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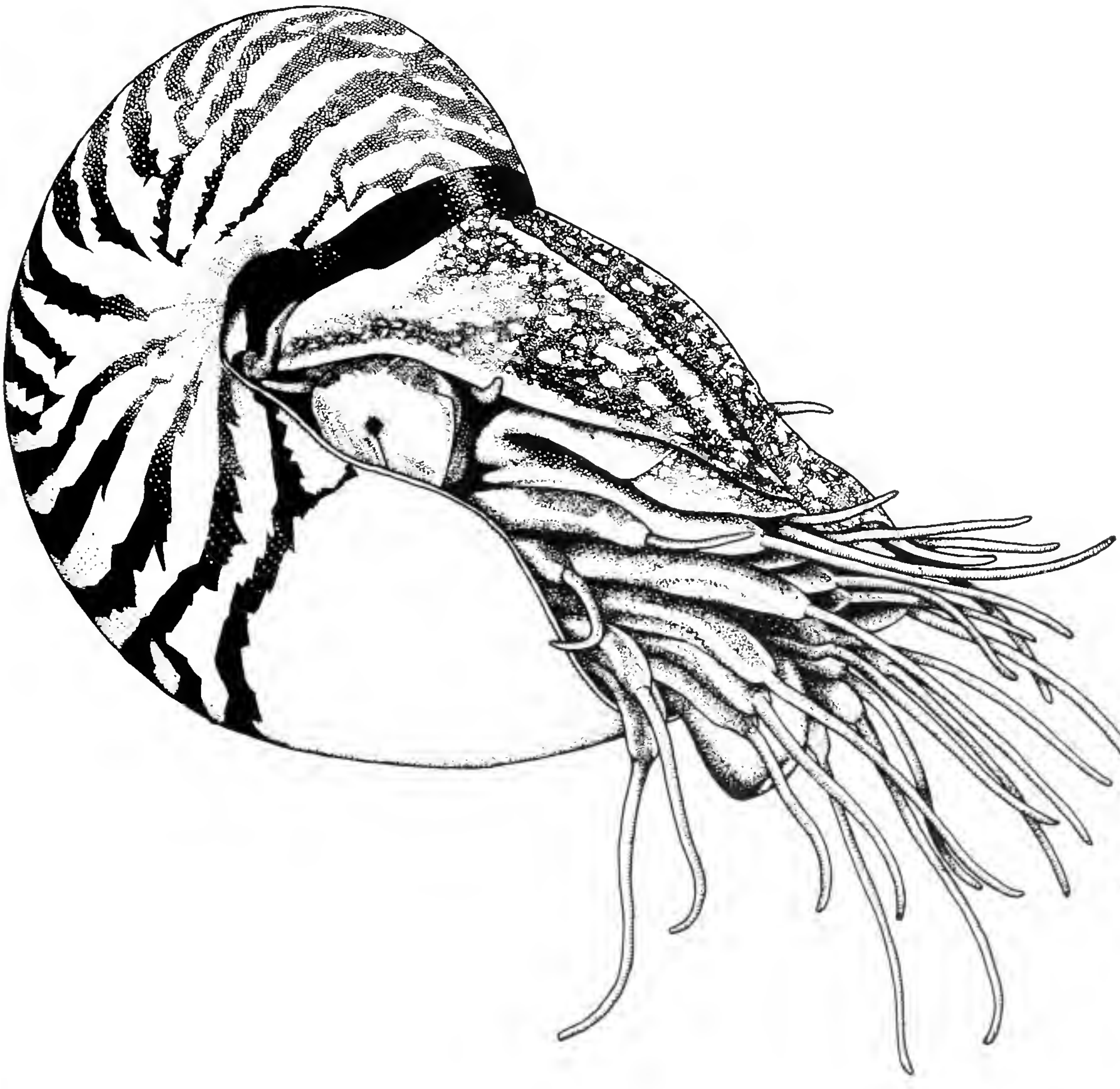

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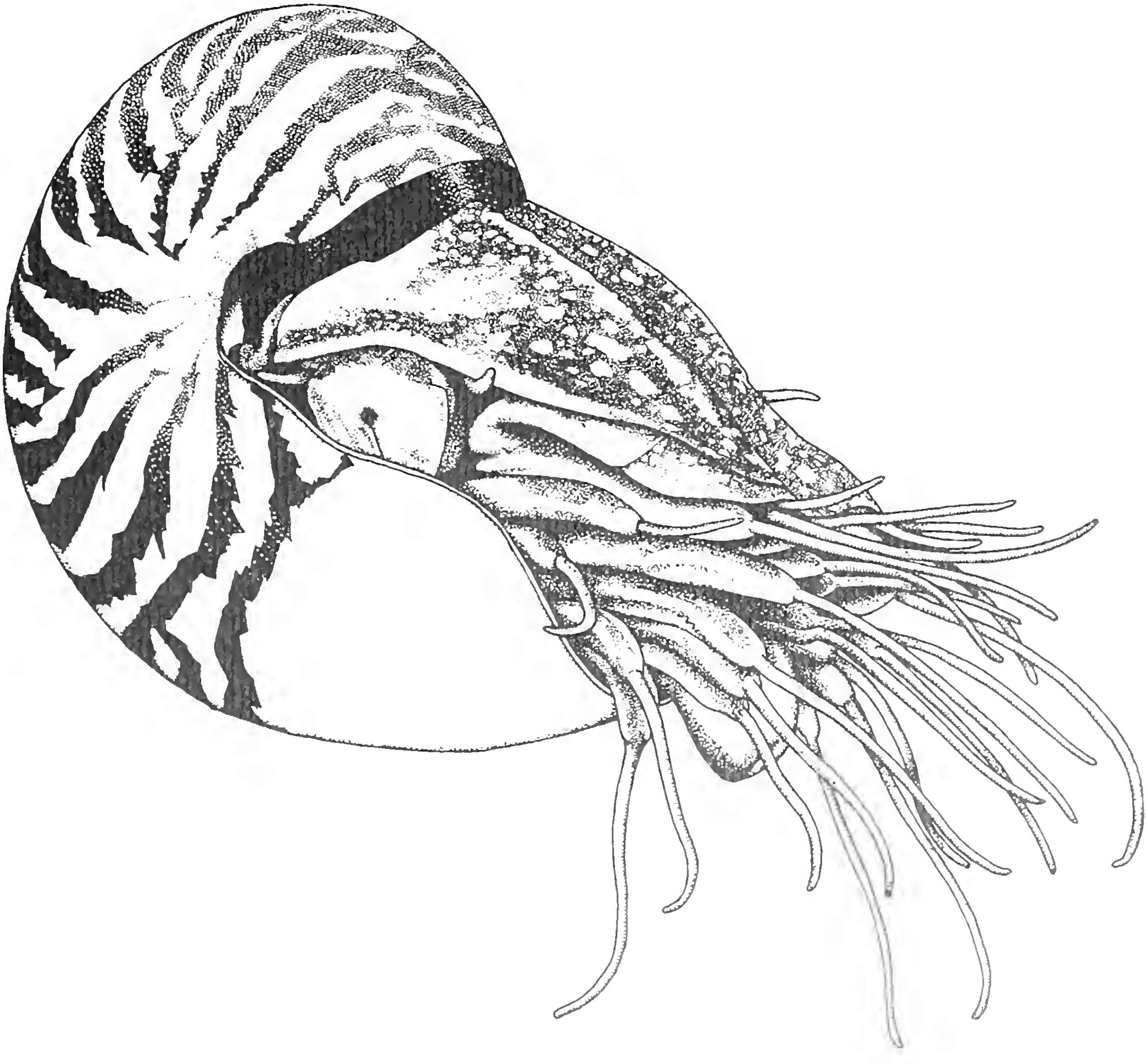

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New Deep-Water Volutidae from off Southeastern Brazil (Mollusca: Gastropoda)

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ABSTRACT

One new genus and three new deep-water species of the Volutidae are described from the southeastern Brazilian coast. According to accepted supraspecific classification of the Volutidae, anatomical characters, such as accessory salivary glands tightly wound around the primary salivary glands, allocate *Odontocymbiola simulatrix* new species, from the upper bathyal zone, to the subfamily Odontocymbiolinae. The rachidian teeth have characteristic "fang-like" cusps present in the genus *Odontocymbiola*. *Tractolira tenebrosa* new species, an upper abyssal species of which only dead shells are known, is conchologically related to the Antarctic species *T. germonae*, differing chiefly in protoconch morphology. The family Zidoninae is represented by the bathyal *Nanomelon viperinus* new genus, new species, which displays the loose association between the two types of salivary glands and opened sperm groove (running to the tip of the penis), diagnostic of the Zidoninae. However, its small, elongated, heavy shell, with strongly clathrate sculpture, the broad rachidian teeth with elongated, straight-edged cusps interlocking with the subsequent teeth, and a large rectal gland that branches anteriorly from a posterior duct are among the characters that differ considerably from those of other genera in the subfamily Zidoninae. An examination of the taxonomic literature on the Volutidae suggests the convergent or primitive nature of characters traditionally considered as diagnostic of the subfamilies Odontocymbiolinae and Zidoninae.

INTRODUCTION

Deep-water operations carried on by the research ship *Marion-Dufresne* in May, 1987, off the southeastern coast of Brazil, yielded 5 volutid species of the subfamilies Odontocymbiolinae and Zidoninae. Dead shells and living specimens were dredged or trawled in depths ranging from 200 to 3,270 m, in a transect conducted perpendicularly to the Brazilian coast, between 21° and 24°S. This material includes deep-water species already known to occur in this sector of the Atlantic, and three undescribed volutid species belonging to two subfamilies. Except for two tropical, shallow-water species of the subfamilies Volutinae (*Voluta ebraea* Linnaeus, 1758) and Lyriinae [[?]*Enaeta guildingii* (Sowerby, 1844)], all known volutids in the southwestern Atlantic belong to subfamilies Odontocymbiolinae and Zidoninae, including species living in the bathyal zone (Rios, 1985).

The subfamily Odontocymbiolinae was described to encompass volutids with "three prong or fang-like denticles" on the rachidian teeth and accessory salivary glands wrapped tightly around the salivary glands (Clench & Turner, 1964). Subsequent workers have provided additional information on radular and anatomical characters of other genera and species in this subfamily (Castellanos, 1970; Weaver & Dupont, 1970; Stuardo & Villarroel, 1974; Klappenbach, 1979; Harasewych, 1987). Based on the Recent distribution and almost complete restriction of the Odontocymbiolinae to the Southern Hemisphere, Harasewych (1987) has suggested that the subfamily evolved in the Weddelian Province after the separation of New Zealand at the end of the Early Paleocene. Three species from three genera of the Odontocymbiolinae were collected during the MD-55 Cruise: *Minicymbiola corderoi* (Carcelles, 1953), *Odontocymbiola simulatrix* new species, a species probably closely related to two temperate South Atlantic species [*O. magellanica* (Gmelin, 1791) and *O. subnodosa* (Leach, 1814)]. The third species collected during our survey, *Tractolira tenebrosa* new species, is an abyssal species probably related to *T. germonae* Harasewych, 1987 from the South Sandwich Islands, Scotia Sea, and from which it differs by conchological characters (only dead shells are known of the new species), particularly protoconch morphology.

The Zidoninae includes 9 living genera, three of which occur in the southwestern Atlantic Ocean. Clench and Turner (1964) characterized the Zidoninae as having uniserial radulae, rachidian teeth with three pointed cusps in one plane, two equal lobes at the base of the siphon, and tubular salivary glands loosely wound around moderately compacted salivary glands (see also Ponder, 1970;

Novelli & Novelli, 1982). The subfamily is represented in the deep-water material of the MD-55 cruise by *Adelomelon riosi* Clench & Turner, 1964, and by a new species that differs considerably in conchological, anatomical and radular characters from other genera in the subfamily. Consequently, a new genus, *Nanomelon* new genus, is here erected to accommodate it.

MATERIAL AND METHODS

Unless otherwise indicated, all material mentioned was obtained during the MD-55 cruise of the *Marion-Dufresne* by P. Bouchet, J. H. Leal, and B. Métivier, in May, 1987. Shells were fractured using a table vise, cleaned in full strength commercial bleach (Clorox) for 30 sec, rinsed in distilled water, and sonicated for the observation of shell ultrastructure. The following abbreviations are used: MNHN, Muséum National d'Histoire Naturelle, Paris, France; MNRJ, Museu Nacional, Rio de Janeiro, Brazil; MORG, Museu Oceanográfico de Rio Grande, Brazil.

DESCRIPTION

Family **Volutidae** Rafinesque, 1815
Subfamily **Odontocymbiolinae** Clench & Turner, 1964
Genus *Odontocymbiola* Clench & Turner, 1964

Odontocymbiola simulatrix new species
(figures 1, 2, 5, 6, 14, 19–21, 26, 27)

Shell (figures 1, 2, 5, 6, 14): Fusiform, reaching 111 mm in length and 41 mm in width. Spire elevated, spire angle about 43°. Earlier teleoconch whorls moderately solid, last whorl thinner and delicate. Shell surface rough and opaque. Periostracum grayish to dark-brown. Shell color cream to pale-orange with straight-edged spiral bands of interrupted, mahogany-brown spots. Three spiral bands in last whorl, one each at base, mid-whorl, and abapical to suture. Preceding whorls with only two bands, mid-whorl band partially occluded by subsequent whorl. Transition protoconch/teleoconch (figure 14) poorly defined. Protoconch (figure 14) smooth, with very fine microscopic spiral striae, with about 2.5 cream-colored whorls. Calcarella small, of slightly darker color. Teleoconch with about 7 whorls, all but last shouldered; concave sutural slope present in shouldered whorls. Suture moderately impressed. Axial ribs triangular in cross-section, stronger and fewer on earlier whorls (about 15 on the first, 23 on the third), changing into a pattern of ill-defined, numerous axial wrinkles (about 70) on last whorl. Spiral sculpture of 140–150 fine raised lines on last whorl, 30–40 on preceding whorls. Spiral lines of same width over teleoconch surface. Aperture elliptical (length/width about 3). Outer lip simple, thin, thinner in larger shells. Parietal region glazed. Glazed surface in larger individuals a thin spiral band adapical to suture of last whorl, as result of shell growth. Columella arched, with siphonal fold and 2–3 columellar plaits. Anterior canal wide, weakly defined. Inner shell surface smooth (see table 1 for shell measurements and whorl counts).

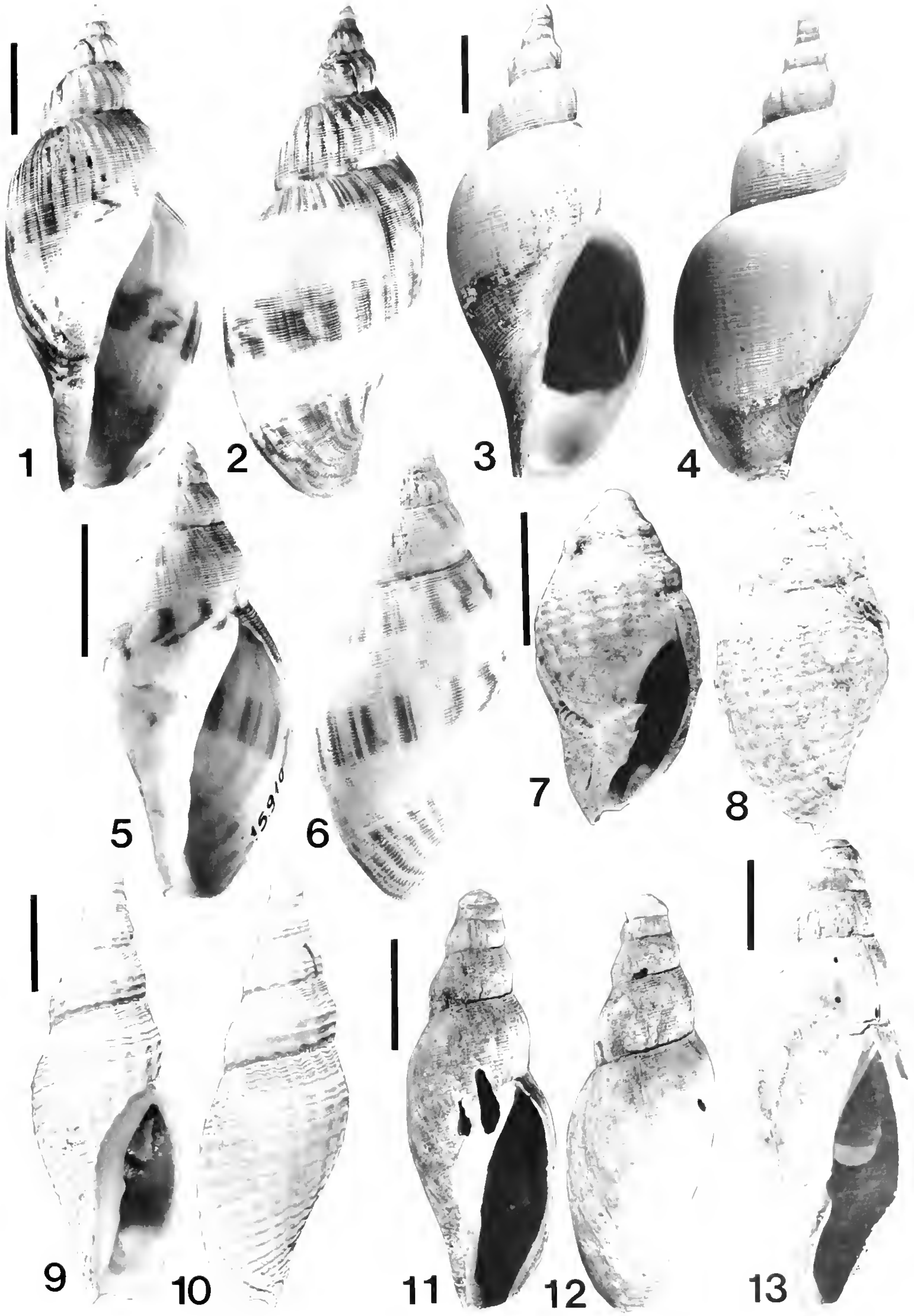
External morphology (figure 26): Living animal with overall light-orange to salmon coloration, foot sole cream-white. Coloration faded in preserved specimens. Head broad, flattened, with large central lobe and two large, semicircular lateral lobes posterior to tentacles. Tentacles tapered, pointed distally. Eyes present. Foot wide (length/width = 1.3, preserved holotype), pointed posteriorly, bilobed anteriorly. Aperture of mucous gland very large, extending slightly around lateral edges of foot. Mantle edge moderately thick. Siphon (si) large, muscular. Two siphonal appendages (lsa, rsa) of equal length, each about half length of siphon (preserved holotype). Siphonal appendages slightly flattened at distal extremity. Ctenidium (ct) leaf-shaped. Osphradium (os) bipectinate with pointed extremities (length/width = 3), ⅔ as long as ctenidium.

Anterior part of the alimentary system (figure 27): Proboscis pleurembolic. Salivary glands (sg) opaque-white, moderately compacted. Ducts of salivary glands (dg) long, opening into posterior part of buccal mass (bm). Accessory salivary glands (as) yellowish-white, ribbon-like, very narrow and long, tightly wound around salivary glands. Ducts of accessory salivary glands open-

Table 1. *Odontocymbiola simulatrix* new species. Linear shell measurements (mm) and whorl counts for the holotype (HOL) and paratypes 1–3 (PA 1–3). For localities see text.

Character	HOL	PA 1	PA 2	PA3
Total length	111.3	70.2	55.0	69.8
Shell width	43.6	29.1	23.2	28.1
Length last whorl	84.9	54.8	43.8	56.7
Aperture length	62.8	44.9	34.1	44.3
Aperture width	22.2	14.0	11.0	15.2
Protoconch diameter	5.0	4.1	4.0	4.0
Teleoconch whorls	7.0	5.0	3.5	5.5
Protoconch whorls	2.5	2.0	2.5	2.5
Length/width	2.55	2.41	2.39	2.48
Aperture length/length	0.56	0.64	0.62	0.63
Aperture length/ap width	2.83	3.21	3.09	2.91

Figures 1, 2. *Odontocymbiola simulatrix* new species. Holotype, 111.3 mm length, 43.6 mm width. **Figures 3, 4.** *Adelomelon riosi* Clench & Turner, 1964. 134 mm length, 54 mm width, off Espírito Santo State, 19°36'S, 38°53'W, 640 m depth. **Figures 5, 6.** *Odontocymbiola simulatrix* new species. Paratype 3, 69.8 mm length, 28.1 mm width. Scale bars = 20 mm. **Figures 7, 8.** *Minicymbiola corderoi* (Carcelles, 1953). 21.5 mm length, 11.1 mm width, off Rio de Janeiro State, 23°36'S, 42°02'W, 200–217 m depth. **Figures 9, 10.** *Nanomelon viperinus* new genus, new species. Holotype, 44.2 mm length, 15.3 mm width. **Figures 11–13.** *Tractolira tenebrosa* new species. **11, 12.** Holotype, 38.3 mm length, 13.8 mm width. **13.** Paratype 2, 41.9 mm length, 15.3 mm width. Scale bars = 10 mm.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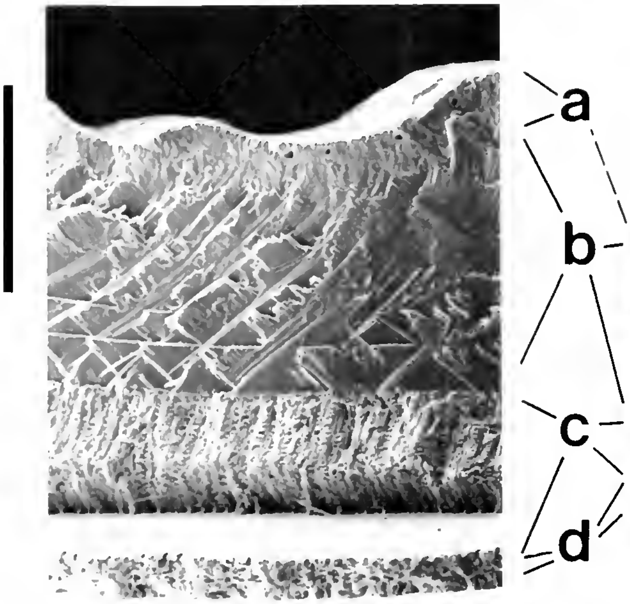

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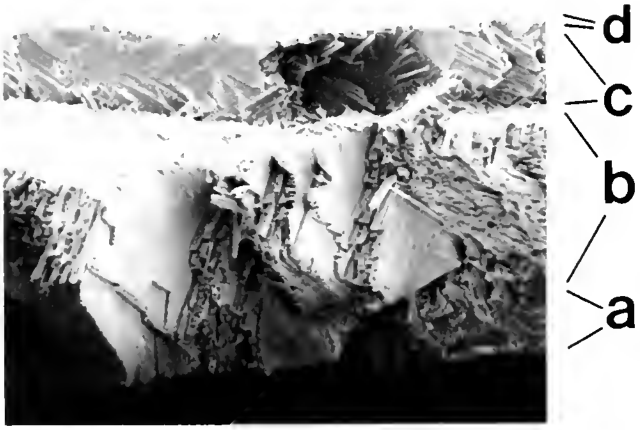

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ing into anteriormost region of buccal mass. Gland of Leiblein (gl) long, convoluted, opening into oesophagus just posteriorly to circumoesophageal nerve ring and valve of Leiblein (vl). Stomach (st) with anterior tubular region (ts).

