MNHN, taken in 569–595 m, SE of Batangas, Luzon, Philippines (13°31′N, 121°24′E) Musorstom-2 sta. CP 36. 1.5×.

Figure 2. *Cancellaria* ***boucheti*** spec. nov., paratype, MNHN, taken in 299–320 m, S of Batangas, Luzon, Philippines (13°49′N, 120°50′E) Musorstom-2 sta. CP 26. 1.5×.

Figure 3. *Cancellaria* ***boucheti*** spec. nov., protoconch of paratype, USNM 242323, taken in 247 m, SW of Destacado Island, Philippines. U.S.B. Fish. sta. 5392. 70×.

Figure 4. *Cancellaria* ***boucheti*** spec. nov., paratype, USNM 238902, taken in 567 m, SE of Pt. Tanon, Cebu, Philippines. U.S.B. Fish. sta. 5535. 1.5×.

Figure 5. *Cancellaria* ***atopodonta*** spec. nov., holotype, MNHN, taken in 441–510 m, SSW of Batangas, Luzon, Philippines (13°49′N, 120°28′E) Musorstom-2 sta. CP 78. 2.5×.

Figure 6. *Cancellaria* ***atopodonta*** spec. nov., paratype, MNHN, taken in 300–330 m, off northwestern Mindoro, Philippines (13°51′N, 120°30′E) Musorstom-2 sta. CP 75, 2.5×.

Figure 7. *Cancellaria* ***aqualica*** spec. nov., holotype, MNHN, taken in 299–320 m, S of Batangas, Luzon, Philippines (13°49′N, 120°50′E) Musorstom-2 sta. CP 26, 1.5×.

Figure 8. *Cancellaria* ***aqualica*** spec. nov., paratype, MNHN, taken in 170–187 m, off the northwestern tip of Mindoro, Philippines (14°00′N, 120°17′E) Musorstom-2 sta. CP 51. 2.0×.

Explanation of Figures 9 to 14

Radula and jaw of *Cancellaria* ***boucheti*** spec. nov., taken from the specimen in Figure 2.

Figure 9. Lateral view of critical-point dried jaw. Scale bar = 500 μm.

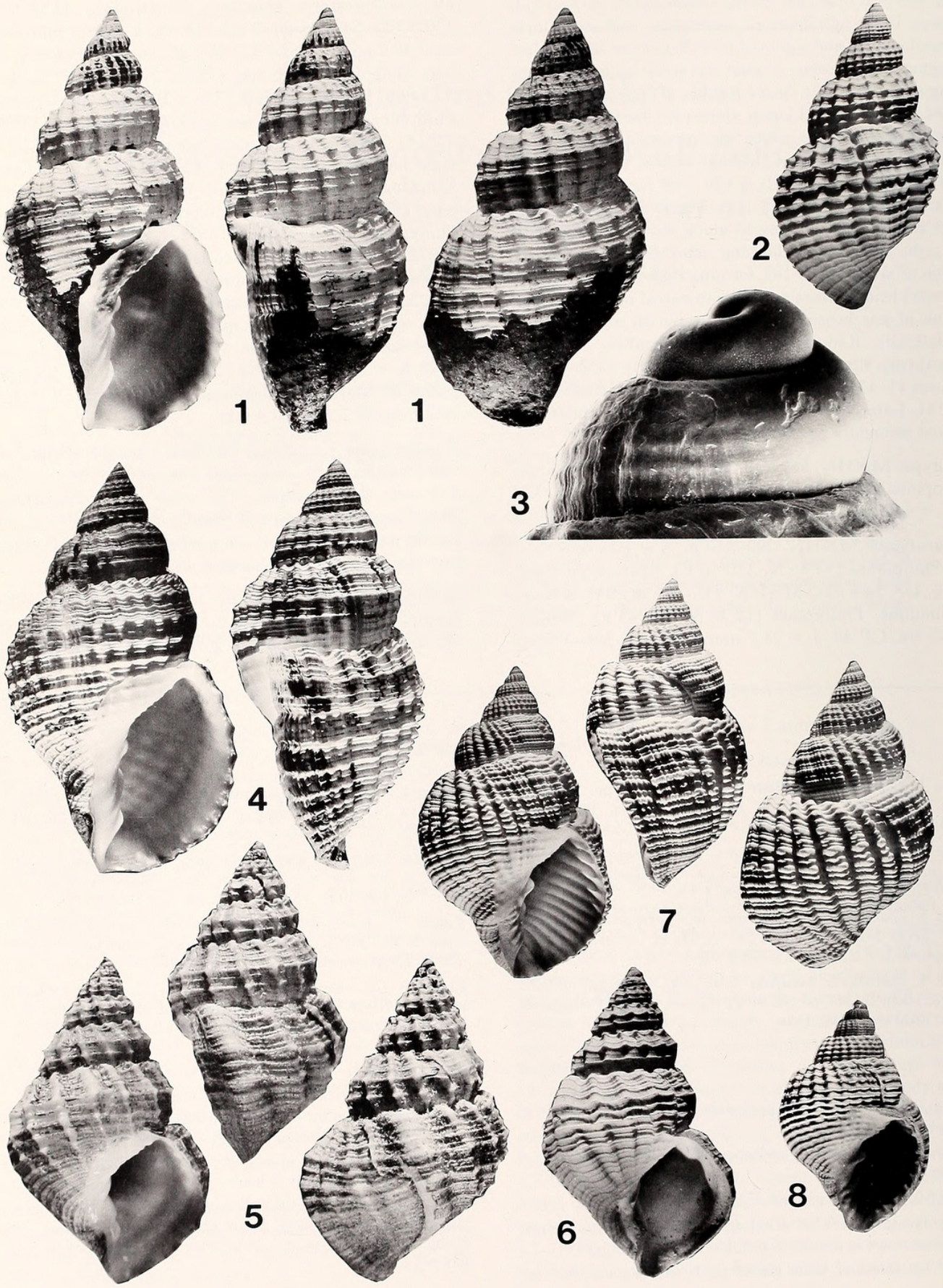
Figure 10. View of distal end of jaw. Scale bar = 25 μm.