Radula (figures 19–21): Radular ribbon (figure 19) uniserial, relatively short (length = 19.6 mm, length width = 24.5, holotype), with about 45 tricuspid rachidian teeth (figure 20), each 0.8 mm wide. Basal plate flattened, chevron-shaped, excavated posteriorly in surface in contact with ribbon. Central cusp at least 1.5 times longer than and 2 times wider than lateral cusps. Central and lateral cusps deeply curved, "fang-like". Central cusp rising from anterior edge of basal plate, pointing posteriorly. Central cusp with very sharp, thin lateral edges and with two, deep lateral longitudinal grooves, giving origin to long, dorsal rib narrower than central cusp. Lateral cusps deeply grooved ventrally (figure 21).

Holotype: MORG 25467, 111.3 mm length, 43.6 mm width, MD-55 station CP-11 (Beam trawl), off Rio de Janeiro State, Brazil (collected alive).

Type locality: Continental slope off the coast of Rio de Janeiro State, Brazil, 21°35′S, 40°06′W, at 248 m depth, muddy bottom.

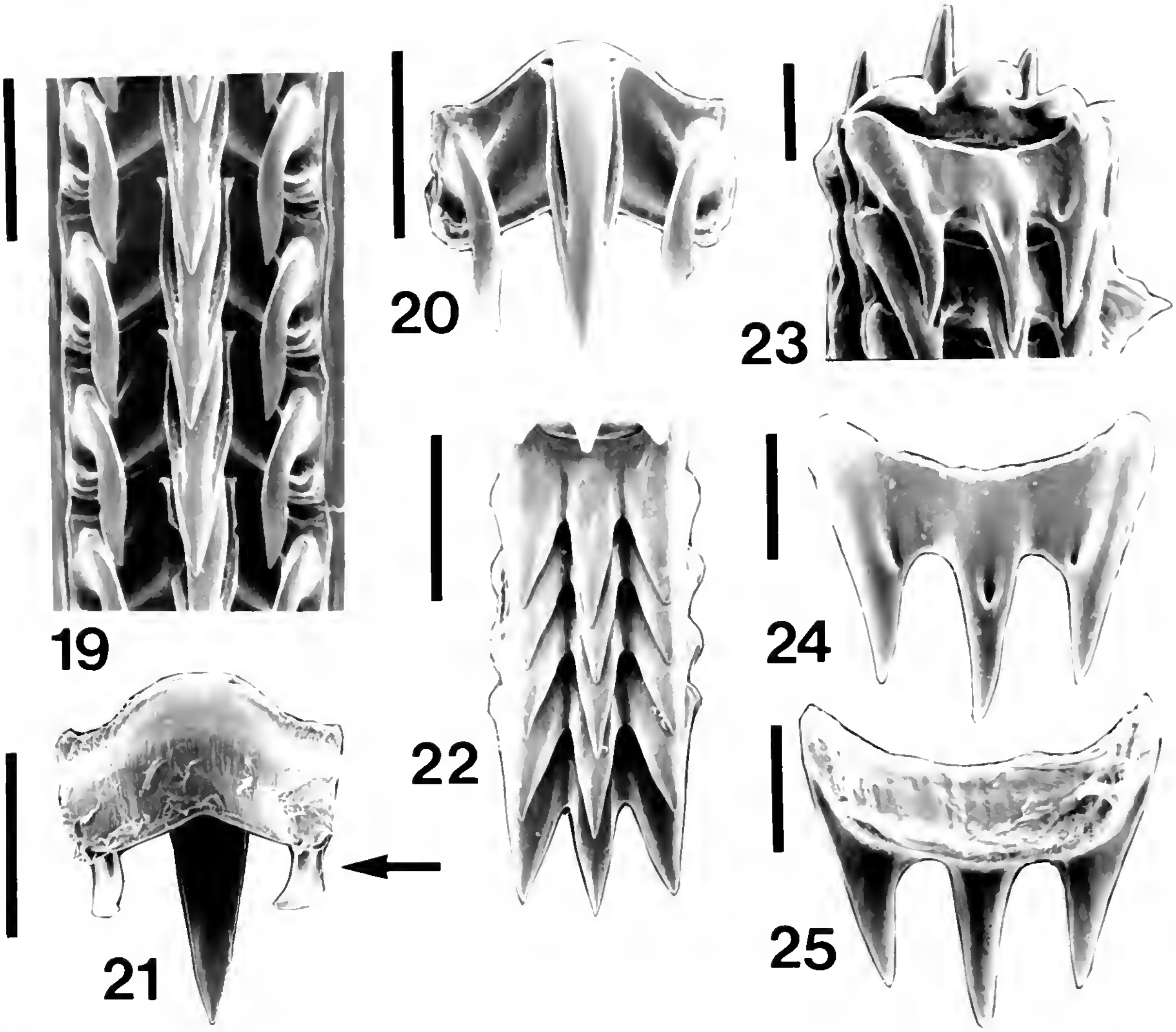
Paratypes: Paratype 1, MNHN, 70 mm length, 29 mm width; Paratype 2, MNHN, 55 mm length, 23 mm width, MD-55 station CB-104 (Blake trawl), 23°42′S, 42°07′W, 430–450 m depth, muddy bottom; Paratype 3, MORG 15910, R/V *Mestre Jerônimo*, off Ilha de Santa Catarina, 28°03′S, 48°11′W, 113 m depth, 07/1971.

Other material examined: One juvenile shell + 1 broken shell, station CB-104 (Blake trawl) (same localities as Paratypes 1 and 2).

Remarks: One dead shell of *O. simulatrix* (Paratype 3, MORG 15910) had been collected off southern Brazil in 1971, and had been recognized as an unidentified volutid. *Odontocymbiola simulatrix* differs from the other five known species of the subfamily in size, shell sculpture, coloration, and radular structure. It can be set apart from *Minicymbiola corderoi* (Carcelles, 1953) by its color pattern of spirally arranged brown spots, larger size (*corderoi* reaches 28 mm, according to Rios, 1985), less prominent sculpture and larger, slender shell with higher spire (compare figures 1, 2, 5, and 6 with 7 and 8). The congeneric *Odontocymbiola americana* (Reeve, 1856), is smaller, has a shorter spire, a smoother shell surface, smaller number of axial ribs, more pronounced shoulders, thicker outer lip, lacks a calcarella at the protoconch apex, and has a more elaborate, delicate color pattern. *Odontocymbiola simulatrix* differs from *O. subnodosa* (Leach, 1814), *O. magellanica* (Gmelin, 1791), and *O. pescalia* Clench & Turner, 1964, by its more elongated shape, narrower aperture, presence of a well-defined spiral color pattern, smaller parietal region, stronger axial and spiral sculpture, and weaker columellar folds. *Odontocymbiola simulatrix* has a radula characteristic of the genus, with "fang-like", deeply curved cusps in the rachidian. However, the rachidian in the new species (figures 20, 21) lacks the extremely elongated central cusp and the blunt extremities of the lateral cusps as in *O. americana*. The lateral edges of the central and lateral cusps are not as sinuated as those of *O. pescalia*, and the basal plate lacks the rounded lateral expansions present in *O. magellanica* (see Clench & Turner, 1964; Weaver & Dupont, 1970; Kaiser, 1977 for descriptions and illustrations of the mentioned species).

Although the soft parts of only one female individual of *O. simulatrix* were examined, the few characters derived from external anatomy (figure 26), alimentary system (figure 27), and radula (figures 19–21) are sufficient to allow subfamilial and generic placement. The long, equal siphonal appendages, very elongated accessory salivary glands, tightly wound around rather compacted salivary glands, a stomach with an elongated anterior section, and the curved, elongated, and basally broadly separated, "prong or fang-like" cusps of the radular teeth are usually accepted as derived characters defining Odontocymbiolinae (see Clench & Turner, 1964; Stuardo & Villarroel, 1974; Harasewych, 1987). The extremely narrow ("fang-like"), elongated, and intricately sculptured cusps "which extend at a right angle from the basal plate and then curve downwards" (Clench & Turner, 1964) are here conditionally considered as the character set that defines the genus *Odontocymbiola*, as opposed to the "prong-like" cusps present in the genus *Miomelon* and *Tractolira* (Harasewych, 1987). Klappenbach (1979), using only shell dimensions and sculpture, has erected the monotypic genus *Minicymbiola* for *Marginella corderoi* Carcelles, 1953. The radular morphology illustrated in the original description of *Minicymbiola* indicates that *M. corderoi* complies with the definition of the genus *Odontocymbiola* by Clench and Turner (1964). Notwithstanding, we conditionally consider *Minicymbiola* to be a valid genus, though only a thorough study of other anatomical characters in the species could corroborate the validity of the extremely divergent shell characters (see figures 7, 8) in the foundation of the genus. As observed in the SEM micrographs of the rachidian in *O. simulatrix*, and in *camera lucida* drawings for the

Figure 14. *Odontocymbiola simulatrix* new species. Protoconch. **Figures 15–18.** *Nanomelon viperinus* new species. **15.** Protoconch. **16–18.** Shell ultrastructure. **16.** Collabral cross-section of last half of last whorl. a, external crossed-lamellar layer; b, middle crossed-lamellar layer; c, third crossed-lamellar layer; d, internal prismatic layer. **17.** Cross-section of third teleoconch whorl at 45° to shell axis; change of orientation of first order lamellae (middle crossed-lamellar layer, b) conforms to whorl curvature. Dashed line indicates that external crossed-lamellar layer (a) is absent. **18.** Cross-section of third teleoconch whorl, approximately perpendicular to shell axis; notice perpendicular relationship between first order lamellae of middle (b) and third (c) crossed-lamellar layers, and very thin internal prismatic layer (d). Scale bars, protoconchs = 1 mm, ultrastructure = 0.50 mm.



Figures 19–21. *Odontocymbiola simulatrix* new species. Radular teeth **19.** Segment of radular ribbon showing relative position of rachidian teeth in non-protracted condition. **20.** Dorsal view of rachidian, notice lateral grooves and longitudinal rib in central cusp **21.** Ventral view of rachidian tooth showing attachment surface, arrow indicates groove in lateral cusp. **Figure 22.** *Adelomelon riosi.* Radular teeth **Figures 23–25.** *Nanomelon viperinus* new genus, new species. Radular teeth. **23.** Radular ribbon, showing relative positions of rachidian teeth in protracted position and "nesting" of the cusp tips in succeeding tooth **24.** Dorsal view of rachidian tooth **25.** Ventral view of rachidian tooth showing attachment surface. Scale bars = 0.50 mm.

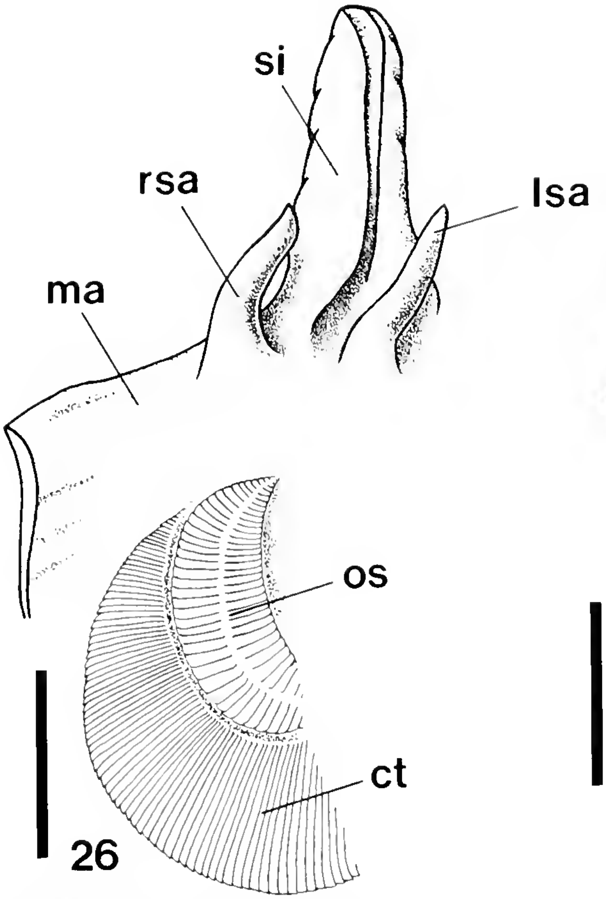
remaining species (Clench & Turner, 1964; Castellanos, 1970; Weaver & Dupont, 1970), all representatives of *Odontocymbiola* exhibit very thin lateral edges and a longitudinal, dorsal rib in the central cusp of the rachidian. The combination of very thin lateral edges and a longitudinal, reinforcing rib probably results in larger cutting effect without weakening of the cusp.

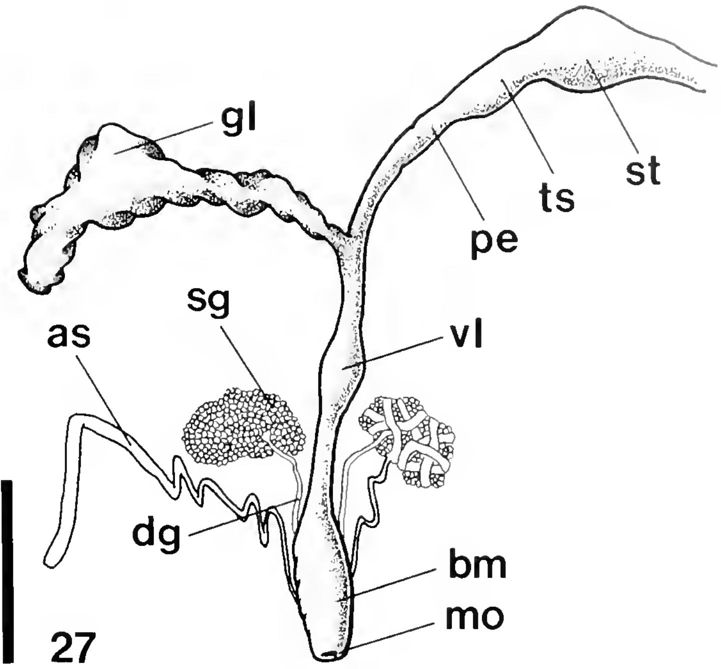
Genus *Tractolira* Dall, 1896

Tractolira tenebrosa new species
(figures 11–13)

Shell (figures 11–13): Elongate, fusiform, reaching about 51 mm length and 17 mm width. Spire elevated, spire angle about 25°. Whole shell surface chalky, dirty white. Shell thin, fragile. Periostracum unknown. Protoconch dome-shaped, with about 5 mm maximum diameter, 2.5 whorls. Teleoconch with up to 4.0 convex whorls. First three teleoconch whorls with about 20 axial ribs. Remainder of teleoconch with axial sculpture of fine growth lines. Spiral sculpture of fine cords, about 20–25 in third teleoconch whorl, 80–100 in the last whorl. Suture excavated. Aperture elongate-elliptical (length/width = 3.5). Outer lip with narrow varix. Parietal region well delimited, with indication of glazed surface (even in badly eroded type-material). Columella arched, with 2–3 columellar plaits (see table 2 for shell measurements and whorl counts).

Holotype: MORG 25468, 38.3 mm length, 13.8 mm width, MD-55 station CP-01 (Beam trawl), off Rio de Janeiro State, Brazil.





Figures 26, 27. *Odontocymbiola simulatrix* new species. Holotype. **26.** Diagram showing the relative positions of some of the organs in the mantle cavity. **27.** Anterior part of alimentary system. Scale bars = 20 mm.

as, accessory salivary gland; bm, buccal mass; ct, ctenidium; dg, duct of salivary gland; gl, gland of Leiblein; lsa, left siphonal appendage; ma, mantle; mo, mouth; os, osphradium; pe, posterior oesophagus; rsa, right siphonal appendage; sg, salivary gland; si, siphon; st, stomach; ts, tubular extension of stomach; vl, valve of Leiblein.

Type locality: Lower continental slope off the coast of Rio de Janeiro State, Brazil, 23°04'S, 40°20'W, at 2,370–2,380 m depth, muddy bottom.

Paratypes: Paratype 1, MNHN, 41.9 mm length, 15.3 mm width, MD-55 station CP-01 (type locality); Paratype 2, MNHN, 51.3 mm length, broken aperture, MD-55 station CP-17, 21°08'S, 38°25'W, 3,250–3,270 m depth, muddy bottom.

Remarks: *Tractolira tenebrosa* is known only from dead shells collected at the upper abyssal zone (between 2,370 and 3,270 m depth). Allocation to subfamilial and generic level is here based solely on shell morphology and previous records of the other two congeneric species, *T. sparta* Dall, 1896 (Gulf of Panama) and *T. germonae* Harasewych, 1987 (South Sandwich Islands, Scotia Sea), from equivalent depths and bottom conditions. *Tractolira tenebrosa* differs conchologically from *T. sparta* and *T. germonae* by having a dome-shaped protoconch instead of the pointed, calcarella-bearing protoconch of the latter two species. Also, the first teleoconch whorls are more crowded, with smaller incremental angles in *T. tenebrosa*. Association of these two conditions produces a blunter, less conical profile in the early teleoconch whorls. The new species is shorter than *T. sparta*, has a proportionally larger aperture, and weaker axial ribs restricted to the two first teleoconch whorls. Axial ribs are absent in *T. germonae*; spiral threads are more numerous in *T. tenebrosa* (80–100, last whorl) than in *T. germonae* (60–80, last whorl), where they are also broader. The new species lacks the flared outer lip and the anteriorly twisted columella and anterior canal, observed in *T. germonae*.

Subfamily **Zidoninae** H. & A. Adams, 1853

Genus *Nanomelon* new genus

Shell: Small [37.6 ± 6.5 mm (n = 11) in the type species]. Spire angle small. Shell surface opaque. Protoconch with about 2.5 whorls. Spiral sculpture of about same intensity as axial sculpture, giving clathrate aspect to shell. Spiral sculpture at sutural ramp of cordlets finer and more closely set than spiral cords on rest of whorl.

Table 2. *Tractolira tenebrosa* new species. Linear shell measurements (mm) and whorl counts for the holotype (HOL) and paratypes 1–2 (PA 1–2). For localities see text.

Character	HOL	PA 1	PA 2
Total length	38.3	41.9	51.3
Shell width	13.8	15.3	—
Length last whorl	28.4	32.8	37.2
Aperture length	21.0	24.8	27.8
Aperture width	6.3	6.6	8.4
Protoconch diameter	4.5	5.3	5.0
Teleoconch whorls	3.50	3.00	4.00
Protoconch whorls	2.25	2.75	2.50
Length/width	2.78	2.74	—
Aperture length/length	0.55	0.59	0.54
Aperture length/ap. width	3.33	3.76	3.31

Axial sculpture absent along the base. Parietal region well defined. Columellar plicae poorly defined. Radula with wide, tricuspid rachidian teeth. Cusps elongated, extremities of cusps nested in small, deep depressions of subsequent teeth. Outer margins of lateral cusps straight.

Type species: *Nanomelon viperinus* new species.

Nanomelon viperinus new species
(figures 9, 10, 15–18, 23–25, 28–33)

Shell (figures 9, 10, 15): Fusiform (length/width about 2.7), imperforate, reaching 45 mm length, 16 mm width. Spire angle about 30°. Shell surface opaque, dirty-white to light-gray. Periostracum very thin, grayish-brown. Shell sometimes eroded where periostracum absent. Transition from protoconch to teleoconch poorly defined (figure 15). Protoconch (figure 15) white, cylindrical, about 2.5 whorls, first 1.5 whorls smooth, remaining whorls sometimes with fine spiral striae. Last protoconch whorl with same diameter as preceding whorl. Teleoconch with up to 4.5 convex whorls, wider at periphery. Suture impressed, sutural ramp slightly concave. Spiral sculpture of about 4 wavy cordlets on sutural ramp and 5 larger spiral cords on remainder of whorl. Interspaces between cords at least three times larger than between narrower, adapical spiral cordlets. Base with about 12 spiral ribs, more crowded abapically. Aperture elongate (length/width about 4). Outer lip simple, thin. Interior of aperture glazed. Parietal region smooth, well defined, and sometimes delimited by narrow glazed band. Columella arched, with siphonal fold and 3–4 columellar plaits. Anterior canal wide (see table 3 for shell measurements and whorl counts).

Shell ultrastructure (figures 16–18): Shell with three crossed-lamellar (CSL) and one internal prismatic layer. External CSL (figures 16, a, 18) about 100 μm thick (in collabral cross-section), observed only in last half of last whorl, horizontal axis of first order lamellae perpendicular to collabral section. Middle CSL (figures 16–18, b) about 550 μm thick, horizontal axis of first order lamellae parallel to collabral section. Middle CSL comprises spiral and axial shell ribs. Third CSL (figures 16–18, c) about 270 μm thick, horizontal axis of first order lamellae perpendicular to collabral section. In middle and third CSL's, second order lamellae in adjacent first order lamellae form an angle of 80° with each other. Innermost prismatic layer (figures 16–18, d) simple, 20–50 μm thick.