Figure 11. Axial view of distal ends of radular teeth. Dorsal tooth with cusps in expanded position. Scale bar = 1 μm.

Figure 12. Detail of distal end of tooth. Stereo pair. The free end of the cusp on the left is locked under the rim of the central cusp. The cusp on the right is free. Scale bar = 1 μm.

Figure 13. Axial view of laterally expanded tooth. Both outer cusps are free. Scale bar = 1 μm.

Figure 14. Lateral view of teeth in Figures 11 and 12. The outer cusps of the ventral tooth are in the interlocked position. The visible cusp on the dorsal tooth is in the expanded position. Scale bar = 5 μm.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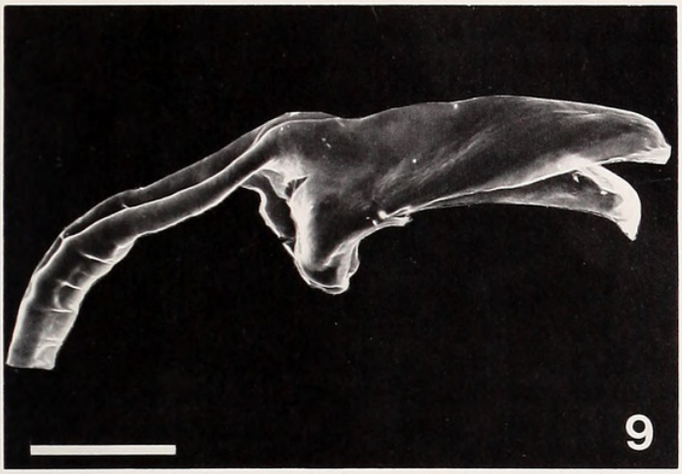
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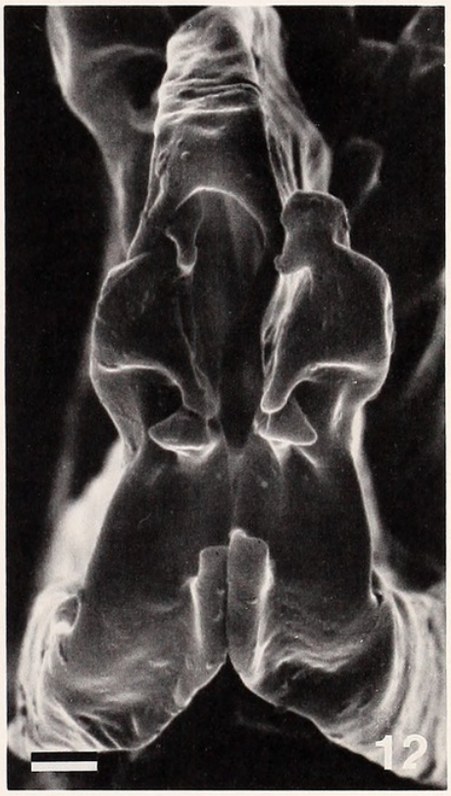
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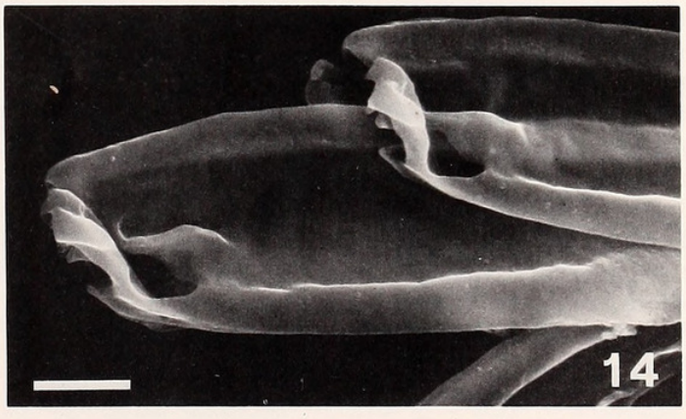
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Table 1