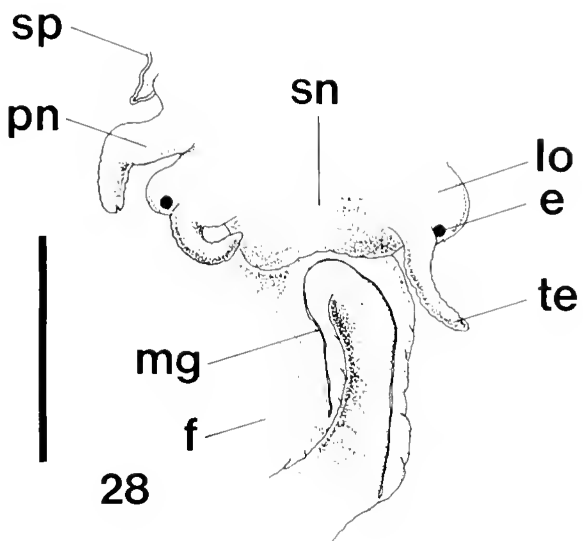
External morphology (figures 28–31): Living animal dull grayish-white. Head broad and flattened, with two semicircular lateral lobes (figure 28, lo) posterior to tentacles. Tentacles (figures 28, 29, te) small and short. Eyes present. Foot (figure 28, f) narrow (length/width = 2, preserved animal), tapered posteriorly. Aperture of mucous gland (figure 28, mg) situated in anterior, broad extremity of foot. Mantle edge thin. Two siphonal appendages (figure 29, lsa, rsa) of equal length, each about ⅓ of length of siphon (figure 29, si); right siphonal appendage with tapered distal extremity, left with blunt, flat distal extremity. Ctenidium (figure 29, ct) leaf-shaped, filaments (figure 30) triangular and elongated laterally, with lateral cilia (figure 30, lc) distributed in well-defined, elongated area at ventral half of filament. Osphradium (figures 29, os, 31) bipectinate, with rounded extremities (length/width = 3), ¾ as long as ctenidium. Hypobranchial gland consisting of delicate, whitish lamellae occupying large area at right side of the mantle cavity. Secretion of hypobranchial gland dark-purple in preserved animals.

Alimentary system (figure 32): Proboscis pleurembolic. Salivary (sg) and accessory salivary glands (as) partially cover circumoesophageal nerve ring (cn) and valve of Leiblein (vl). Salivary glands grayish-white, well compacted. Ducts of salivary glands (dg) opening into anterior oesophagus, close to buccal mass (bm). Accessory salivary glands white, loosely wound, situated anteriorly to salivary glands. Valve of Leiblein slightly anterior to circumoesophageal nerve ring. Gland of Leiblein (gl)

→

Figures 28–33. *Nanomelon viperinus* new genus, new species. Male specimen. **28.** Anterior part of animal. **29.** Diagram showing the relative positions of some organs of the mantle cavity. **30.** Ctenidial filament in frontal view. **31.** Pair of osphradial lamellae in frontal view. **32.** Alimentary system. **33.** Anterior part of male reproductive system, arrow indicates prostate opened ventrally. Scale bars = 5 mm, except for 26, 27, bar = 1 mm, and 29, bar = 2 mm.

an, anus; as, accessory salivary gland, bm, buccal mass; cn, circumoesophageal nerve ring, ct, ctenidium; dd, duct of digestive gland; dg, duct of salivary gland, do, dorsal groove of prostate; dr, duct of rectal gland, e, eye; f, foot; gl, gland of Leiblein; in, intestine; lb, nerve of gland of Leiblein, lc, lateral cilia of ctenidium, lo, lateral cephalic lobe, lp, lateral glandular lobes of prostate; lsa, left siphonal appendage, ma, mantle; mo, mouth; mw, mantle wall, pe, posterior oesophagus, pn, penis, pr, prostate; os, osphradium; re, rectum, rg, rectal gland, rs, radular sac; rsa, right siphonal appendage; sg, salivary gland, si, siphon, sn, snout, sp, sperm groove; st, stomach, te, tentacle; vd, vas deferens; vl, valve of Leiblein, vo, ventral opening of prostate.



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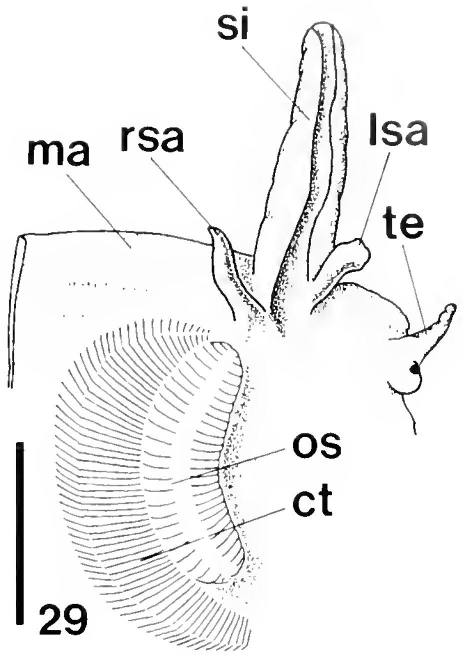

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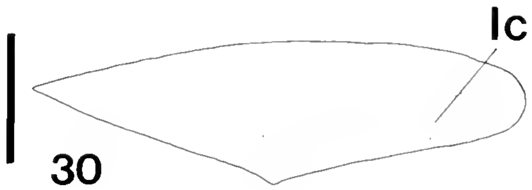

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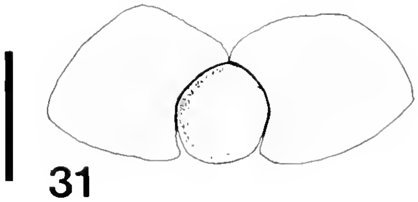

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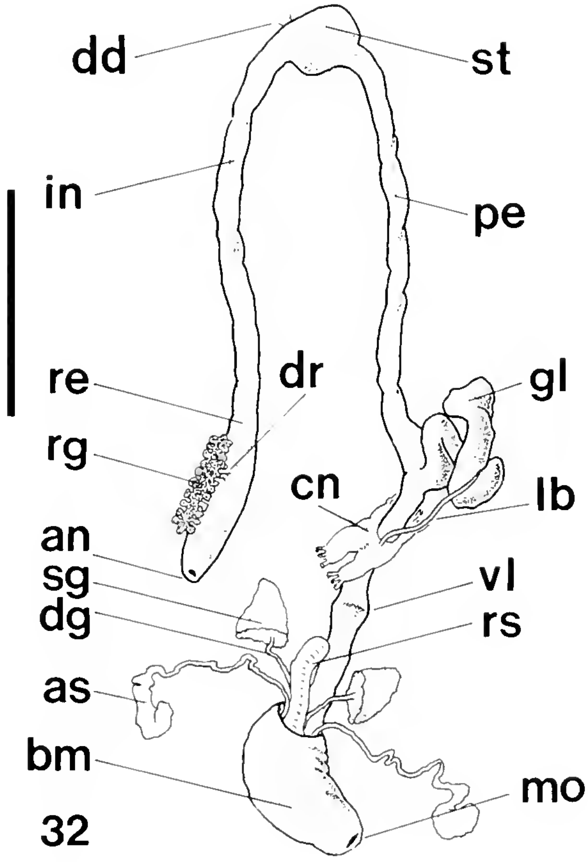

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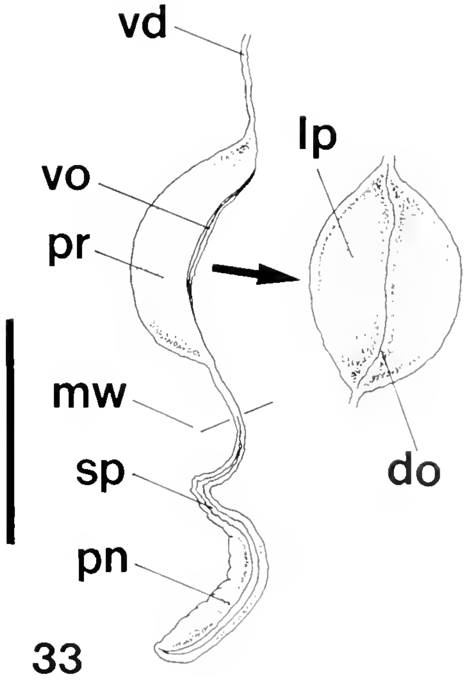

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Table 3. *Nanomelon viperinus* new genus, new species. Linear shell measurements (mm) and whorl counts. All specimens from the type locality, off Rio de Janeiro State, 23°47'S, 42°10'W, 610 m depth (n = 11, including holotype and paratypes 1–7).

Character	Range	$\bar{x}$	SD
Total length	27.3–45.4	37.6	6.5
Shell width	11.2–16.6	13.6	1.7
Length last whorl	19.2–31.9	25.9	4.2
Aperture length	14.7–24.3	19.6	3.5
Aperture width	4.1–5.8	4.9	0.6
Protoconch diameter	3.3–3.9	3.5	0.2
Teleoconch whorls	5.75–7.00	6.59	0.51
Protoconch whorls	2.25–3.00	2.70	0.19
Axial ribs last whorl	15–24	19	3
Length/width	2.37–3.02	2.73	0.19
Aperture length/length	0.49–0.54	0.52	0.02
Aperture length/ap. width	3.38–4.42	3.97	0.31

relatively short, tightly wound, surrounded by connective tissue, innervated, through its anterior extremity, by nerve of gland of Leiblein (lb). Nerve of gland of Leiblein originating at left buccal ganglion in circumoesophageal nerve ring. Posterior oesophagus (pe) very long. Stomach (st) short, embedded in digestive gland and showing as slight swelling of posterior oesophagus. Intestine (in) relatively long. Rectum (re) slightly swollen in preserved specimens. Rectal gland (rg) brownish-gray, elongated, with many lateral, short and blunt branches. A short, posterior duct (dr) connects rectal gland to dorsal surface of rectum. Anus (an) with weak anal papilla.

Radula (figures 23–25): Radular ribbon (figure 23) uniserial. Rachidian teeth (figures 24, 25) 0.14 mm wide, tricuspid, with crescent-shaped basal plate. Cusps situated in approximately same plane as basal plate, growing from its posterior margin. Central and lateral cusps curved, all about same length, extremity of central cusp slightly more posterior than extremities of lateral cusps. Dorsal surface of rachidian deeply impressed by cusps of preceding teeth. When teeth are in same plane (parts of radula not in protracted condition), extremities of cusps (figure 23) interlock with base of cusps of adjacent tooth.

Male reproductive system (figure 33): Testis grayish-white, situated along adapical part of digestive gland. Seminal vesicle extremely convoluted, anterior to kidney. Vas deferens (vd) straight, joins prostate. Prostate (pr) cream-white, ventrally opened (vo), internally and dorsally grooved (do), laterally bilobed (lp). Prostate and rectum loosely joined by connective tissue. Sperm groove (sp) becomes open posterior to anus. Open sperm groove runs to distal extremity of penis. Penis (pe) small, without papilla, situated immediately behind right lateral head lobe, not folded back inside mantle cavity.

Holotype: MORG 25469, 44.2 mm length, 15.3 width, MD-55 station CB-105 (Blake trawl), off Rio de Janeiro State, Brazil (collected alive).

Type locality: Continental slope off the coast of Rio de Janeiro State, Brazil, 23°47'S, 42°10'W, 610 m depth, muddy bottom.

Paratypes: Paratypes 1–5, MNHN, MD-55 station CB-105 (Blake trawl) (type locality); Paratypes 6, 7, MNRJ 5762, MD-55 station CB-104 (Blake trawl), 23°42'S, 42°07'W, 430–450 m depth, muddy bottom.

Other material examined: MNHN, 7 juvenile specimens, 10 juvenile or damaged shells; MNRJ 5763, 3 shells, 10 juvenile or damaged shells; MORG 25470, 3 specimens, 8 juvenile specimens, 3 juvenile shells + 2 dissected animals, MD-55 station CB-105 (Blake trawl) (type locality); MORG 25471, 1 juvenile shell, MD-55 station CB-106 (Blake trawl), 23°54'S, 42°11'W, 830 m depth, muddy bottom; MORG 25472, 10 juvenile or damaged shells, MD-55 station CB-104 (Blake trawl) (same locality as Paratypes 6, 7).

Remarks: *Nanomelon* differs in shell and radular morphology from all known zidonine genera; shell sculpture is similar to *Minicymbiola corderoi* and *Miomelon alarconi* Stuardo & Villarroel, 1974, having a similar, clathrate and chalky white surface. Clathrate or reticulate sculpture is also found in some species of the operculate volutid genus *Fusivoluta* (Calliotectinae), from deep-water off South Africa (Weaver & Dupont, 1970; Liltved & Millard, 1986). *Nanomelon viperinus* has a very elongated shell for a Zidoninae (length/width = 2.73 ± 0.19 mm, n = 10); see table 3 for other measurements and Weaver and Dupont (1970) for shell dimensions in other genera. Within the subfamily, general similarity is restricted to the New Zealand species comprising the genus *Alcithoe* [*flemingi* Dell, 1978, *lutea* (Watson, 1882), *wilsonae* (Powell, 1933); see Dell, 1978]. *Nanomelon viperinus* is easily separated from the *Alcithoe* species group by its smaller total shell length and relative smaller apertural size, general shell proportions (table 3), fainter columellar plicae, clathrate sculpture, characteristic set of crowded spiral cordlets in the sutural shelf, and larger number of protoconch whorls. The shell ultrastructure agrees with the basic arrangement described by Harasewych (1987) for *Tractolira germonae*, the most remarkable difference being the presence of a thin, internal lining of prismatic crystals (figures 16–18, d). Boggild (1930), examining thin sections of the shell of "*Voluta* sp.", described three layers: the most external layer finely prismatic, and the second and third layers crossed-lamellar. The third layer was portrayed by Boggild as composed of two sub-layers. The new genus also has distinct radular characters. Cusps of the rachidian teeth are very elongated for a zidonine, the basal plate is wide but not much curved (compared to those of *Alcithoe*), the lateral cusps have straight outer margins, and the tips of the cusps produce characteristic, relatively deep depressions in subsequent teeth.

The alimentary system of *Nanomelon* is characterized by accessory salivary glands loosely connected to the primary salivary glands, not tightly wound around them, and the stomach lacks an anterior tubular extension.

Clench and Turner (1964) have considered the small degree of physical association between the two types of salivary glands as one of the characters distinguishing Zidoninae from Odontocymbiolinae, in which the accessory salivary glands are tightly wound around the principal salivary glands.

Nanomelon viperinus has a relatively large rectal gland that opens in to the rectum through a duct situated in its posterior part, as opposed to that in *Alcithoe arabica* (Gmelin, 1791) (Zidoninae, Ponder, 1970) and *Tractolira germonae* (Odontocymbiolinae, Harasewych, 1987), in which the rectal gland branches posteriorly from an anterior duct situated immediately behind the anus. The new species has a male reproductive system typical of the Zidoninae; Novelli and Novelli (1982) have noted that the presence of a ventrally opened prostate, and an open sperm groove running to the distal extremity of the penis are characters unique to the subfamily. Their conclusions were based on their own work on *Adelomelon ancilla* (Lightfoot, 1786), *A. beckii*, *A. brasiliana*, *Zidona dufresnei*, and *Provocator corderoi* and on data from Woodward (1900), Clench and Turner (1964), and Ponder (1970). The Odontocymbiolinae have a closed sperm duct along the mantle cavity floor and penis (Clench & Turner, 1964; Harasewych, 1987).

DISCUSSION

In the process of assigning the above species and genera to the different subfamilies, it became evident that some traditionally used characters are convergent, or primitive at their respective levels of utilization. For instance, shell size, general outline, number and shape of axial ribs in early teleoconch whorls, and shape and internal coloration of the aperture render *O. simulatrix* superficially similar to subadults of *Adelomelon riosi* Clench & Turner, 1964. The latter zidonine volute has accessory salivary glands loosely wound around moderately compacted salivary glands, and rachidian teeth with the cusps and basal plate roughly in the same plane (figures 3, 4, 22). The two species were found microsympatrically during the MD-55 cruise, Blake trawl CB-104, at 430–450 m depth. The new species is also conchologically similar to the Fulgorariinae species *Nipponomelon prevostiana* (Crosse, 1978), *N. magna* (Kuroda & Habe, 1950), *Musashia hirasei* (Sowerby, 1912), and *M. cancellata* Kuroda & Habe, 1950, all from the western Pacific (see descriptions and illustrations in Kuroda & Habe, 1950; Shikama, 1967; Weaver & Dupont, 1970; Moore, 1984; Okutani *et al.*, 1988).

Convergence in shell shape between representatives of the volutid subfamilies Odontocymbiolinae and Zidoninae has been observed previously. The conchological mixing of *Odontocymbiola magellanica* and *Adelomelon ancilla* (Lightfoot, 1786) by Pilsbry and Olsson (1954) and the consequent taxonomic implications at supraspecific levels were noted by Clench and Turner (1964) in the original description of Odontocymbiolinae. The superficial conchological convergence of *Odontocymbiola simulatrix* with certain species of Fulgorariinae as well as with *A. riosi*, provides further evidence of the unreliability of shell characters in the supraspecific volutid taxonomy.

Some anatomical characters used in subfamilial taxonomy may also be convergent. The "loosely wound" condition of the accessory salivary glands, considered to be diagnostic of the Zidoninae, is found not only in all known alimentary systems in the subfamily (this paper; Clench & Turner, 1964, Ponder, 1970; Novelli & Novelli, 1982), but also in the odontocymbioline *Miomelon alarconi* Stuardo & Villarroel, 1974, and probably in *Tractolira germonae* Harasewych, 1987 (the illustration given in the original description of this species depicts a relationship between the two types of salivary glands more likely to be found in a zidonine species).

Radular and male reproductive system characters are apparently more adequate to define the above subfamilies, although much variation in radular morphology is found in the Zidoninae (see Weaver & Dupont, 1970). This latter family can also show convergence in radular morphology with the Fulgorariinae (Stuardo & Villarroel, 1974). The presence of a ventrally open prostate, and an open sperm groove are characteristic of the Zidoninae, as opposed to the sperm duct closed from the mantle floor to the penis of the Odontocymbiolinae; one of the two conditions is most probably primitive at the subfamilial level. The suitability of the above characters to formulate a higher classification of the Volutidae will be decided only after careful phylogenetic analysis of the family on a world-wide basis, a task which is beyond the scope of this regionally based work.

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Pleioptygmatidae, a New Family of Mitriform Gastropods (Prosobranchia: Neogastropoda)

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ABSTRACT

A new family of mitriform gastropods is proposed, comprising only the genus *Pleioptygma* Conrad, 1863, based on examination of the foregut of *P. helenae* (Radwin & Bibbey, 1972). *Pleioptygma helenae* is the only known Recent species of this genus, known otherwise only from species from the Neogene of the southeastern United States. The unique configuration of the foregut separates this group from the Mitridae, Costellariidae, Volutidae, and Turridae. Features characterizing Pleioptygmatidae include a proboscis introvert not connected to the head, presence of a proboscis bulb, buccal mass divorced from the proboscis, and hypertrophied rhachidian tooth.

Key words: Pleioptygmatidae, systematics; *Pleioptygma helenae*, anatomy.

INTRODUCTION

The genus *Pleioptygma* Conrad, 1863 (type species *Voluta carolinensis* Conrad, 1840), comprises a small group of species with medium to large (attaining 150 mm in length) mitriform shells bearing conspicuous spiral cords, columellar plicae, and siphonal notch. Three nominal species and one subspecies [*P. carolinense*, *P. lineolatum lineolatum* (Heilprin, 1887), *P. lineolatum saginatum* (Tucker & Wilson, 1933), and *P. prodroma* (Gardner, 1937)] and possibly two additional unnamed species are represented in the Tertiary formations of the southeastern United States (W. G. Lyons, personal communication). Only one Recent species, *P. helenae* (Radwin & Bibbey, 1972), is known. Numerous specimens of *P. helenae* have been collected from the continental shelf off northern Honduras (Caribbean), an area in which several endemic, relict genera have been found (Petuch, 1981, 1982a,b; Houbrick, 1986).

MATERIALS AND METHODS

Prior to the summer of 1983, all known specimens of *P. helenae* were shells that had been carried into lobster pots by hermit crabs. However, through the efforts of Mr. Louis Kotora, a St. Petersburg shell dealer, a live-collected specimen of *P. helenae* (male, shell length 69 mm; figure 1) was obtained from lobster fishermen in July–August, 1983. The specimen, collected near Honduras, was preserved in commercial rubbing alcohol (isopropanol) and brought to W. G. Lyons at the Florida Marine Research Institute, Department of Natural Resources, for examination. The animal was extracted from the shell and given to me by Lyons for dissection. A preliminary report on that specimen was presented at the 1984 American Malacological Union Meeting (Quinn & Lyons, 1984). Subsequently, Mr. Kotora provided another live-collected specimen (female, shell length 107 mm) preserved in rum and collected from the same area as the first specimen. Because the shells were to be maintained intact, the animals were extracted by hooking them with a dental probe and pulling with a twisting motion, with consequent loss of most of the posterior portions of the two animals. This report describes the anatomy of the anterior portions, especially the foregut morphology, and proposes the new family Pleioptygmatidae, based on differences from the foregut morphologies of the Mitridae, Costellariidae, Volutidae, and Turridae.

SYSTEMATICS

Superfamily **Muricoidea** Rafinesque, 1815
(*sensu* Ponder & Warén, 1988)

Family **Pleioptygmatidae** Quinn new family
(type genus *Pleioptygma* Conrad, 1863, Miocene–Recent)

Genus *Pleioptygma* Conrad, 1863
(type species *Voluta carolinensis* Conrad, 1840, Pliocene)

Superfamilial placement follows Ponder and Warén (1988). Foregut anatomy of *Pleioptygma helenae* (Radwin & Bibbey, 1972) (discussed below) suggests a taxonomic ranking equal to that of the Mitridae and Cos-

Figure 1. *Pleioptygma helenae* (Radwin & Bibbey, 1972). Ventral and dorsal views of shell of 69 mm male specimen.

tellariidae. *Pleioptygma* is derived from the Greek *pleios*, full, and *ptygma*, a fold. Contrary to common usage, the genus name is neuter, not feminine. Species names in this account are emended accordingly.

Pleioptygma helenae (Radwin and Bibbey, 1972)

Type locality: Gorda Bank, Honduras (here emended).

The type material of *P. helenae* was reported to be from Cay Sal Bank, Bahamas (Radwin & Bibbey, 1972), obtained from lobster pots by a commercial lobster fisherman. Subsequent attempts to collect this species from Cay Sal have failed. Instead, numerous specimens have been collected from the banks off Honduras. I believe the original types were mislocalized and here propose that the type locality be emended to the Gorda Bank, Honduras.