Cancellaria ***boucheti*** spec. nov. Measurements of shell characters. Linear measurements in mm. n = 10.

Character	Mean	Standard deviation	Range
Shell length	35.6	10.2	19.5–46.5
Shell width	19.6	4.9	10.8–24.5
Aperture length	20.7	6.2	11.2–29.3
Aperture length / Shell length	0.579	0.026	0.548–0.640
No. whorls, protoconch	1.53	0.24	1.33–2.00
No. whorls, teleoconch	5.53	0.65	4.67–6.67
Spire angle	53.0°	3.1°	48.5–59.0°

in the examination of the distal ends of the teeth, but makes accurate measurement of tooth length very difficult. Previous work has shown that the length of the tubular portion of the jaw approximates tooth length (Olsson, 1970; Harasewych & Petit, 1982, 1984). Both tooth length (about 1.1 mm) and tooth width (about 16 μm) are in the range reported for other cancellariids.

Etymology: This species honors Dr. Philippe Bouchet, of the Department of Malacology, Muséum National d'Histoire Naturelle, Paris, who brought this material to our attention.

Cancellaria ***atopodonta***
Petit & Harasewych, spec. nov.

(Figures 5, 6, 15, 16; Table 2)

Description: Shell small, reaching 22 mm, heavy, conispiral, with rounded anterior. Protoconch of 1¼ glossy, pitted whorls, slightly deflected from coiling axis. Transition to teleoconch marked by appearance first of spiral then axial sculpture. Teleoconch with up to 5⅔ convex whorls. Suture impressed. Axial ribs major sculptural feature, numbering 13–16 on body whorl, 10–13 on early whorls. Internal varices, first detected on outer surface of shell between 3rd and 4th postnuclear whorls, occur every 120° thereafter. Spiral sculpture of 10–13 major cords on body whorl, 3–4 on penultimate whorl, with 3–5 fine spiral threads between adjacent cords. Aperture ovate, deflected from coiling axis by 20–25°. Lack of shallow indentation marking juncture of siphonal canal on outer lip may be artifact, as all specimens heavily scarred by predators. Inner surface of outer lip with 9 or 10 strong, short lirae lining last internal varix. Inner lip adpressed posteriorly, with 2 simple columellar folds and siphonal fold. Shell white within and without. Internal structure not studied. Periostracum thin, yellow, finely lamellose, forming fine hairs along spiral threads. Intact jaw not recovered. Radular teeth long, ribbonlike. Central cusp with ventrally recurved rim and 2 dorsal, posteriorly recurved barbs (Figure 16). Thickening of basal areas (Figure 16) less pronounced than in preceding species. Lateral cusps distally expanded, each with 4 secondary, anteriorly directed cusps (Figures 15, 16).

Holotype: MNHN, 441–510 m, SSW of Batangas, Luzon, Philippines (13°49′N, 120°28′E) Musorstom-2 sta. CP 78, L = 21.5 mm.