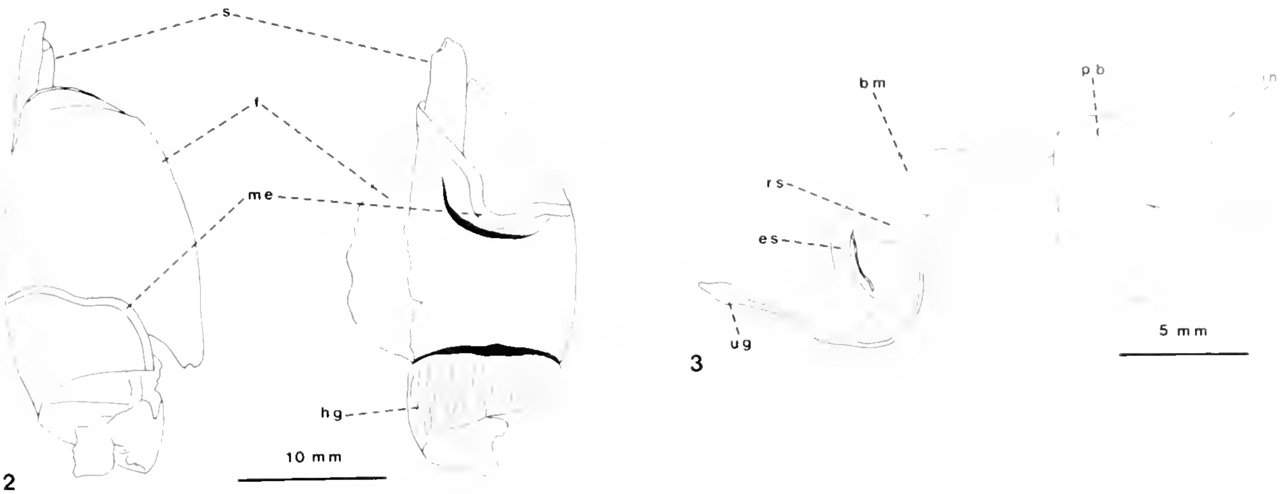
ANATOMY

External features: The remains of the animals after extraction comprise about one whorl each (figure 2); the posterior portion of the mantle cavity and all organs posterior to that were lost. The foot is large, very muscular, uniformly tan to cream in the larger specimen; the smaller is dark chocolate-brown on the sole, fading to grayish buff above. The head is small relative to the foot, with conical snout; the tentacles are short, tapering to rather blunt tips, with conspicuous black eyes located at about midlength. The penis is broad, dorsoventrally flattened, folded to right, and located to the right of the head. The mantle is very thin except for a narrow (1–2 mm wide), muscular band along the edge; the posterior portion and right side are badly torn in both specimens. The siphon is large, thick-walled, muscular, and lacks siphonal appendages. The remains of the ctenidium and osphradium are broad but otherwise unremarkable. The remains of the hypobranchial gland indicate that it is large and rather thick. The columellar muscle is broad and thick.

Proboscis complex: Situated anteriorly is a large, broad introvert (figures 3, 4, 7). The base of the introvert attaches to the right anterior face of the proboscis bulb. The walls of the introvert are thick near the base but rapidly become thin; they are composed principally of circular muscle forming an outer tube or "sheath" and measuring 11–13 mm long when contracted. Distally, the introvert invaginates, runs back through the outer tube/sheath, and enters the proboscis bulb (figure 3). In the larger specimen (figures 4, 7), the introvert turns sharply, runs to the left side of the bulb lumen, then continues diagonally to the right posterior and attaches to a muscular mound on the floor of the bulb. The total length of the contracted introvert is approximately 45 mm. In the smaller specimen, the inner tube of the introvert enters the proboscis bulb, where it is packed in a convoluted mass, exits through the right posteroventral wall of the proboscis bulb, and finally joins the buccal mass. The total length of the introvert is approximately 65 mm.

The proboscis bulb is a large, conspicuous, roughly rectangular structure attached to the floor of the cephalic cavity close to the anterior body wall (figures 3, 4, 7). The bulb of the larger specimen measures 17.0 × 18.5 mm, and that of the smaller 3.5 × 7.5 mm; the greater length of both is perpendicular to the longitudinal axis of the head-foot. The bulb is attached to the cephalic cavity floor by a broad, rather thick band of muscle originating in the foot and inserting along the anterodorsal edge of the bulb. The bulb walls are very thick and are composed of several layers of muscle oriented at right angles to each other. In the smaller specimen, there are four distinct layers oriented transversely-longitudinally-transversely-longitudinally (outer to inner layers, respectively, direction relative to axis of head-foot). The muscle layers of the bulb in the larger specimen are less distinctly demarcated, especially the middle two, because of the addition of much oblique muscle.

Buccal mass: The buccal mass is a muscular, pear-shaped organ lying, *in situ*, on its left side just to the right of the proboscis bulb, its longitudinal axis parallel to the head-foot longitudinal axis and its morphological anterior end topologically posterior (figures 5, 6). The morphological anterior end is separated from the proboscis bulb by a 1.5–2.0 mm length of introvert in the smaller specimen. However, in the larger specimen, the anterior part of the buccal mass extends through the wall of the proboscis bulb and protrudes into the bulb lumen as a prominent mound to which the introvert attaches (figure 7). In the left center of the mound is a narrow, elongate opening leading from the introvert to a small pouch into which the true mouth protrudes. A narrow, thick-walled tube leads from the mouth to the buccal cavity, a distance of about 9 mm, of which the first 6 mm run to the right through the posteroventral wall of the proboscis bulb.



Figures 2, 3. *Pleioptygma helenae.* **2.** Diagrammatic sketch of animal of 69 mm specimen removed from shell, right lateral and dorsal views. **3.** Diagrammatic sketch of foregut of 69 mm specimen. Structures not in life positions. bm, buccal mass; es, esophagus, f, foot; hg, hypobranchial gland; in, introvert, m, muscular mantle edge; pb, proboscis bulb, rs, radula sac; s, siphon; ug, unpaired foregut gland.

The buccal mass walls are very thick, ranging from about 3 mm at the anterior end to about 1.5 mm near the opening of the esophagus (figure 8). The buccal cavity is spacious, and its floor has a prominent transverse ridge just posterior to the oral tube opening. The opening of the radula sac is subrectangular and is located in the center of the buccal cavity floor. The radula sac is broad, comprising the posteroventral ⅔ of the buccal mass. Just behind and above the posterior edge of the radula sac opening is a small (2 mm long, 1 mm wide) caecum. Directly above the caecum is the opening of the anterior esophagus.

Radula: The triserial ribbon is broad and short (length : width = 1.3–1.6:1), about 5% of shell length, with about 70–100 transverse rows of teeth (figures 9–11). The posterior 60% of the rows are above the bending plane, the anterior 40% below. The rhachidian teeth of the larger specimen are 1.05 mm wide and the lateral teeth are 1.30 mm wide at the bending plane. The rhachidian and lateral teeth are similar in structure, each having a broad, narrow basal plate and numerous equal, sharp, narrowly triangular cusps (the rhachidian tooth has about 25 cusps, the lateral teeth about 35).

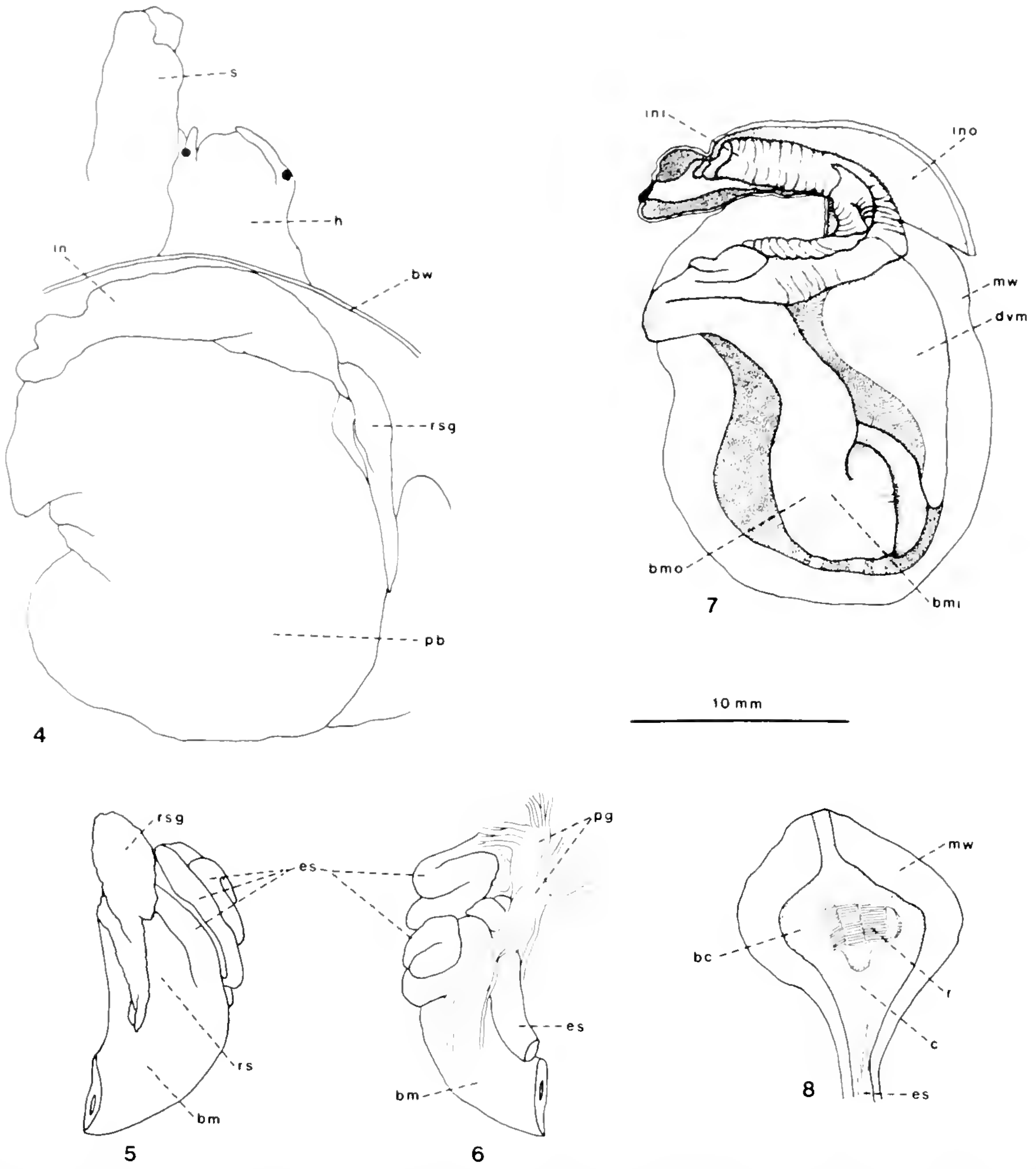
Esophagus: Upon exiting the buccal cavity, the esophagus curves slightly to left, makes a 180° ventral turn and runs underneath itself for about 5 mm, continues through the nerve ring and turns upward, forms a convoluted mass of half-loops, and finally runs posteriorly and diagonally to the left beneath the proboscis bulb (figures 5, 6). A valve of Leiblein was not found.

Salivary glands: These glands are elongate, roughly lanceolate organs lying along either side of the radula sac and are fused at the broad ends (figures 4, 5). The salivary ducts are short and do not pass through the nerve ring; the right duct enters the right side of the radula sac just posterior and ventral to the external separation of the esophagus from the buccal mass; the left duct enters on the left side slightly more ventrally than does the right duct. No accessory salivary glands were observed.

Unpaired foregut gland: The duct is long (about 25 mm), and coiled into a ball to the right of the buccal mass (figure 3). The duct terminates in a muscular, lanceolate bulb 4 mm long and 1.8 mm in greatest width. This organ was found only in the smaller specimen, and the connection of the duct with the foregut was not found.

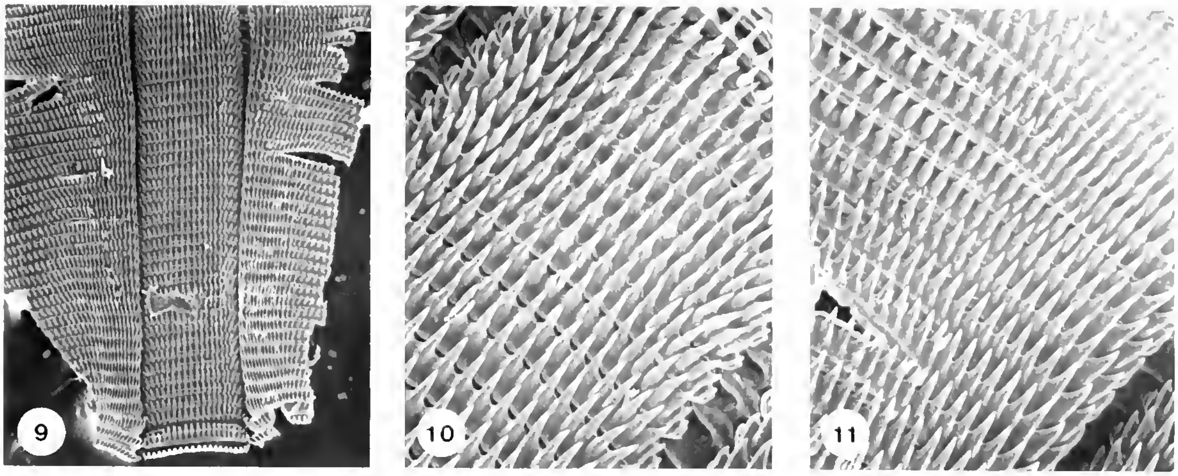
DISCUSSION

Familial placement of *Pleioptygma* has always been controversial. Conrad (1840) first described the type species of *Pleioptygma* as *Voluta* but soon (Conrad, 1842) transferred the species to *Mitra*, a placement followed by Tuomey and Holmes (1856). However, Conrad (1863) seemingly reversed himself by assigning his new genus *Pleioptygma* to Volutidae. Heilprin (1887) ignored *Pleioptygma* and maintained the species group in *Mitra*. Dall (1890) noted Conrad's placement of *Pleioptygma* in Volutidae but treated it as a subgenus of *Mitra*, a classification followed by Cossmann (1899), Tucker and Wilson (1933), Gardner (1937), Mansfield (1937), Olsson and Harbison (1953), and Dubar (1958, 1962). Cernohorsky (1970:61) stated unequivocally that *Pleioptygma* was not referable to Mitridae but instead possessed many features "all consistent with the Volutidae. An assignment to the Scaphellinae might be appropriate." Radwin and Bibbey (1972:95–96) rejected that placement, stating that characters Cernohorsky (1970) used to exclude *Pleioptygma* do occur in some Mitridae, and concluded "We are thus tentatively placing the subgenus *Pleioptygma* in the Mitridae, pending examination of the radular dentition of *M.* (*P.*) *helenae*." Cernohorsky (1976: 282) ignored Radwin and Bibbey and maintained that



Figures 1–8. *Pleioptygma helenae* Foregut morphology of 107 mm specimen **4.** Diagrammatic sketch of proboscis complex in relation to head, cephalic cavity opened dorsally **5, 6.** Diagrammatic sketches of buccal mass and associated organs **5.** Dorsal (morphological right side) view **6.** Ventral (morphological left side) view **7.** Dissection of proboscis bulb and introvert, opened dorsally **8.** Dissection of buccal mass, opened dorsally bc, buccal cavity, bm, buccal mass, bmi, inner opening to buccal mass, bmo, outer opening to buccal mass, bw, body wall; c, caecum of buccal mass; dvm, dorsoventrally oriented muscle mass, es, esophagus, h, head, in, proboscis introvert, ini, inner tube of introvert, ino, outer tube of introvert, mw, muscular wall of proboscis bulb, pb, proboscis bulb, pg, pedal ganglia, r, radula, rs, radula sac, rsg, right salivary gland, s, siphon

"shell features of *Pleioptygma* are consistent with the Volutidae, and the genus should be referred to the Volutid subfamily Scaphellinae." Weaver and duPont (1970) omitted *Pleioptygma* from their monograph of worldwide Volutidae. In all cases, judgments of affinities of *Pleioptygma* were based entirely on shell characters. Although by no means complete, the anatomical data presented above provide an opportunity to re-evaluate the relationships of *Pleioptygma*. The following discussion compares the anatomy of *Pleioptygma helenae* with that of the Mitridae, Costellariidae, and Volutidae, the families to which *Pleioptygma* has traditionally been assigned, and the Turridae, a group that has some superficial similarities of foregut anatomy to that of *Pleioptygma*. Table 1 summarizes the comparison of characters of *Pleioptygma* and the four families cited above.



Figures 9–11. *Pleioptygma helenae.* SEM micrographs of radula. **9.** View of portion of intact ribbon. × 25. **10.** Rhachidian teeth. × 100. **11.** Lateral teeth. × 100.

Ponder (1972) investigated the anatomies of several mitriform gastropods from the southwestern Pacific. In that study, he found that the Mitridae, as then perceived, actually comprised two families, the Mitridae *sensu stricto* and the Costellariidae (as Vexillidae). I am here following that decision and will compare *Pleioptygma* to each group separately. Terminology of anatomical structures follows Ponder's (1973) review of the comparative anatomy of the Neogastropoda. The shells of the Mitridae and *Pleioptygma* are rather similar in shape and sculpture, with spiral ridges predominating; however, the shells of *Pleioptygma* are larger and lighter. The radulae of the two groups are also quite similar, both having comb-like lateral teeth and multicuspid rhachidian teeth (except in *Pterygia*, which lacks lateral teeth). *Pleioptygma*, however, has hypertrophied rhachidian teeth that are only slightly less broad than the lateral teeth. Mitrids, on the other hand, have rhachidian teeth that are noticeably narrower than the lateral teeth. The radula of *Mitra sigillata* Azuma, 1965 (Cernohorsky, 1970, fig. 26), is most similar to that of *P. helenae* in that the rhachidian has about 20 cusps and the laterals have about 22. However, the rhachidian is only about 60% of the width of the laterals, compared to 80% in *P. helenae.* The soft parts of *Pleioptygma* offer a number of important characters that differ from the Mitridae. The foot of *Pleioptygma* is relatively large, whereas that of mitrids is small. The head of *Pleioptygma* has a distinct, relatively large snout; that of the Mitridae has no such structure. An epiproboscis, one of the hallmarks of the Mitridae, is missing in *Pleioptygma*. The proboscis mouth of mitrids has a strong, muscular sphincter, the "peristomal rim" of Ponder (1972). In *Pleioptygma* the proboscis "mouth" has no such rim, the opening of the snout having assumed that function. In fact, the true mouth of *Pleioptygma* has been divorced from the extensible portion of the proboscis. Mitrids have a proboscis sac, but it is a very thin-walled structure, in contrast with the extremely thick-walled, muscular proboscis bulb of *Pleioptygma*; however, it is not yet possible to determine whether the two structures are homologous. The prominent unpaired foregut gland of *Pleioptygma* is totally absent in the Mitridae.

Members of the Costellariidae differ from *Pleioptygma* in the following characters: 1) axial, rather than spiral, shell sculpture is predominant; 2) lateral teeth of the radula are simple and sickle-shaped; 3) the rhachidian is much narrower; 4) an introvert and proboscis bulb are absent; 5) a pair of accessory salivary glands is present; and 6) an unpaired foregut gland is present, but it comprises only the Gland of Leiblein (see Ponder, 1972).

The volutids are distinguished from *Pleioptygma* by the following characters: 1) the dominant shell sculpture, when present, is axial; 2) the radula is usually uniserial with a uni-, tri-, or multicuspid rhachidian that is comparatively much smaller; 3) siphonal appendages are present; 4) an introvert is absent; 5) there is no proboscis bulb; 6) paired accessory salivary glands are present; and 7) an unpaired foregut gland is present but comprises only the Gland of Leiblein.

The proboscis complex of *Pleioptygma* is superficially similar to that of some turrids, particularly to some members of the subfamily Daphnellinae (Smith, 1967). In the Turridae, the buccal mass has also been divorced from the proboscis tip; there is an introvertible proboscis, at least in *Philbertia* (Smith, 1967); and the poison gland resembles the unpaired foregut gland of *Pleioptygma*. However, the proboscis bulb of *Pleioptygma* and the hypertrophied rhachidian teeth with comb-like laterals are not similar to any described turrid, and most of the similarities in other structures are analogous, not homologous.

Considering the anatomical differences separating *Pleioptygma* from other similar neogastropod families, it is evident that *Pleioptygma* cannot be accommodated in any defined family. Therefore, I propose that *Pleioptygma* represents a family separate from other mitriform gastropods, defined principally by the autapomorphous proboscis complex, the position of the buccal mass, and the hypertrophied rhachidian tooth. The morphologies

Table 1. Comparison of shell and anatomical characters of Pleioptygmatidae, Mitridae, Costellariidae, Volutidae, and Turridae. Characters of Mitridae and Costellariidae from Ponder (1972, 1973); Volutidae from Clench and Turner (1964) and Ponder (1973); and Turridae from Smith (1967).

Character	Pleioptygmatidae	Mitridae	Costellariidae	Volutidae	Turridae
Shell size	Medium to large	Medium to large	Small to large	Small to large	Small to large
Predominant sculpture	Spiral	Smooth or spiral	Axial	Smooth or axial	Smooth, axial or spiral
Radula					
Lateral teeth	Multicuspid	Multicuspid or absent	Simple, curved	Usually absent	Usually absent, multicuspid if present
Rhachidian teeth	Wide multicuspid	Usually relatively small, multicuspid	Relatively large, 3 or more cusps	Small to large, uni-, tri-, or multicuspid	Usually absent, rudimentary if present
Foot	Large relative to shell	Small relative to shell	Moderate relative to shell	Large relative to shell	Small relative to shell
Siphonal appendages	Absent	Absent	Absent	Present	Absent
Alimentary canal					
Proboscis	Introvert	Pleurembolic	Pleurembolic	Pleurembolic	Polyembolic or intraembolic
Proboscis bulb	Present	Absent	Absent	Absent	Absent
Epiproboscis	Absent	Present	Absent	Absent	Absent
Mouth	At base of proboscis complex, no peristomal rim	At tip of proboscis, with peristomal rim	At tip of proboscis, no peristomal rim	At tip of proboscis	At base of proboscis, with peristomal rim
Accessory salivary glands	Absent?	Absent	Present, paired	Present, paired	Usually absent, paired if present
Unpaired foregut gland	Present	Absent	Present	Present	Present, poison gland
Valve of Leiblein	Absent	Small or absent	Large	Large	Absent

of radula and shell suggest that the Pleioptygmatidae may be derived from an ancestor in common with the Mitridae.

The function of the proboscis complex of *Pleioptygma* can only be surmised. In both specimens dissected for this study, the anterior portion of the introvert was lying free in the cephalic cavity, wedged between the anterior face of the proboscis bulb and the body wall. Evidence was lacking of any previous attachment to the walls of the snout. This position may have been the result of extreme retraction in response to contact with the preservative. In life, the introvert probably lies partially within the snout and is everted by a combination of contractions of the intrinsic circular muscle of the introvert and muscular contraction of the proboscis bulb. The length of the everted introvert must be quite extensive, as the wrinkled and folded appearance of the contracted organ indicates. The length of the introvert, combined with the dissociation of the radula from the proboscis complex, suggests that *Pleioptygma helenae* feeds on soft-bodied prey, probably tubicolous and crevice-dwelling worms such as sipunculans and polychaetes. The position of the radula suggests that it acts principally in triturating prey and transferring food into the esophagus.

Two major differences were observed between the two specimens. The presence of an unpaired foregut gland in the smaller specimen, but not in the larger, cannot be explained. Differences in the length and morphological relationship of the introvert and proboscis bulb, as well as the morphological relationship of the proboscis bulb and buccal mass, may be explained by ontogenetic changes. Apparently, the total length of the introvert develops relatively early in ontogeny, at least by the time the shell reaches a length of about 70 mm. With growth, the length remains about the same, but the width increases. Increasing the volume of the lumen of the proboscis bulb also allows the enclosed introvert to become less convoluted. In a similar manner, growth of the proboscis bulb, especially the thickening of the bulb walls, encroaches upon and eventually envelops the morphological anterior end of the buccal mass, creating the mound on the floor of the proboscis bulb.

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The Reproductive Anatomy and Taxonomic Status of *Philomycus venustus* Hubricht, 1953 and *Philomycus bisdosus* Branson, 1968 (Pulmonata: Philomycidae)

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ABSTRACT

Specimens of *Philomycus venustus* and *P. bisdosus* were collected from their type localities. Reproductive-system morphology of these two species is described. Comparisons of external characteristics reveal clear, consistent differences in mantle pattern, length, and foot-edge color. Comparisons of the reproductive systems demonstrate species-specific differences in penial anatomy. These data support the recognition of *Philomycus bisdosus* as a distinct species.

INTRODUCTION

Thirty years ago it was not unusual to describe terrestrial gastropods using only external characters. One such description was that of *Philomycus venustus* Hubricht, 1953. *Philomycus bisdosus* Branson, 1968 was described on the basis of external and selected reproductive-system characteristics. Hubricht (1974:33) placed *P. bisdosus* in the synonymy of *P. venustus* noting that the latter species was "... a rather variable species and *P. bisdosus* represents one extreme of that variation." Because no comparative data were presented in support of the synonymization, the present study was initiated. Specimens of *P. venustus* and *P. bisdosus* were collected, and comparisons involving their external and reproductive-system morphologies were made. The goals of this study were: (1) to describe the reproductive-system anatomy of *Philomycus venustus* and of *P. bisdosus* and (2) to obtain comparative data in support of the above noted synonymization.

MATERIALS AND METHODS

Specimens of *Philomycus venustus* were collected on May 22, 1986 and May 21, 1987 at the type locality for this species (Comer's Rock, Jefferson National Forest, Grayson County, Virginia) under the bark of down dead trees (elevation *ca.* 1,220 meters). Specimens of *Philomycus bisdosus* were collected from the type locality (Breaks Interstate Park, Dickensen County, Virginia) on May 23, 1986 and May 22, 1987. The specimens were found approximately 0.3 kilometers northwest of Cold Spring, crawling on trees (elevation *ca.* 540 meters).

External characteristics were compared with species descriptions to ensure correct identification (*i.e.*, length, mantle color and pattern, and color of foot edge). All specimens were drowned in distilled water and then dissected. Complete reproductive systems of each species were stained and mounted using Gregg's (1959) procedure. Additional reproductive systems of each species were dissected so that the internal structure of the penis could be described. The Student's *t*-test was used to test for statistical differences between species. All material was preserved in 70% ethanol subsequent to dissection. Collection and dissection dates were essentially the same in each year to remove those differences in anatomy attributable to differences in the phase of the life cycle.

Voucher specimens have been deposited in the National Museum of Natural History, Smithsonian Institution (USNM 860412 and USNM 860413 for two specimens of *Philomycus venustus*; USNM 806414 and USNM 860415 for two specimens of *Philomycus bisdosus*).

RESULTS

A total of eight specimens of *Philomycus venustus* (two in 1986, six in 1987) and seven specimens of *P. bisdosus* (one in 1986, six in 1987) were collected. The mantle colors and patterns of these specimens agreed with the type descriptions for each species (figures 1-4). The total length of each specimen was measured, the results are shown in table 1. Measurements were taken from active, but not crawling, slugs. A Student's *t*-test indicated a significant difference between the lengths of these species. All of the *P. bisdosus* had gray foot margins, all *P. venustus* had white foot margins.

Table 1. Measurements of slug length and results of a Student's *t*-test comparing the means of the measurements. Length in millimeters, standard deviation in parentheses.

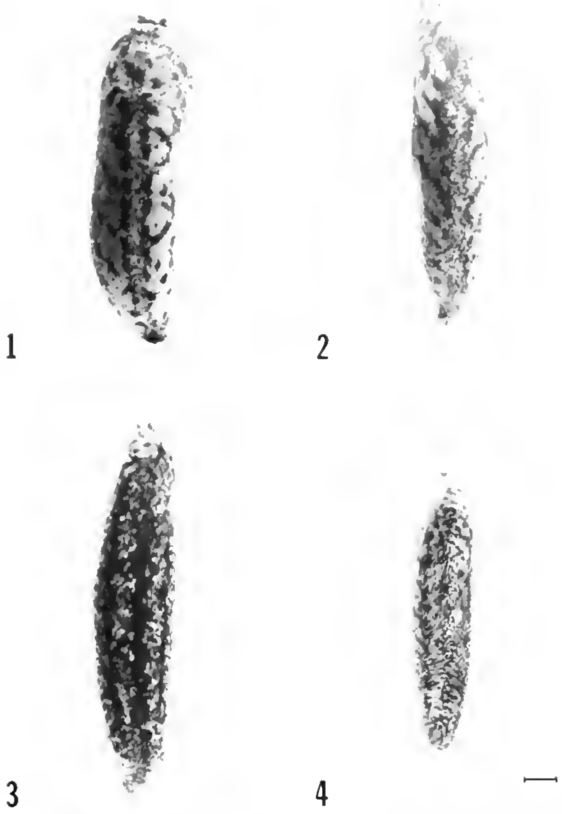
	Philomycus bisdosus	*Philomycus venustus*
N	7	8
Range	40–55	50–65
Mean	46.9 (6.31)	56.8 (4.46)
	$t = 3.46$	$p = <0.01$[1]

[1] Degrees of freedom = 13

Of the specimens collected, the reproductive systems of four *Philomycus bisdosus* and six *P. venustus* were stained and mounted on glass slides. The reproductive systems of three *P. bisdosus* and two *P. venustus* were prepared such that the internal anatomy of the penises could be observed.

GENITALIA OF *Philomycus venustus* HUBRICHT, 1953 (FIGURES 6, 8)

Atrium approximately 80% penial length, glandular on outer surface. Vagina approximately 10% penial length. Spermathecal duct diameter greater than that of oviduct, length slightly less than that of oviduct, slight taper toward spermatheca. Spermatheca round. Dart sac and dart smaller than spermatheca diameter. Penis thick, straight, slightly tapered distally; penial sheath reaching junction of vas deferens and penis. Internally, penis with chamber at distal end, chamber containing several papillose ridges; chamber length equal to approximately 40% of penial length. Vas deferens encircles distal end of penis, entering penis along outer edge. Vas deferens approximately 2½ times length of spermathecal duct, approximately same diameter throughout its length. Penial retractor as wide as distal end of penis, length approximately 80% penial length. Accessory retractor present, small compared to accessory retractor of *P. bisdosus*.



Figures 1–4. Mantle patterns. **1, 2.** *Philomycus venustus*. **3, 4.** *Philomycus bisdosus*. Scale bar equals 5 mm

GENITALIA OF *Philomycus bisdosus* BRANSON, 1968 (FIGURES 5, 7)

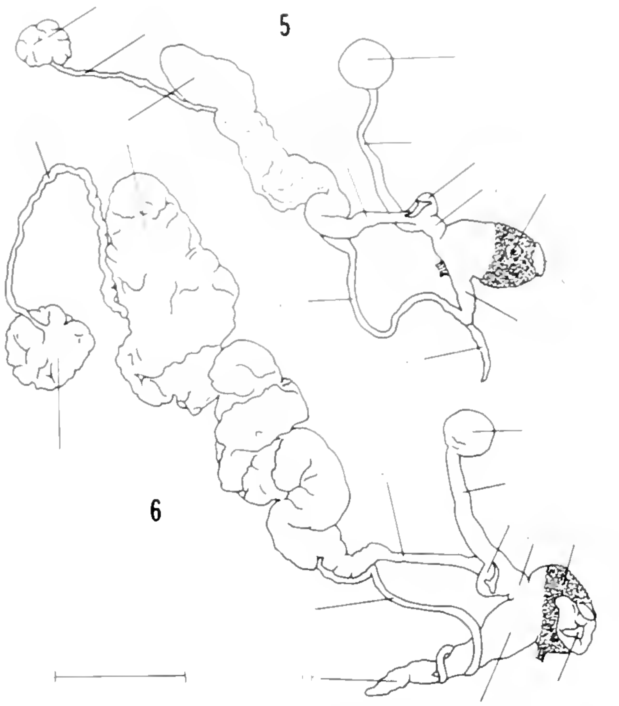
Atrium length approximately equal to penial length, glandular on outer surface. Vagina approximately 15% penial length. Spermathecal duct diameter about same as that of oviduct, length approximately 1½ times that of oviduct, slight taper toward spermatheca. Sperma-

Table 2. Reproductive system measurements and results of Student's *t*-tests comparing the means of the measurements. Measurements in millimeters obtained *via* an ocular micrometer. Standard deviation in parentheses.

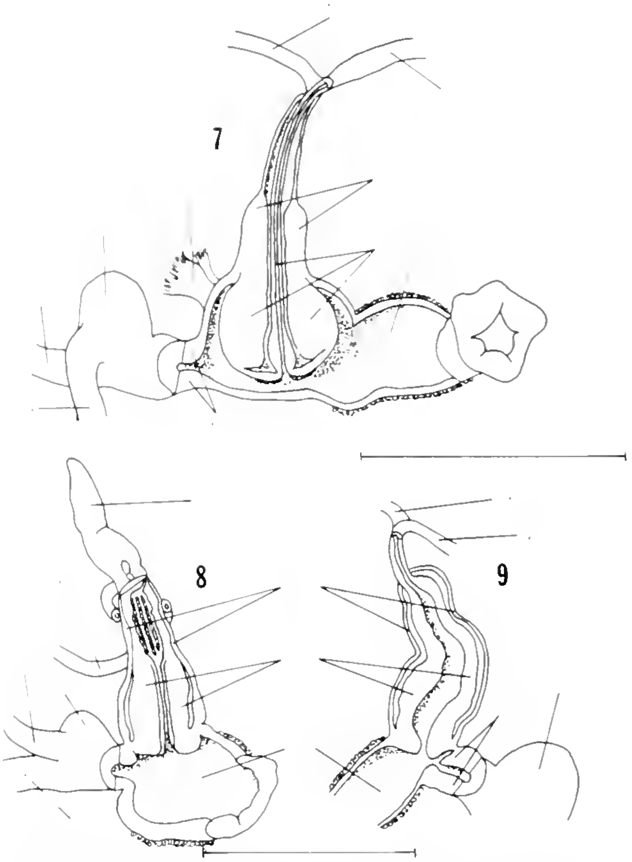
	Philomycus bisdosus (N = 3)		*Philomycus venustus* (N = 4)			
	Range	Mean	Range	Mean	t	Probability[1]
Spermatheca diameter	2.4–3.9	3.2 (0.76)	3.8–5.5	4.7 (0.75)	2.60	<0.05[2]
Length of spermathecal duct	9.1–10.3	9.8 (0.64)	8.6–13.8	10.5 (2.26)	0.59	>0.50
Maximum diameter of spermathecal duct	1.0–1.2	1.1 (0.12)	1.2–1.5	1.4 (0.13)	3.16	<0.05[2]
Length of oviduct	6.9–8.1	7.6 (0.62)	10.9–16.0	13.2 (2.25)	4.74	<0.01[2]
Maximum diameter of oviduct	0.7–1.0	0.9 (0.15)	0.8–1.2	1.0 (0.17)	0.82	>0.40
Length of vas deferens	17.9–19.8	19.1 (1.02)	18.8–22.4	21.3 (1.66)	2.16	>0.05
Maximum diameter of vas deferens	0.4–0.7	0.6 (0.15)	0.5–0.7	0.6 (0.10)	—	—
Length of penial retractor	4.3–7.2	5.4 (1.57)	2.2–8.1	4.9 (2.55)	0.32	>0.50
Maximum width of penial retractor	0.5–0.8	0.7 (0.15)	0.9–1.7	1.4 (0.36)	3.50	<0.02[2]

[1] Degrees of freedom = 5.

[2] Significant difference at 5% level.



Figures 5, 6. Genitalia. **5.** *Philomycus bisdosus.* **6.** *Philomycus venustus.* Scale bar equals 10 mm. A, atrium. AG, albumen gland. DS, dart sac. G, gonad. GP, genital pore; HD, hermaphroditic duct. P, penis. PR, penial retractor. S, spermatheca. SD, spermathecal duct. UV, free oviduct. V, vagina. VD, vas deferens.



Figures 7–9. Longitudinal sections of the penises. **7.** *Philomycus bisdosus.* **8.** *Philomycus venustus.* **9.** *Philomycus togatus* (9 from Fairbanks, 1986). Scale bars equal 10 mm. A, atrium; AR, accessory retractor; DS, dart sac; P, penis; PR, penial retractor, PS, penial sheath; SD, spermathecal duct. UV, free oviduct; V, vagina, VD, vas deferens.

theca round. Dart sac and dart smaller than spermatheca diameter. Penis diameter at proximal end approximately 5 times distal diameter, with distal diameter slightly less than diameter of vas deferens. Penial sheath reaches junction of penis and vas deferens. Internally, penis with apparent continuation of the vas deferens reaching proximal end of penis. Proximal end of penis projected into upper atrium. Vas deferens enters distal end of penis at its center. Vas deferens approximately 1½ times length of spermathecal duct, somewhat swollen at penial end, but approximately same diameter throughout its length. Penial retractor width approximately equal to vas deferens diameter, length equal to length of penis. Accessory retractor present, two times accessory retractor width of *P. venustus.*

Nine measurements of various organs of the reproductive systems were obtained (table 2). Student's t-tests indicate significant differences (probability < 0.05) in four of the measurements: spermatheca diameter; maximum diameter of spermathecal duct, length of oviduct; maximum width of penial retractor.

DISCUSSION

In their discussion of terrestrial slugs, Chichester and Getz (1968:159) stated that "In almost all species the distal genitalia are specifically diagnostic." Fairbanks (1986) has shown species-specific differences in the distal genitalia (penial anatomy) for two sympatric species of *Philomycus*, *P. togatus* Gould, 1841 and *P. carolinianus* Bosc, 1802. Comparisons of the reproductive system anatomy of *P. bisdosus* and *P. venustus* (this study) demonstrated consistent comparable differences in penial anatomy (figures 7, 8). These two species have not been shown to be sympatric, however each is sympatric with *P. togatus* and *P. carolinianus*. Four other reproductive-system characteristics (table 2) provided additional support for species-specific differences between *P. bisdosus* and *P. venustus*.

Examination of external characters of *Philomycus venustus* and *P. bisdosus* also revealed diagnostic differences between these two species. The mantle patterns were clearly different (figures 1–4), so the specimens were always easily separable. *P. venustus* was a significantly larger slug than *P. bisdosus* (table 1). A consistent difference in foot margin color provided a third discriminating character.

Hubricht (1974) did not specify which characters were used to provide the basis for the synonymization of *Philomycus bisdosus* with *P. venustus*. Because no definitive data were available for comparisons of reproductive-system anatomy, one might conclude that the mantle pattern was the primary criterion. However, in the present study, *P. venustus* always had transverse oblique bands, either solid or broken into spots. *P. bisdosus* had no transverse bands. This, coupled with the size difference, foot margin color difference and the differences in penial anatomy, lead to the conclusion that the specimens examined for this study were representatives of two different species. Accordingly, *Philomycus bisdosus* Branson, 1968 should be recognized as a distinct species.

Based upon external appearance and size, *Philomycus bisdosus* was most similar to *P. togatus* (see Fairbanks, 1986). The mantle patterns of these two species were similar, and the reproductive systems appeared similar in gross morphology. However, the foot margin of *P. bisdosus* was gray, whereas that of *P. togatus* was orange. In addition, the penial anatomy was different (figures 7, 9) and *P. bisdosus* had a dart sac and dart that was approximately 65% the size of the dart sac and dart of *P. togatus*.

ACKNOWLEDGEMENTS

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Shell and Pallet Morphology in Early Developmental Stages of *Teredo navalis* Linné (Bivalvia: Teredinidae)

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ABSTRACT

Dimensions of the shell and provinculum distinguish *Teredo navalis* larvae from the larvae of other bivalve mollusks. In the present scanning electron microscopic study of shell and pallet morphology during early ontogenetic stages of this species, the characteristic teredinid provinculum, with two interlocking pairs of small teeth and a wide central tooth and socket, was well-developed in shells 90 μm long. Provinculum length ranged from 44 to 51 μm during the larval period. Average lengths of provincular teeth of the left valve were 9.6 μm for the anterior tooth and 8.2 μm for the posterior tooth; in the right valve, lengths were 7.2 μm for the anterior tooth, 16.4 μm for the central tooth, and 6.6 μm for the posterior tooth. Larval shell height prior to metamorphosis was just under 230 μm.

Formation of a ligament pit preceded secretion of the dissoconch and development of the apophyses, condyles, and exterior denticulated ridges. Shell loss along the posterior margin of the right valve accompanied a shift in the axis of articulation from the dorsal to the posterior plane; subsequent secretion of the dissoconch restored bilateral symmetry. The initial triangular shape of the pallet blade became increasingly rectangular and finally elongate with growth along the distal margin.

Key words: Larvae, post-larvae, shell morphology, pallets; *Teredo navalis*, teredinid, shipworm

INTRODUCTION

The common shipworm *Teredo navalis* Linné, 1758, is distributed worldwide in temperate waters (Turner, 1966, 1971; Abbott, 1974). This larviparous bivalve releases veligers at the straight-hinge stage of development (Sigerfoos, 1908; Grave, 1928; Jørgensen, 1946; Sullivan, 1948, Loosanoff & Davis, 1963; Loosanoff *et al.*, 1966; Turner, 1966, 1971; Scheltema, 1971; Turner & Johnson, 1971). Early morphology of *T. navalis* has been described with optical photomicrographs and gross shell dimensions at various developmental stages (Jørgensen, 1946; Sullivan, 1948; Imai *et al.*, 1950, Loosanoff & Davis, 1963; Loosanoff *et al.*, 1966, Chanley & Andrews, 1971; Culliney, 1975). Jørgensen (1946) characterized the teredinid provinculum as having three teeth on the right valve and two teeth on the left valve; however, dimensions of the larval hinge teeth are not documented for this species. Growth rates of *T. navalis* during larval and post-larval stages were tabulated by Imai *et al.* (1950). Morphology of the shell and pallets of *T. navalis* during post-larval stages has not been described to date.

The present scanning electron microscopic study provides a comprehensive description of the morphological features of the shell and pallets of *T. navalis* during early developmental stages. Provinculum length and dimensions of provincular teeth of *T. navalis* larvae are compared with the same measurements of previously described teredinid larvae to facilitate identification of specimens isolated from plankton samples. Scanning electron microscopic methods for reproducible and consistent orientation of post-larval specimens are described. Details of the rapid changes in shell morphology during metamorphosis are elucidated with micrographs of sequential developmental stages.

MATERIALS AND METHODS

Adult specimens of *Teredo navalis* were collected from a subtidal stake of sweet gum (*Liquidambar styraciflua* Linné) located in a coastal bay near Wachapreague Inlet, Virginia. Larvae (initial shell stages) were removed from three of these adult shipworms and were reared in filtered (50 μm mesh) baywater (salinity range = 29.5 to 34.5‰; temperature range = 22 to 28 °C) using standard culture techniques (Loosanoff & Davis, 1963). During metamorphosis, animals colonized several pieces of conditioned wood that were floated in the culture tank.