2 Paratypes: MNHN, 300–330 m, off northwestern Mindoro, Philippines (13°51′N, 120°30′E) Musorstom-2 sta. CP 75, L = 20.6 mm, 20.8 mm.

Comparisons: This species differs so markedly from other described taxa that it is difficult to make comparisons. Its columellar structure is similar to that of *Cancellaria garrardi* (Petit, 1974), but the latter species has more rounded whorls and lacks a deep suture and a distinct shoulder. *Cancellaria* ***atopodonta*** most closely resembles the Japanese Pliocene shell figured as "*Cancellaria* (*Merica*) *reevei laticostata* (Löbbecke)" by Shuto (1962:72, pl. 13, fig. 12), which also has rounded whorls and lacks a pronounced shoulder. The names "*reevei*" and "*laticostata*" are incorrect spellings of *reeveana* Crosse, 1861, and *laticosta* Löbbecke, 1881, respectively, although neither of these names can, in our opinion, be correctly applied to the shell figured by Shuto. We have been unable to find an available name for this Japanese fossil.

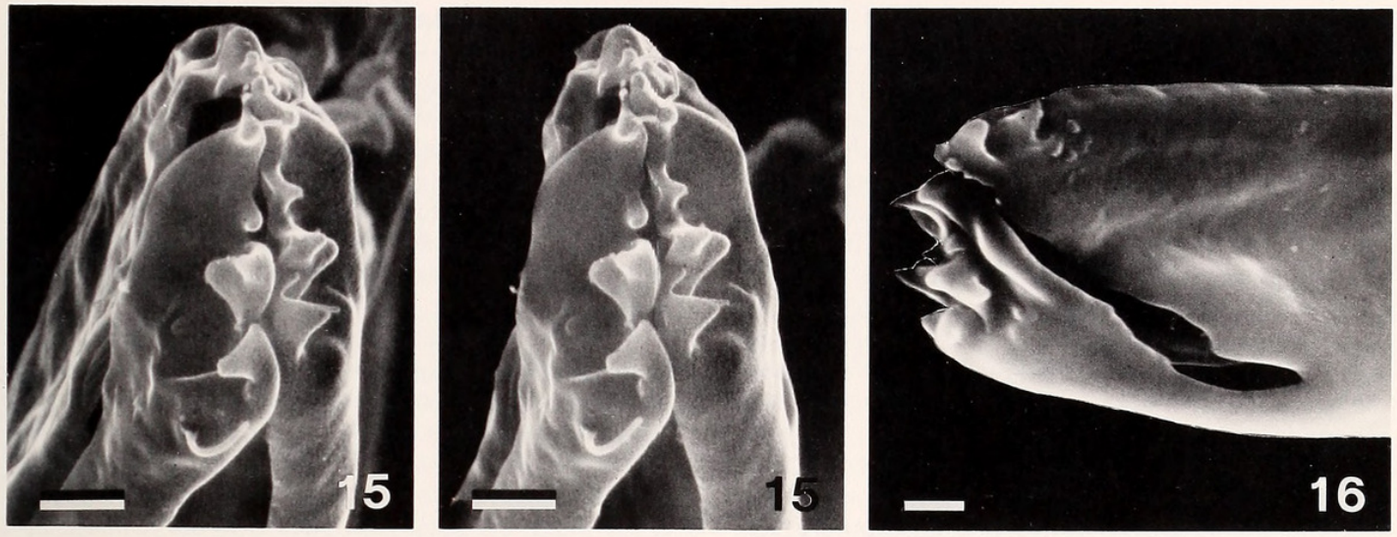
Remarks: The presence of recurved barbs on the central cusps of the radula of *Cancellaria* ***atopodonta***, a feature previously reported only from radulate species of Admetinae, suggests that such barbs are a primitive character, and were present in the common ancestor of all cancellariids. Such an interpretation implies that *C.* ***atopodonta*** is a primitive member of the lineage giving rise to the Cancellariinae and the Trigonostominae, as these barbs are absent in most species of these two "subfamilies."

Etymology: The specific name is derived from the Greek *atopos,* meaning anomalous or out of place, and the Greek *odontos,* meaning tooth, and refers to the unusual structure of the radular teeth.

Cancellaria ***aqualica***
Petit & Harasewych, spec. nov.