Larval and post-larval samples were treated with a 5.25% sodium hypochlorite solution for 10 minutes to remove soft tissues (after Rees, 1950); disarticulated valves and pallets were rinsed several times with distilled water and were stored in 95% ethanol. Specimens were mounted on silver tape, were coated with approximately 600 Å of gold-palladium, and were examined using an ETEC Autoscan scanning electron microscope (SEM). Consis-

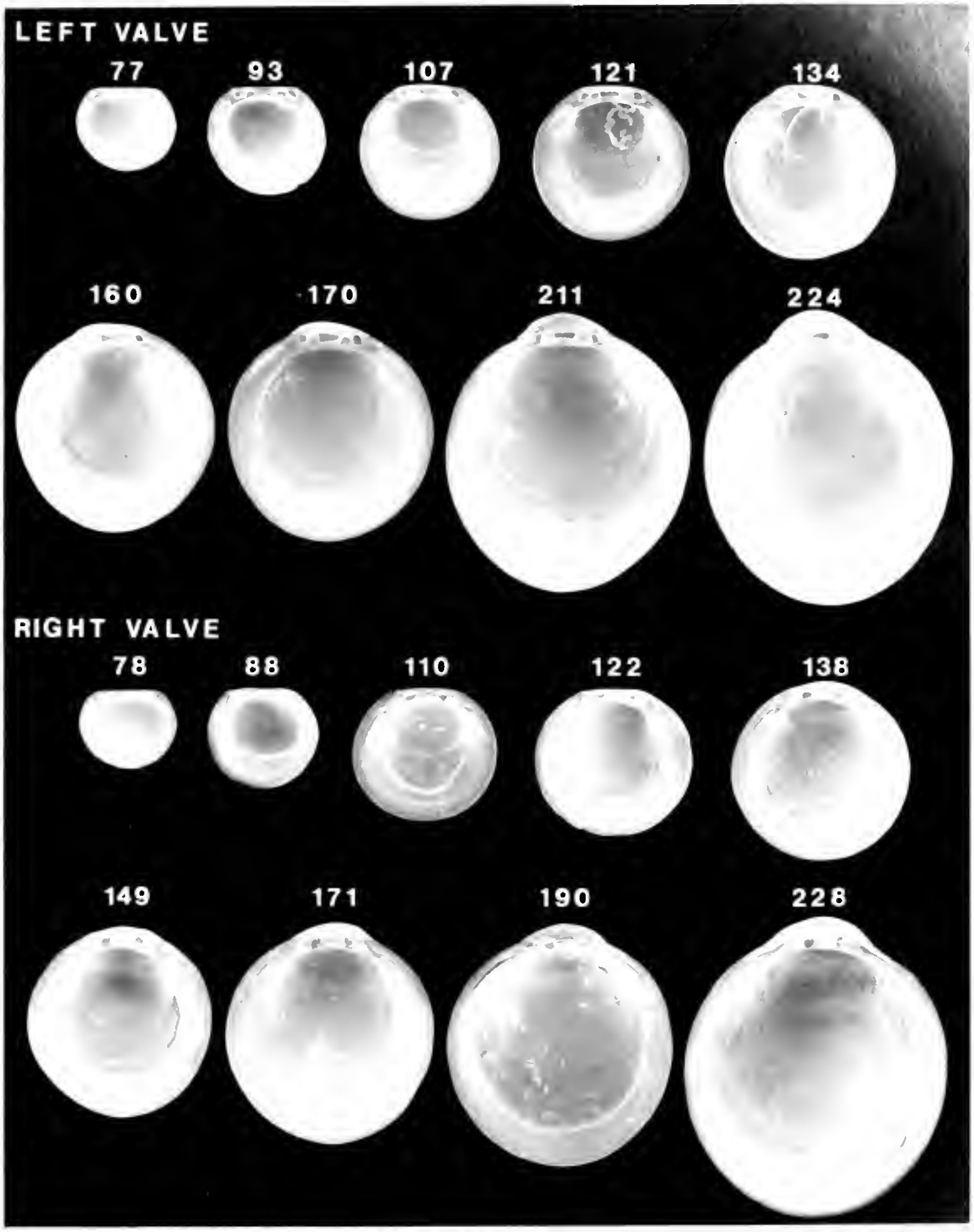


Figure 1. Scanning electron micrographs of disarticulated valves of *Teredo navalis* larvae. Numbers indicate greatest shell dimension in μm.

tent orientation for documentation of shape was obtained by positioning larval shells with points of the shell margin aligned in a plane normal to the electron beam of the SEM. [For further details of SEM methods for larval shells, see Fuller *et al.* (1989).] Similar orientation of post-larval valves was impossible because points along the post-larval shell margin do not lie in a single plane. Throughout the post-larval developmental period, however, points along the dorsoventral margin of the anterior slope (except those at the extreme ventral region) comprise a plane (figure 3). Thus, consistent orientation of post-larval shells was achieved by positioning specimens such that this plane was parallel to the electron optical axis. Additional adjustments were made so that dorsal and ventral condyles were at an equal working distance. Shells mounted for documentation of external shell mor-

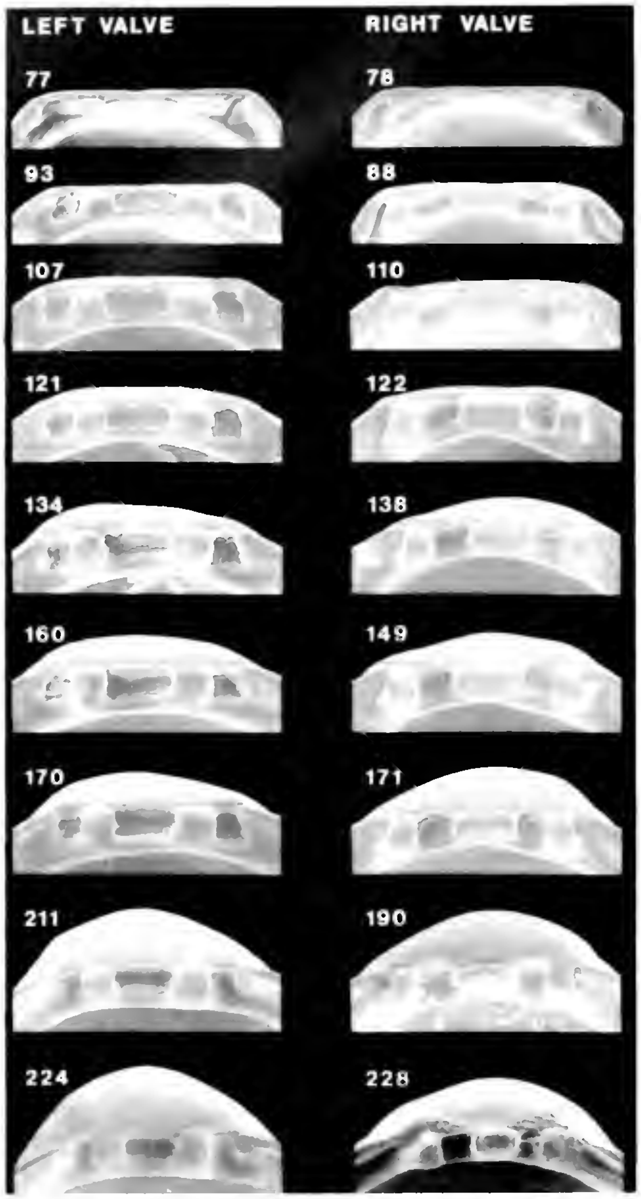


Figure 2. Scanning electron micrographs of the hinge of disarticulated valves of *Teredo navalis* larvae seen in figure 1. Numbers indicate greatest shell dimension in μm

phology were placed with the condyles and posterior slope resting on a specimen mount, which was tilted slightly for maximal visibility of the external surface.

Shell height is defined as the greatest dorsoventral dimension. Shell length is defined as the greatest anteroposterior dimension roughly parallel to the hinge line in larval and early post-larval specimens; measurements of this dimension include the anterior and posterior slopes as they developed in late post-larvae. Shell nomenclature is taken from Turner (1966, 1971).

Outer surface morphology of the pallets was documented with the blade positioned approximately perpendicular to the electron optical axis. Pallet length is the distance between proximal and distal ends (see Turner, 1971:26, for pallet terminology).

RESULTS

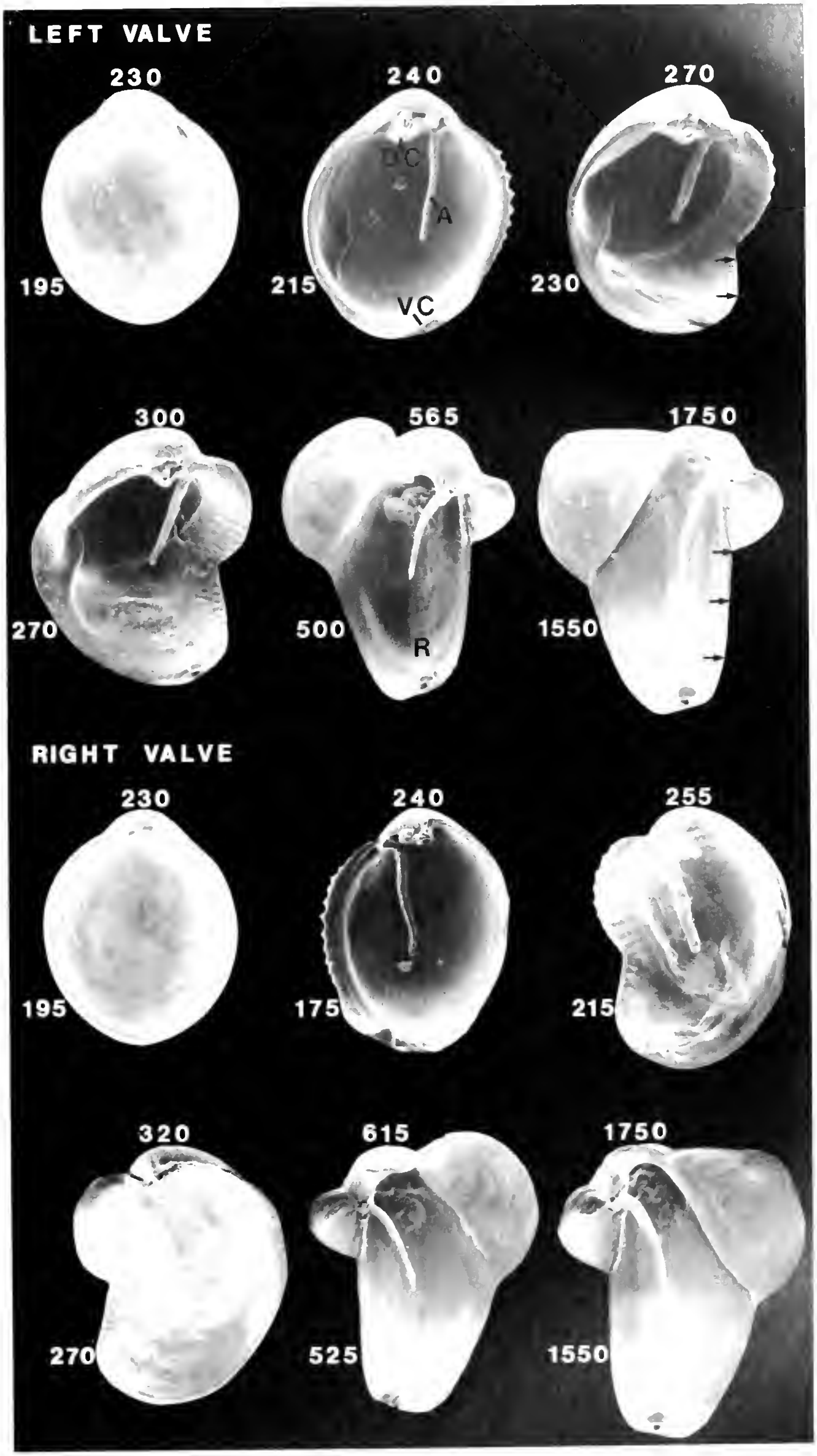
Scanning electron micrographs of disarticulated valves and hinges of sequential ontogenetic stages of *Teredo navalis* larvae are shown in figures 1 and 2. Straight-hinge larval shells ranged from 77 to 87 μm long ($\bar{x} \pm$ SD = 81.5 ± 3.3 μm; n = 30) and from 66 to 70 μm high ($\bar{x} \pm$ SD = 66.6 ± 1.5 μm; n = 30). Larvae 90 μm long had a well-developed provinculum, with two interlocking pairs of small teeth and a wide, central tooth and socket. Provinculum length ranged from 44 to 51 μm ($\bar{x} \pm$ SD = 47.7 ± 1.7 μm; n = 21) during the larval period. Measurements of provincular teeth are summarized in table 1. A low umbo formed in shells approximately 120 μm long. During mid-larval stages, the longest valve dimension shifted from an anteroposterior to a dorsoventral axis; larvae were equidimensional at approximately 150 μm. Length of larvae just prior to metamorphosis ranged from 195 to 210 μm ($\bar{x} \pm$ SD = 202.0 ± 4.8 μm; n = 30); height was just under 230 μm at this stage.

The first morphological evidence of metamorphosis was formation of a ligament pit, which was observed when valves were approximately 230 μm high (figures 3, 4). Immediately following formation of the ligament pit, dramatic morphological changes occurred in the shell and hinge. An apophysis grew from a base beneath the anterior tooth and socket; this base extended below the entire hinge area and expanded at the posterior end to form an early dorsal condyle (figures 3, 4, height 240 μm, DC). Formation of the ventral condyle began with an inward protrusion of the ventral margin (figure 3, height 240 μm, VC). Shell loss along the posterior margin of the right valve began at this stage (figures 3, 5, height 240 μm). An initial denticulated ridge formed on the anterior margin of the shell exterior (figure 5, height 240 μm).

A shift in the axis of articulation from an anteroposterior to a dorsoventral orientation occurred when shell height was between 230 and 240 μm (figure 6). Loss of approximately 25 to 40 μm of the shell along the posterior margin of the right valve accommodated this shift (figures 5, 7). New ridges were added on the external surface of the anterior margin (figure 5, height 250 μm).

→

Figure 3. Scanning electron micrographs of disarticulated valves of *Teredo navalis* post-larvae. Numbers above the shells indicate shell height (greatest dorsoventral dimension); numbers beside the shells indicate shell length (greatest anteroposterior dimension). Dimensions are in μm and are accurate to within 5 μm. Arrows designate the dorsoventral margin of the anterior slope; points on this margin were aligned in a plane for consistent orientation of valves. A, apophysis; DC, dorsal condyle; VC, ventral condyle; R, umbonal-ventral ridge


LEFT VALVE
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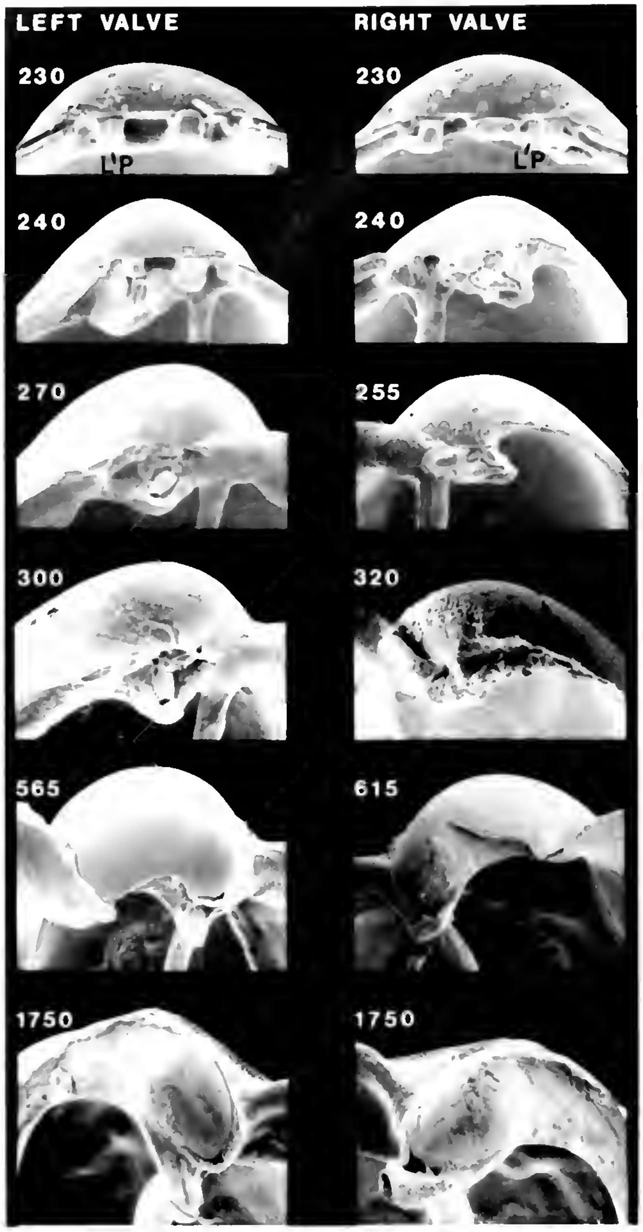


Figure 4. Scanning electron micrographs of the hinge of disarticulated valves of *Teredo navalis* post-larvae seen in figure 3. Numbers indicate shell height (greatest dorsoventral dimension) in µm. LP, ligament pit.

In shells approximately 255 to 275 µm high, the ventral condyle had developed into a prominent knob, and the provinculum was no longer recognizable (figures 3, 4). Rapid growth along the ventral margin increased the depth of the valves and caused articulated shells to become nearly spherical. Protrusion of ventral condyles further separated right and left valves. Five to 12 ridges covered the external surface of the anterior slope (figure 5, height 265/275 µm). Demarcation of the posterior slope began in valves 300 µm high (figures 3, 5). Posterior margins of right and left valves were symmetrical; unequal secretion of the dissoconch along this margin restored earlier asymmetry of the valves (figure 8).

External growth lines marked the pronounced ventral extension of the valves (figure 5, height 330/295 µm). As development continued, the posterior slope became more prominent (figure 3, height 565/615 µm). The umbonal-ventral ridge appeared on the interior surface of the shell (figure 3, height 565/615, 1,750 µm). The dorsal condyle developed (figure 4, height 565/615 µm) from the early expanded base of the apophysis (figure 4, height 240, 270/255, 300/320 µm) and was positioned posterior to the apophysis (figure 9). At a shell height of approximately 1 mm, the posterior gape was well-developed (figure 10).

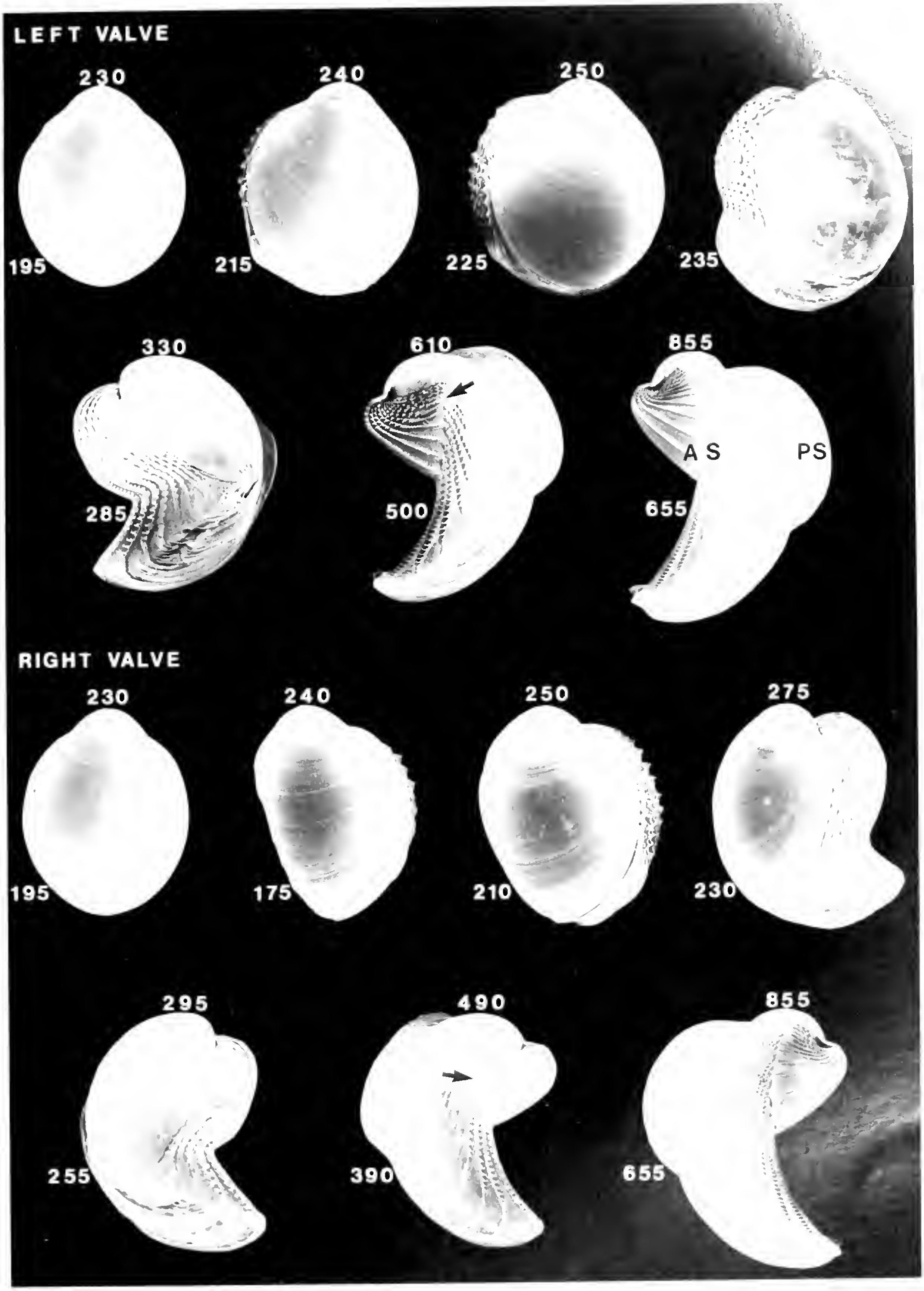
The external surface of the anterior slope of both valves was sculptured with closely-spaced, denticulated ridges in early post-larvae. Subsequent ridges were more widely-spaced, so that the relationship of shell length to number of ridges over the entire post-larval period was logarithmic (figures 5, 11). In contrast to early post-larval ridges with uniform denticles, late post-larval ridges had fine denticles in the anterior section, while large, coarse denticles marked posterior ridges (figure 5, height 610/490, 855 µm). In addition, these late post-larval ridges formed a sharp angle at the ventral junction of the anterior and posterior sections of the anterior slope.

The earliest pallets were removed from animals with a shell length of approximately 240 µm. The pallet blade at this stage was triangular, with the margin of the inner face extending further distally than that of the outer face (figure 12, 75 µm). The shape of the blade became more rectangular with additional growth of the inner margin (figure 12, 125/110 µm). Inner and outer margins of the pallet blade elongated, and the margin of the outer face became considerably more concave than that of the inner face (figure 12, 200/195, 285/265, 485/470 µm).

Throughout development of the pallets, each pair had a symmetrical shape. Close examination of an individual pallet, however, revealed that the ventral surface was longer than the dorsal surface of the blade. The resulting asymmetry of the blade was increasingly evident as ventral and dorsal surfaces rounded and the dorsal distal tip extended further than the ventral distal tip (figure 12, 715/795, 1,025/1,035 µm). Further growth was greatest in a distal direction, resulting in an elongate shape of pallets approximately 1,500 µm long (figure 12).

Pallet length increased more rapidly than shell length during initial post-larval stages. After anterior and posterior slopes were well-developed, pallet length and shell length increased at approximately equal rates (figure 13).

Figure 5. Scanning electron micrographs of the exterior surface of disarticulated valves of *Teredo navalis* post-larvae. Numbers above the shells are shell height (greatest dorsoventral dimension); numbers beside the shells are shell length (greatest anteroposterior dimension). Dimensions are in µm and are accurate to within 5 µm. Arrows mark late post-larval ridges, which are comprised of both fine and coarse denticles. AS, anterior slope, PS, posterior slope.


LEFT VALVE
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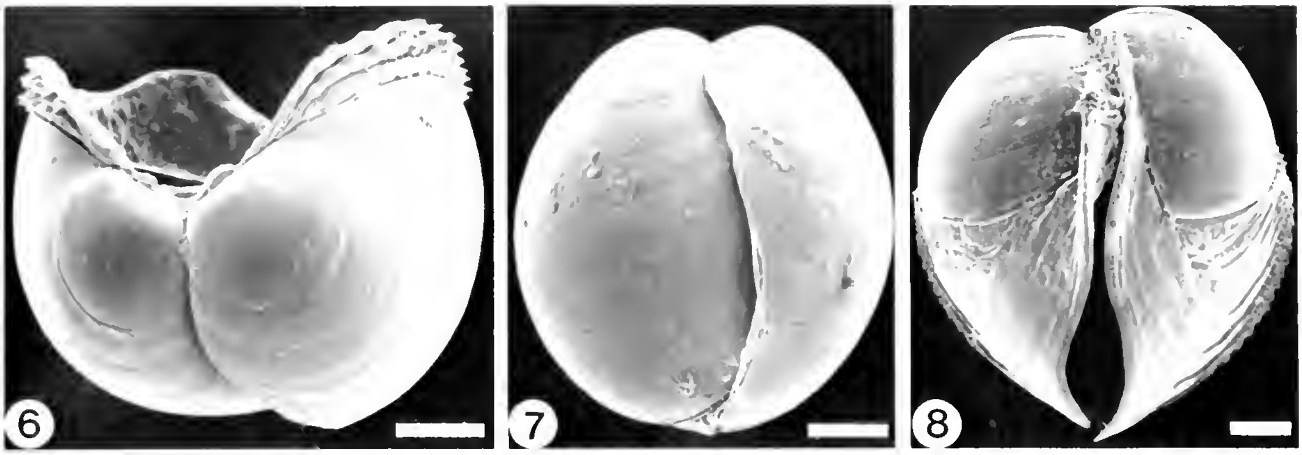

Figures 6–8. Scanning electron micrographs of early post-larval shell specimens of *Teredo navalis*. **6.** Dorsal view after the shift in axis of articulation to a dorsoventral orientation. Scale bar = 50 µm. **7.** Posterior view after the shift in axis of articulation to a dorsoventral orientation. Scale bar = 50 µm. **8.** Posterior view when symmetry of right and left posterior margins is nearly complete. Scale bar = 50 µm.

Figures 9, 10. **9.** Scanning electron micrographs of a left valve of a post-larval specimen of *Teredo navalis*. Stereo pair was taken with an 8° angular displacement between exposures. **10.** Scanning electron micrograph of an articulated post-larval shell specimen of *Teredo navalis*; posterior view. Scale bar = 200 µm.

DISCUSSION

Larval Development

Previously reported shell dimensions of *Teredo navalis* larvae are summarized in table 2. Dimensions of straight-hinge larvae in the present study were consistent with those in previous descriptions. Mean provinculum length of *T. navalis* in the present study was 47.7 µm, close to the 51.3 µm mean given by Culliney (1975) and within the 45 to 50 µm range given by Chanley and Andrews (1971). Umbones appeared when larvae were about 120 µm long, similar to the 123.3 µm mean length reported by Culliney (1975) and within the 110 to 150 µm length range given by Sullivan (1948), but larger than the 95 to 100 µm length range found by Chanley and Andrews (1971). Shell length and shell height were equal when larvae of this species were approximately 150 µm, which was the size given by Imai *et al.* (1950) but was larger than the 123 and 122 µm sizes of equidimensional larvae found by Culliney (1975) and Mann and Gallager (1985), respectively. Size at metamorphosis was smaller than that reported by Sullivan (1948), Imai *et al.* (1950), and Mann and Gallager (1985) and approximately the same as that reported by Loosanoff and Davis (1963), Loosanoff *et al.* (1966), Chanley and Andrews (1971), and Culliney (1975). Difficulty in achieving consistent shell orientation due to great convexity of the valves during late larval stages may account for the discrepancies among measurements. Measurements of disarticulated valves, aligned with the shell margin in a plane, would improve accuracy.

Scheltema (1971) summarized previous descriptions of teredinid larvae from the North Atlantic. He emphasized that features included in these early descriptions, such as larval size ranges and color, are not always sufficient for positive identification of unknown species. On the other hand, differences in external shell surface sculpture revealed by scanning electron microscopy distinguished

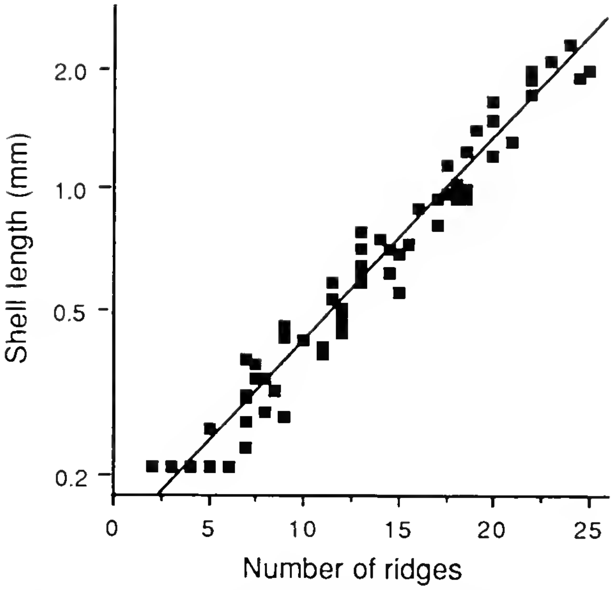

Figure 11. Relationship between shell length (greatest antero-posterior dimension) and number of (early and late post-larval) ridges on the exterior surface of shells of *Teredo navalis*. Regression equation is $y = -0.28 + 0.08x$; $r^2 = 0.93$.

several species of the Teredinidae (Scheltema, 1971; Turner & Boyle, 1975; Calloway & Turner, 1979). Also, Turner and Johnson (1971) illustrated the distinct nature of the velum in two teredinids and suggested use of this character as an aid in species identification.

The value of hinge structures for identification of larval bivalves is well-documented (Jorgensen, 1946; Sullivan, 1948; Rees, 1950; Loosanoff *et al.*, 1966; Chanley & Andrews, 1971; Le Pennec, 1980; Lutz *et al.*, 1982; Jablonski & Lutz, 1983). In teredinids, provinculum length is constant throughout the larval period (Rees, 1950); therefore, identification of teredinid species based on provinculum length can be made without regard to larval size or stage of development. In specimens of *T. navalis* larvae examined in the present study, dimensions of provincular teeth showed individual variation but were independent of developmental stage or size.

Provinculum length of *Teredora m*[illegible] Turton 1822) (= *Teredo thomsonii* Tryon. Tu[illegible] Scheltema, 1971) is approximately 70 μm (Rancur[illegible] 1) and of *T. navalis* averages 47.7 μm (pre[illegible]; therefore, larval specimens of *T. navalis* and *T.* [illegible] are easily distinguishable on the basis of provinculum length. Furthermore, measurements and shapes of individual teeth of *T. malleolus* reported by Rancurel (1965 differ from shapes and dimensions of teeth of *T. navalis* in the present study.

Scanning electron micrographs of a disarticulated right valve of *Lyrodus pedicellatus* (Quatrefages, 1849), another larviparous teredinid, were presented by Turner and Johnson (1970. figs. 1, 2). Although measurements of teeth from these micrographs are approximate, measurements of the length of the central tooth relative to the anterior and posterior teeth indicate distinct differences in the provinculum of the right valve of *T. navalis* and *L. pedicellatus*.

Dimensions of provincular teeth of *T. navalis* also differ from those of *Bankia martensi* (Stempell, 1899) (table 1). The most striking difference in the provinculum of these two species, however, is the shape of the anterior tooth of the right valve, which is J-shaped in *B. martensi* and rectangular in *T. navalis* (B. Campos, personal communication). A J-shaped anterior tooth is also noted in the provinculum of the right valve of *Bankia setacea* (Tryon, 1863) (Quayle, 1951: fig. 8).

METAMORPHOSIS

Lutz and Hidu (1979) suggested that development of the ligament pit was among the earliest morphological changes that occur in planktonic bivalves during metamorphosis. Further evidence of the early formation of the ligament pit is seen during metamorphosis of *Teredo navalis*. In this species, the ligament pit formed ventral to the hinge structure in post-larval shells approximately 230 μm high. Secretion of the dissoconch and formation of apophyses, dorsal and ventral condyles, and external ridges occurred subsequently, when shipworms were approximately 240 μm high.

Table 1. Lengths (distance across center of tooth and parallel to hinge line) in μm of provincular teeth of *Teredo navalis* and *Bankia martensi*.[1]

	Teredo navalis		*Bankia martensi*	
Position	Range	$\bar{x} \pm$ SD	Range	$\bar{x} \pm$ SD
	Left valve (n = 9)		Left valve (n = 10)	
Anterior	8.8–10.2	9.6 ± 0.5	8.5–12.8	9.1 ± 1.0
Posterior	7.7–8.6	8.2 ± 0.3	4.2–8.5	6.4 ± 1.0
	Right valve (n = 12)		Right valve (n = 9)	
Anterior	6.3–8.3	7.2 ± 0.6	4.2–6.4	5.2 ± 1.2
Central	13.7–18.2	16.4 ± 1.1	14.9–17.0	16.4 ± 0.8
Posterior	6.0–7.0	6.6 ± 0.3	4.2–8.5	5.9 ± 1.0

Data on *Bankia martensi* were provided by B. Campos, Universidad de Valparaíso, Viña del Mar, Chile. Specimens were sampled from Valparaíso Bay, Chile.

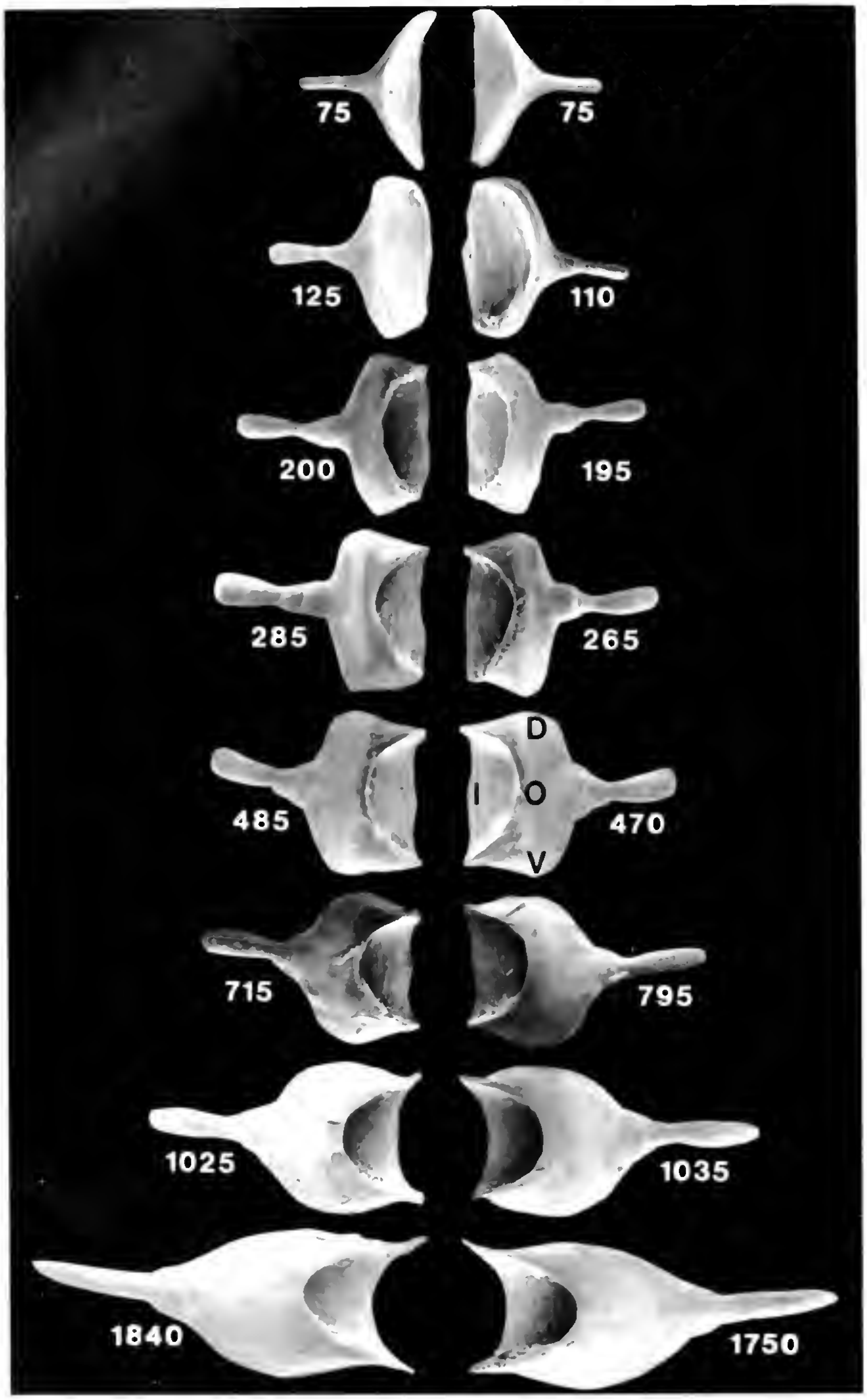

Figure 12. Scanning electron micrographs of the outer face of pallets of *Teredo navalis* post-larvae. Micrographs of similarly-sized right and left pallets are not necessarily from the same individual. Numbers indicate distance between distal and proximal ends in μm. I, inner margin, O, outer margin, D, dorsal surface, V, ventral surface.

In *T. navalis*, major modifications of the shell enable post-larvae to penetrate wood. Preparation for these changes begins in mid-larval stages with increased growth along the ventral shell margin, so that the new axis of articulation is oriented along the longest shell dimension. The shift in axis of articulation from the dorsal to the posterior plane is accomplished by shell loss along the posterior margin of the right valve. Quayle (1959) described similar shell loss along the posterior margin of the right valve of *Bankia setacea* following settlement and suggested that the loss was due to shell erosion. The shift occurs rapidly in *T. navalis*; shells approximately 230 μm high articulated along an anteroposterior axis, and shells approximately 240 μm high articulated along a dorsoventral axis. Subsequent adjustments for this rearrangement, however, occur more gradually with growth of the animal. These include further separation of the valves by an inward protrusion of the condyles until shells articulate against the condyles rather than against dorsal and ventral shell margins. Also, depth of the shell valves increases until articulated shells are nearly spherical. Separation of the valves allows extension of the foot and siphons.

The sudden shift in the axis of articulation is followed by an abrupt change in the orientation of growth axes. Growth axes of the anterior section of the anterior slope are roughly similar to larval growth axes. Growth at the extreme ventral margin of the dissoconch, however, is roughly perpendicular to the larval shell margin (figure 9).

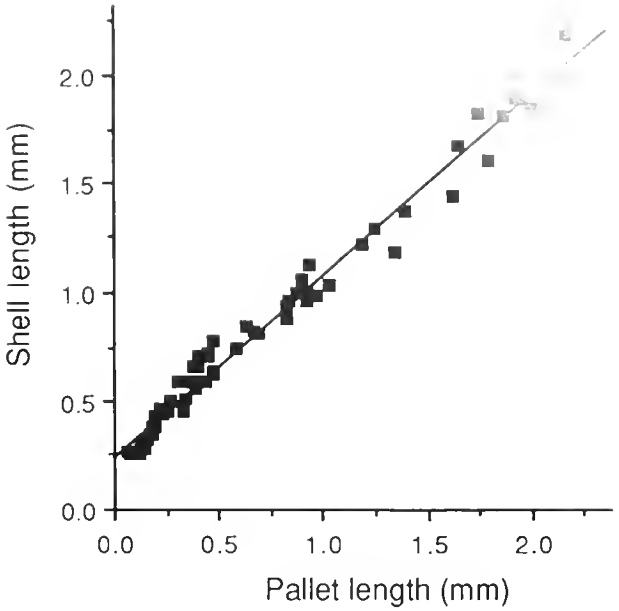

Figure 13. Relationship between shell length (greatest anteroposterior dimension) and pallet length (distance between proximal and distal ends). Each point represents an individual animal; when right and left values differed, the average was used. Regression equation is $y = 0.23 + 0.84x$, $r^2 = 0.99$.

Table 2. Summary of literature reports on larval shell dimensions (in μm) of *Teredo navalis* at (1) time of release from parent, (2) appearance of umbones; (3) equidimensional stage; and (4) metamorphosis. For comparative purposes, l = anteroposterior dimension; h = dorsoventral dimension, p = provinculum length

Source	Release	Umbones	Equi-dimensional	Metamorphosis
Grave (1928)	l = 85–90 h = 70–75	—	—	—
Jørgensen (1946)	l = 80 ($\bar{x}$)	—	—	h ≈ 250
Sullivan (1948)	h × l ≈ 80 × 95	l = 110–150	—	h × l ≈ 250 × 220
Imai *et al.* (1950)	l = 85 ($\bar{x}$) h = 72 ($\bar{x}$)	—	≈150	l = 215 ($\bar{x}$) h = 235 ($\bar{x}$)
Loosanoff and Davis (1963)	h × l = 70 × 80 (min) l = 90 (max) l = 85–95 (average)	—	—	l > 200 l = 190 (min) h = 206 (min) l = 200 (max) h = 231 (max)
Loosanoff *et al.* (1966)	h × l = 70 × 80 (min) l = 90 (max)	—	—	l > 200
Chanley and Andrews (1971)	l = 70–90 (min) p = 45–50	l = 95–100	130–140	l = 190–>200

Culliney (1975)	l = 87.7 ($\bar{x}$);
	range = 77–95
	h = 75.4 ($\bar{x}$);
	range = 66–85
	depth range = 55–57
	p = 51.3 ($\bar{x}$);
	range = 46–54
		l = 123.3 ($\bar{x}$)
		h = 123.3 ($\bar{x}$)
		depth = 90
			≈123	[1]l = 205.5,
				range = 200–216
				h = 239.2,
				range = 192–260
				depth = 190

Mann and Gallager (1985)	l = 89.3 ($\bar{x}$) h = 76.1 ($\bar{x}$)	—	≈122	[2]l = 212.1 h = 230.0
Present study	l = 81.5 ($\bar{x}$); range = 77–87 h = 66.6 ($\bar{x}$), range = 66–70	l = 120	≈150	l = 202.0 ($\bar{x}$) range = 195–210

[1] Pediveliger

[2] First appearance of pediveliger

EXTERNAL SHELL MORPHOLOGY

Numerous, closely-spaced denticulated ridges cover the external surface of the anterior slope of early post-larval shells of *Teredo navalis*. Although the number of ridges found in early stages is variable, observations show a consistent decrease in total number of ridges after formation of the posterior slope (compare figure 5, right valves, heights 275 and 295 μm). This decrease suggests that early post-larval ridges are obliterated as late post-larval ridges (ridges with both fine and coarse denticles) are added at the anterior shell margin.

Hill and Kofoid (1927) described the function of exterior ridges of the adult shell of *T. navalis*. By carving in an anterior direction, shipworms deepen burrows with the fine serrations on anterior ridges; at the same time, posterior ridges with coarser teeth increase the diameter of the burrow. Slightly curved early ridges have uniformly sized denticles (figure 5, height 330/295 μm). As described by Sigerfoos (1908) for *Bankia gouldi* (Bartsch, 1908), a difference in spacing at the dorsal and ventral ends of the shell of *T. navalis* gradually increases the curvature of a single ridge until a sharp right angle forms at the junction of the anterior and posterior sections of the anterior slope. In *T. navalis*, fine denticles form in the central portion of the ridge at this stage (figure 5, height 610/490 μm). Successive ridges are comprised of only fine denticles on the anterior section and only coarse denticles on the posterior section of the anterior slope (figure 5, height 855 μm).

PALLET DEVELOPMENT

Pallet morphology during early post-larval developmental stages was one of the characters used in determining phylogenetic relationships of species within the family Teredinidae (Turner, 1966). Unfortunately, development of pallets is described for only a few species. Pallets of *Lyrodus pedicellatus* were described by Isham and Tierney (1953) from first appearance until an estimated length of 80 μm. Rancurel (1955) described developmental stages of pallets approximately 400 μm long and larger for *Teredora malleolus*. Early pallet blades of both *Teredo navalis* in the present study and of *L. pedicellatus* described by Isham and Tierney (1953) are initially triangular in shape and then grow distally. Early pallets differ in the two species, however, in that the stalk of the pallets in *L. pedicellatus* is thin and transparent, while the stalk of the pallets in *T. navalis* is calcified and opaque. Also, in *L. pedicellatus* the stalk forms before the blade (Isham & Tierney, 1953: fig. 20), whereas the earliest pallets examined of *T. navalis* had a blade (figure 12, 75 μm). In *T. malleolus*, the blade of pallets nearly 600 μm long is circular in cross-section and, with subsequent elongation, develops a medial fissure (Rancurel, 1955: fig. 4; Turner, 1966). In *T. navalis*, the blade of pallets approximately 700 μm long is circular in cross-section and then becomes elongate, but development of a fissure does not occur (figure 12).

The degree of individual and environmental variation in pallet morphology of adult *T. navalis* was demonstrated by Miller (1923). Turner (1966) stated that two pallets removed from an individual shipworm often showed unequal erosion, breakage, and deformation. Pallets in the present study were less subjected to effects of an adverse environment because of controlled culture conditions and collection at an early age. In general, sampled pallets had similar morphology, and sequential developmental stages were consistent. A striking symmetry of opposing pallets was observed throughout the post-larval developmental period (figure 12).

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Shell Tubules in *Corbicula fluminea* (Bivalvia: Heterodonta): Functional Morphology and Microstructure

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INTRODUCTION

Narrow tubules are relatively common structures that permeate bivalve mollusc shells (Oberling, 1964; Kobayashi, 1969; Taylor *et al.*, 1969, Omori *et al.*, 1976; Robertson & Coney, 1979; Waller, 1980; Prezant, 1981; Watabe, 1988). Although well documented, they remain poorly understood. According to Waller (1980) these tubules are more common in epifaunal than infaunal bivalves. There have been several hypotheses concerning the function of these tubules. Waller (1980) summarized these in a publication on the shell and mantle of arcoid bivalves. Briefly, these include: windows for photoreception (allowing transduction of light to underlying pallial photoreceptors); anchorage sites for the mantle; aqueducts involved with, and as a means of, expanding surface area for respiratory exchange; protection against boring organisms; and a site for mobilization of calcium and carbonate ions to buffer extrapallial fluid during acidification events as might occur in long periods on adduction. Additionally, such tubules could be involved with embryonic nourishment (Rosso, 1954) or monitoring water conditions (Robertson and Coney, 1979).