(Figures 7, 8; Table 3)

Description: Shell of moderate size, reaching 39 mm, heavy, biconic, pseudoumbilicate. Protoconch of 1 to 1⅓ whorls, smooth, glassy, slightly bulbous, deviated from shell axis by 10–15°. Transition to teleoconch evidenced by onset of spiral sculpture, followed within ¼ whorl by first appearance of axial ribs. Teleoconch with up to 6 strongly convex, highly sculptured whorls. Suture deeply impressed. Shell surface strongly cancellated by intersecting axial ribs and spiral cords. Axial sculpture of 14–16 prosocline ribs on early whorls, up to 19 on body whorl. Ribs strong, evenly spaced, becoming weak and more nu-



Explanation of Figures 15 and 16

Radula of *Cancellaria* ***atopodonta*** spec. nov., taken from the holotype.

Figure 15. Detail of distal end of tooth. Stereo pair. The free ends of both outer cusps are locked under the rim of the central cusp. Scale bar = 1 μm.

Figure 16. Lateral view of the same tooth as in Figure 15. The outer cusps are distally expanded. The central cusp has 2 dorsal barbs. Scale bar = 1 μm.

merous every 120°, giving appearance of single, broad rib marking location of broad internal varices. Spiral sculpture of 13–17 major cords on body whorl, 6–8 on penultimate whorl, with 1–3 fine threads between neighboring cords. Aperture large, hemi-elliptical, deflected from coiling axis by 18–25°. Outer lip with very shallow indentation posterior to siphonal canal and 11–13 strong, slightly recessed lirae extending ¼ whorl into aperture. Inner lip adpressed posteriorly, with 2 columellar and 1 siphonal fold. Folds simple, exhibiting periodic variation in size, reaching maximum extension into aperture in opposition to apertural lirae. Siphonal canal very short. Base color white, with light brown to ginger markings as in *Cancellaria reticulata* (see HARASEWYCH & PETIT, 1982). Aperture white. Soft parts and periostracum unknown.

Holotype: MNHN, 299–320 m, S of Batangas, Luzon, Philippines (13°49′N, 120°50′E) Musorstom-2 sta. CP 26, L = 34.0 mm.

3 Paratypes: MNHN, 326–330 m, WSW of Batangas, Luzon, Philippines (13°55′N, 120°29′E) Musorstom-2 sta. CP 15, L = 38.3 mm; MNHN, 170–187 m, off the northwestern tip of Mindoro, Philippines (14°00′N, 120°17′E) Musorstom-2 sta. CP 51, L = 15.7 mm, 19.5 mm.

Comparisons: *Cancellaria* ***aqualica*** most closely resembles *C. elegans* Sowerby, 1822, as figured by GARRARD (1975: fig. 1[1]), from which it may be distinguished by its stronger axial and spiral sculpture, its lack of color bands, and by having a more swollen body whorl.

Table 2

Cancellaria ***atopodonta*** spec. nov. Measurements of shell characters. Linear measurements in mm. n = 3.

Character	Mean	Standard deviation	Range
Shell length	21.0	0.6	20.4–21.6
Shell width	13.2	0.3	12.8–13.5
Aperture length	10.4	0.2	10.1–10.5
$\frac{\text{Aperture length}}{\text{Shell length}}$	0.494	0.016	0.485–0.512
No. whorls, protoconch	1.22	0.19	1.00–1.33
No. whorls, teleoconch	5.33	0.34	5.00–5.67
Spire angle	54.2°	0.8°	53.5–55.0°

Table 3

Cancellaria ***aqualica*** spec. nov. Measurements of shell characters. Linear measurements in mm. n = 4.

Character	Mean	Standard deviation	Range
Shell length	26.9	11.0	15.7–38.2
Shell width	16.8	6.3	10.0–23.1
Aperture length	14.8	5.6	9.2–20.4
$\frac{\text{Aperture length}}{\text{Shell length}}$	0.557	0.022	0.535–0.587
No. whorls, protoconch	1.16	0.19	1.00–1.33
No. whorls, teleoconch	5.08	0.92	4.00–6.00
Spire angle	62.0°	1.4°	60.0–63.0°

Remarks: Our concept of *Cancellaria elegans* does not agree with Garrard's interpretation. As mentioned by GARRARD (1975:4), the type lot (British Museum [Natural History] 1968387) contains 3 specimens. This lot is labelled "*C. elegans* Baclayon, Bohol. Id., Philippines" on the back of an old board. It is possible that two specimens with locality data were added later, as only one specimen has an old label with the number "4," the same sort as used by Sowerby, glued inside the aperture. In any event, the specimens in this lot are brown, with a brown protoconch, lack the white band present in many related species, and agree in all respects with the type figure. These specimens and the type figure have a finely cancellate sculpture that is quite distinct from the Australian species.

Although a color photograph of the holotype of *Cancellaria asprella* Lamarck, 1822, is available to us, we are unable to determine if *C. asprella* and *C. elegans* are conspecific, and this determination must await the opportunity to physically examine Lamarck's type. In any event, the specimens that we consider to represent *C. elegans* as well as the holotype of *C. asprella* have apertures that are ⅔ the total length of the shell, while *C.* ***aqualica*** has an aperture that is only ½ as long as the shell.

Etymology: From the Latin *aqualicus,* meaning belly or paunch, referring to the swollen body whorl of this species.

FUNCTIONAL MORPHOLOGY OF THE NEMATOGLOSSAN RADULA

Other than one anecdotal report of *Cancellaria crawfordiana* feeding on pieces of fish and egg capsules of squid and whelks (TALMADGE, 1972), there have been no published reports on the food or feeding of any cancellariid. Although examinations of the gut contents of a number of species have failed to uncover any identifiable traces of solid food (GRAHAM, 1966; HARASEWYCH & PETIT, 1982, 1984), several speculations as to the diet of cancellariids have been based on the unusual morphology of the anterior alimentary system, especially the radula (GRAHAM, 1966; OLSSON, 1970; OLIVER, 1982; HARASEWYCH & PETIT, 1982, 1984). Data presented in this paper on the morphology of the jaws and radulae of *Cancellaria* ***boucheti*** and *C.* ***atopodonta***, as well as figures of these organs of other cancellariids (OLSSON, 1970; OLIVER, 1982; Harasewych & PETIT, 1982, 1984), permit the following observations and inferences regarding their functional morphology.

Although the length of the teeth is extreme, the cancellariid radula is formed and functions as a normal radular ribbon, with teeth produced posteriorly and migrating anteriorly, contrary to OLSSON's (1970:21) suggestion that teeth are either added from the center of the ribbon and directed anteriorly or posteriorly, or are no longer added once the radula is fully formed. HARASEWYCH & PETIT (1982) observed several teeth in the process of being redirected from posterior to anterior. GRAHAM (1966) suggested that such redirection is accomplished by a change in the thickness and tension of the subradular membrane.

The majority of the cusps, both primary and secondary, on each tooth are directed anteriorly, parallel to the line of motion of the tooth rather than perpendicular to it, indicating a piercing or grappling rather than a rasping function for the radula. The extreme flexibility of the radular teeth limits their ability to transmit force. Like ribbons, they only transmit tensile and not compressive force.

Figure 12 reveals a mechanism by which the distal ends of the lateral cusps interlock under the recurved rim of the central cusp. The left cusp is shown in a locked position, the right cusp is free. Thickened areas on either side of the central cusp may serve to buttress the lateral cusps when they are in a locked position. When the radula is protruded, the distal-most tooth is in the compact, interlocked form. During the rasping motion, as each tooth slides posteriorly over the tooth ventral to it, its lateral cusps are pushed into the unlocked, laterally expanded position (Figures 11, 14) by the distal end of the tooth below. In the reverse action, the free distal end of each tooth passes under the next dorsal tooth, and the cusps are again compressed into an interlocked position. We suggest that this interlocking mechanism functions in the following manner. Each radular tooth is applied to the prey tissue in the compact, interlocked position, the anteriorly directed cusps impaling or entangling the tissue. The tissue is spread laterally when the cusps are pushed into the unlocked position by the next tooth, which repeats the action, penetrating deeper into the tissue. The length of the teeth and the tubular nature of the jaw make it unlikely that the cusped distal ends of the teeth can be retracted sufficiently to convey food to the esophageal opening, but instead suggest that their function is limited to the penetration of the tissues of prey organisms, or as suggested by TALMADGE (1972), of the walls of molluscan oothecae, in order to reach the internal fluids, on which the cancellariids then feed suctorially.

ACKNOWLEDGMENTS

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W. O. Cernohorsky, Auckland Institute and Museum, furnished us with a color photograph of the type of *Cancellaria asprella* Lamarck.

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