Corbicula fluminea (Müller, 1774), unlike the corbiculids *Polymesoda caroliniana* (Bosc, 1901) (Tan Tiu, 1987) and *P.* (*Geloina*) *erosa* (Solander, 1786) (Prezant & Tan Tiu, 1986), possesses numerous shell tubules. These tubules, which are filled by mantle extensions, could be involved in lightening juvenile shells thereby decreasing the drift load during "planktonic" dispersal, and help in anchoring the mantle to the shell during locomotion or biomineralization.

MATERIALS AND METHODS

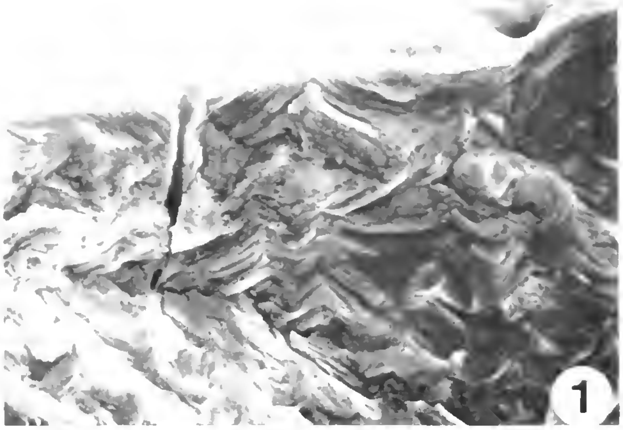
Shell microstructure of 30 specimens drawn randomly from some 250 specimens of *Corbicula fluminea* collected at different seasons and from various habitats in southern Mississippi and ranging in size from 7 to 38 mm shell length, were closely scrutinized for possession of shell tubules. Exact details of collection times and sites can be found in Prezant and Tan Tiu (1986) and Tan Tiu (1987). Whole or fractured valves were critical point dried in a Denton DCP-1 Critical Point Drier using liquid carbon dioxide as a transfer agent from absolute ethanol, either without prior treatment or following treatment in 50% (v/v) hydrochloric acid or 50% (v/v) commercial Clorox (sodium hypochlorite). Specimens were coated with a thin layer of gold in a Polaron SEM Coating Unit E5100, and examined at accelerating voltages of 30 kV in an AMR 1000 scanning electron microscope.

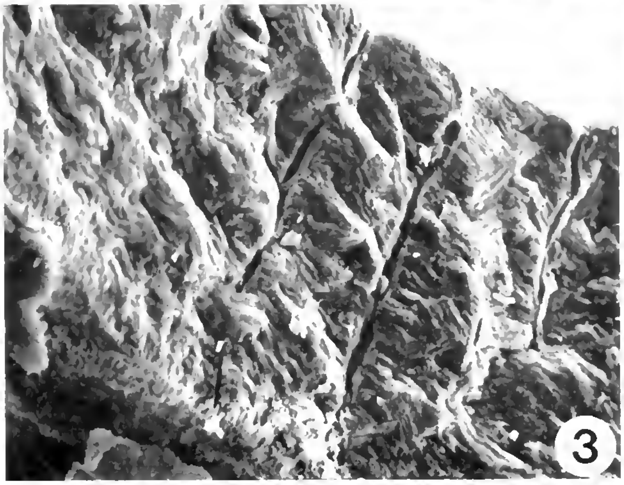
RESULTS

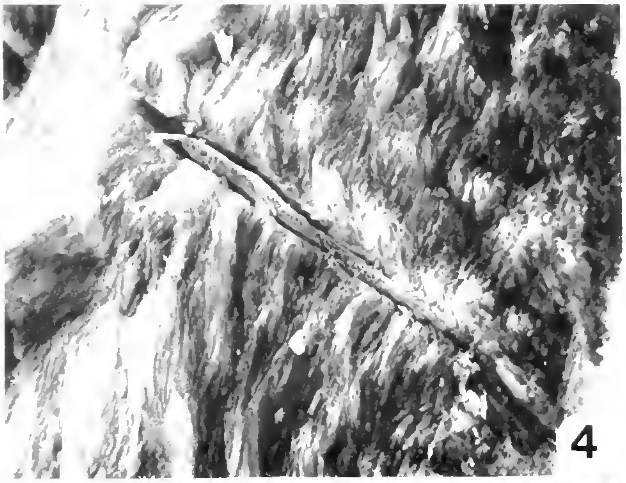
Narrow tubules, circular in cross-section, are a common feature of the early dissoconch shell of *Corbicula fluminea*. The extent of shell that has tubules covers a concentric band about 2 mm wide parallel to the curvature of the shell margin. The proximal border is about 700 μm from the hinge. Tubules averaging 6 μm in diameter consistently permeate the early dissoconch in this band, but not the prodissoconch nor the later dissoconch shell in all specimens examined.

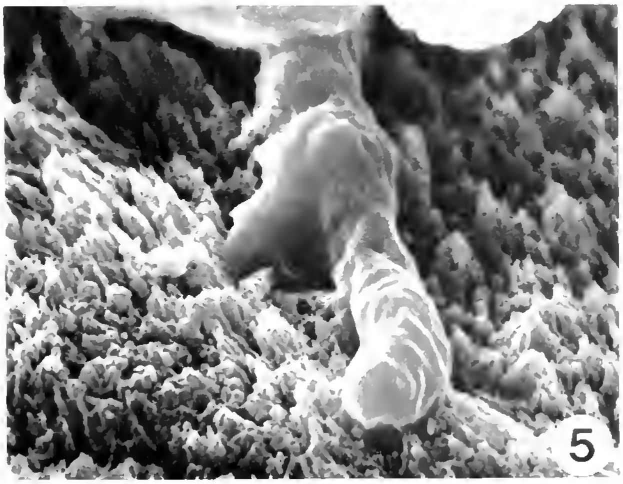
Straight or sinuous tubules penetrate "well formed" cross-lamellar shell microstructures (figures 1, 2) and are usually oriented roughly perpendicular to the shell surface (figure 3) up to the vicinity of the periostracum. Here they are infrequently deflected to become roughly parallel to the inner surface of the periostracum. This occasionally is revealed in specimens treated with acid. In these the surface shell is eroded and remnant surface shell has rarely shown a single mantle extension exiting one tubule in cross-section and entering another along a plane parallel to the shell surface. Internally, tubules are filled by extensions of the mantle (figure 4). The leading end of this finger-like mantle projection is smooth (figure 5). These tissues occasionally show a bifurcating or anastomosing tip (figures 5, 6) toward the shell exterior.

The relatively uniform distribution of mantle extensions into tubules is illustrated in figure 7. This micrograph shows the basal regions of mantle extensions on the shell-facing surface of a reflected portion of the mantle. Disregarding shell tubule branchings and anastomoses, and assuming that the tubules were perfect cylinders, a conservative estimate of volume occupied by









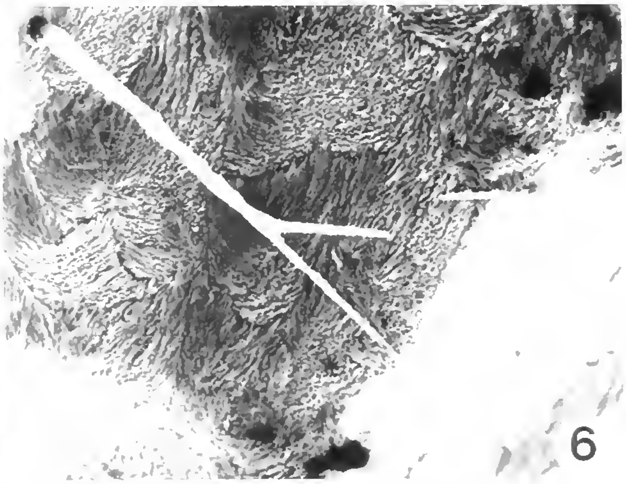


Figure 1. Shell fracture showing flared end of tubule on inner surface (top of photo) of shell, and normal crossed-lamellar microstructure of tubular wall. Horizontal field width (HFW) = 192 μm. **Figure 2.** Shell fracture showing normal crossed-lamellar microstructure of tubular wall (inner surface of shell towards lower right). HFW = 16 μm. **Figure 3.** Shell fracture showing tubules traversing the entire calcareous shell component. Shell tubules are oriented roughly perpendicular to the shell surface (inner surface of shell towards upper right). Portions of periostracum are visible on lower left of photo. HFW = 332 μm. **Figure 4.** Shell fracture showing mantle extension in a tubule (inner surface of shell towards upper left). HFW = 89 μm. **Figure 5.** External surface of shell [periostracum and thin layer of shell digested by 50% (v/v) hydrochloric acid for 30 seconds] showing leading edge of mantle extension. HFW = 16 μm. **Figure 6.** External surface of shell [periostracum and thin layer of shell digested by 50% (v/v) hydrochloric acid for 30 seconds] showing bifurcation of tubular extension. HFW = 228 μm.

tubules relative to total volume of shell possessing tubules ranged from 0.8 to 2.1%. Figure 8 shows the inner shell surface with an estimated density of 196 tubule openings per square millimeter, which is about four times greater than the density of possible tubule openings in the external shell surface (figure 9).

DISCUSSION

We believe this is the first recorded observation of the distal tips of mantle extensions associated with shell tubule formation. The mantle extensions in *Corbicula fluminea* do not penetrate the periostracum, as is true for the pisidiids (Robertson & Coney, 1979) and arcoids (Waller, 1980). The tubules can detour away from the periostracum and anastomose laterally, as viewed from the shell exterior in a partially decalcified shell. Unlike shell tubules in arcoids (Oberling, 1964; Waller, 1980) and pisidiids (Robertson & Coney, 1979), which are distributed throughout the shell medial to the pallial line, shell tubules in *C. fluminea* are restricted to the early dissoconch. It is uncertain whether the dissolution occurs only proximally in early shell deposition or distally and radially along the base and length of the pallial extension. In fact, without cyto- or histochemical analyses, we can only speculate that the mantle extensions filling the tubules are responsible for penetration of the shell and likely do so through chemical means. It is possible that an acid, as found in the mantle of *Lithophaga* Röding, 1798 (Morton, 1983), or a proteolytic enzyme similar to those produced by the accessory boring organs of muricid gastropods (Carriker & Williams, 1978), is involved in shell tubule formation by dissolution. It is also possible, though unlikely, that shell biomineralization occurs around an inhibitory mantle extension.

We propose that supplementary anchorage of mantle to shell is the primary function of the tubular tissues in *Corbicula fluminea*. This is suggested by the orientation of the mantle extensions that branch or anastomose toward the shell exterior, thus forming a root or anchor within the shell. During early stages of juvenile development, including small mature clams (7–14 mm shell length), *C. fluminea* is able to disperse through the water column using ctenidial-produced mucous drouge lines (Prezant & Chalermwat, 1985). During this drifting period the valves remain widely abducted. This, as well as the usually active behavior of benthic juveniles (Kraemer, 1986), could place strain on the mantle–shell juncture. Mantle extensions could aid in maintaining this connection. Moreover, the decrease in shell volume directly attributed to the shell tubules could offer the bivalve a slightly lighter shell with less mineral content. As drifting occurs in smaller clams and the tubules are only found in the early dissoconch shells of *C. fluminea*, there is a possible correlation between drifting and possession of lighter shell. Beyond the drifting stage, the tubules possibly become a liability rather than an asset as suggested by the differential erosion of the external shell surface at the umbonal region, as observed by Kat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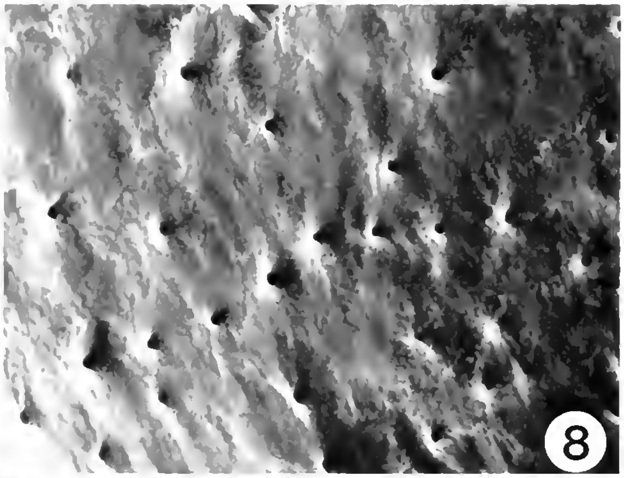
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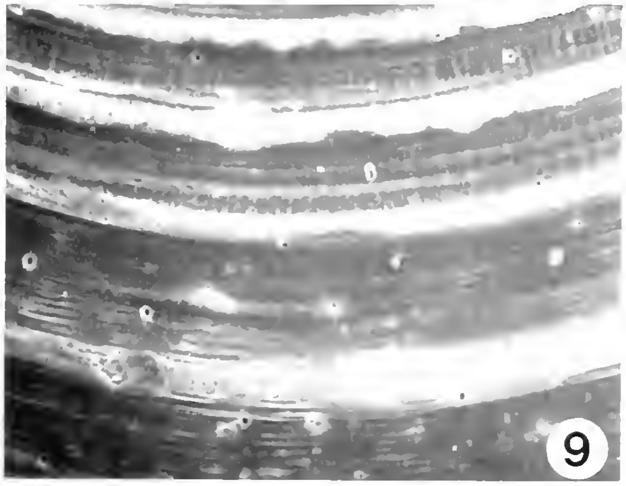
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Figure 7. Mantle reflected to show uniform distribution of mantle extensions on surface facing shell tubules (upper right). HFW = 707 μm. **Figure 8.** Opening of tubules on inner surface of shell (estimated density = 196 tubules per square millimeter). Umbo towards the top. HFW = 453 μm. **Figure 9.** Density of tubule openings on external surface of untreated shell is four times lower (estimated density = 45 tubules per square millimeter) than on inner surface (see figure 8). HFW = 660 μm.

(1982), in clams inhabiting acidic waters. The mantle extensions anchored to the wall via shell tubules could facilitate biomineralization by bringing the mantle in close apposition to the deposition site, *i.e.*, shell. This could be particularly important in the umbonal region as, under certain conditions, this is the thinnest part of the shell (*i.e.*, in those with eroded umbos). It is also possible that whenever the mantle extensions of *C. fluminea* are exposed, due to extreme external erosion of shell, the mantle extensions secrete substances to the outer surface of the shell, preventing further shell erosion (Fritz *et al.*, 1988). Some shell tubules that penetrated the periostracum (figure 9) and as noted by Fritz *et al.* (1988) are likely preservation and erosion artifacts, respectively. At present, all proposed functions of shell tubule and associated mantle extensions remain speculative.

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Reoccurrence of *Cyclonaias tuberculata* in the Huron River, Michigan

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In 1935, mussels virtually paved the bottom of shoal-like niches of the Huron River in southeastern Michigan. Characteristic assemblages existed in the small, medium, and large-river zones, as well as in creeks and river-lakes (Van der Schalie, 1970). Since then, human activities have brought about serious depletion among the 25 species of mussels that occupied long stretches of the Huron. One of those species, *Cyclonaias tuberculata* (Rafinesque, 1820), was abundant between the cities of Dexter and Ann Arbor in the 1930's but was designated as a rare and endangered species by Michigan's 1975 Natural Features Inventory.

Water quality in this river segment was improved in recent years (Gannon & Meier, 1986) and currently supports a top quality, warm water fishery. In this note we report findings of a survey conducted between Ann Arbor and Dexter during the summer of 1986 to determine if *Cyclonaias tuberculata* had reestablished itself in this portion of the Huron River.

The study area is a 16-km reach, between river miles 60 and 70. In this river segment, width ranges between 12 and 45 m and depth between 0.9 and 9.0 m (Say & Jansson, 1976), except for low flow conditions when depths of 0.15 m were recorded. The 24-year annual mean discharge ranges between 3.96 m^3/sec and 16.7 m^3/sec.

Six sampling locations were identified as having suitable substrate for *Cyclonaias tuberculata*. Preliminary collecting established the presence of living or dead *Cyclonaias* at each of the sites. Where site conditions permitted, 76 randomly sampled 1-m^2 plots were surveyed, 36 on each side of the river, six times between June and August. Shells were hand-picked from the shallows, digging several inches below the surface. Dead valves deposited as middens by muskrats and raccoons were included. The length of each shell was recorded, as well as whether the specimen was live or dead. Living specimens were returned to the river.

Of the 370 specimens of *Cyclonaias tuberculata* found, 23.5% were live animals. The three upriver stations yielded 70% of the live specimens. Other genera found in this reach of the river were *Lampsilis*, *Villosa*, *Anodonta*, *Elliptio*, *Ligumia*, and *Pisidium*. The age of *Cyclonaias*, approximated by the length of the shell, ranged from about 3 to 20 years (2.6 to 11.0 cm); the average age for both live animals and dead shells was approximately 13–15 years (7.3 cm).

While the species has managed to recolonize this area since its decimation some 50 years ago, its numbers remain well below prior population levels (Van der Schalie, 1970). A greater number of living specimens were located in upriver sampling sites compared to downriver sites; this may correlate with improved water quality. In recent surveys the water quality of those upper reaches was rated as very good (Gannon & Meier, 1986). The lower rated downriver area is impacted by Mill Creek, the largest source of agricultural non-point pollution to this river reach. During our study, plumes of silt and suspended sediment were observed entering the river from Mill Creek, possibly suffocating organisms. This deleterious effect may also be exacerbated by the effluent of the Dexter Sewage Treatment Plant.

Theoretical life history data suggest that a healthy population would contain greater numbers of young valves relative to older valves than were found in this survey. Three hypotheses may explain the deviation between the size frequency distribution found in this survey (figure 1) and the expected theoretical distribution. (1) Annual recruitment may be low compared to 13 to 15 years ago. (2) Greater selective mortality of young, relative to older valves, may be occurring now with small dead shells being washed to the nearest impoundment where current is slowed. (3) Sample methodology used may not be sensitive to the smallest mussels. Because young mussels are approximately 0.32 cm long at age 1 year (Neves, 1985), hand sampling is likely to miss this group. In addition, the juvenile state may occupy habitats other than those of the adult that we sampled (D'Eliseu, 1972).

The latter hypotheses were tested in the summer of 1987 when the 1986 sample sites were revisited and

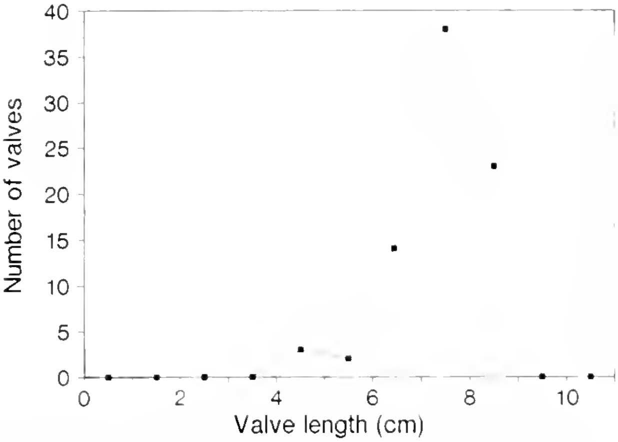

Figure 1. Size-frequency distribution of live and dead *Cyclonaias tuberculata* found in the Huron River study area

sampled using a 2-mm mesh sieve. Three non-adult habitat types were also sampled: macrophytes, loose substrate downstream of boulders, and deep pool areas. Sampling with sieves allowed a higher percentage of live adults (53%) to be found compared to 23% in the 1986 survey. However, only one early juvenile (less than 17 mm) and four late juveniles (greater than 17 mm but less than 4 years old) were found in 450 0.25-m^2 samples. An abundance of Sphaeriidae of the desired size category were found, ruling out inefficient sampling as the problem but raising the additional concern of species competition. It has been postulated (Neves & Widlak, 1987) that the juvenile stage of Unionidae is probably the most susceptible stage to competitive interactions for food or space. Because Sphaeriidae has a competitive advantage in terms of adaptability, young Unionidae may suffer as Sphaeriidae prosper.

This survey has determined that *Cyclonaias tuberculata* has been reestablished in the Huron River between Ann Arbor and Dexter. However, the population size-frequency distribution suggests there may be cause for additional concern. More information is needed to assess if annual recruitment of *Cyclonaias tuberculata* is sufficient to maintain a healthy mussel assemblage.

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Occurrence of the Ribbed Mussel, *Geukensia demissa*, on the Book Gills of a Horseshoe Crab, *Limulus polyphemus*[1]

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While collecting specimens of the flatworm, *Bdelloura candida* Girard, 1850, from the gills of the horseshoe crab, *Limulus polyphemus* Linné, 1758, we observed a single specimen of the Atlantic ribbed mussel, *Geukensia demissa granosissima* Sowerby, 1914, attached by byssal threads to a gill filament of one of the *L. polyphemus*. This was the only occurrence of fouling by a mollusk in well over 200 *Limulus* examined over a 2 day period. The *Limulus* were collected in March of 1985 from the Indian River in Florida near the Volusia–Orange County line.

It is of particular interest that the mussel was attached to the gills of the *Limulus* since the latter species possesses an appendage (the flabellum) specialized for cleaning the gill filaments. Most, if not all, aquatic arthropods groom the body surfaces, including the gills, extensively (Bauer, 1981). The flabellae of the fouled *Limulus* were fully functional. The mussel would not remain attached to the *Limulus* beyond the next molt, as the byssal threads did not penetrate the exoskeleton. The shell length of the *G. demissa*, which probably settled on the horseshoe crab as a larva, was 18 mm, suggesting that the animal was about a year old (Lutz & Castagna, 1980). The *Limulus* had a carapace width of 15.5 cm.

Reports of fouling bivalves on arthropods are uncommon. Wolff (1959) found 12 *Mytilus edulis* Linné, 1758 on a green crab, *Carcinus maenas* Linné, 1758, as well as several 5–6 year old *Crassostrea virginica* on an individual of another crab species, *Hyas araneus* Linné, 1758. The age of the fouling oysters on this *H. araneus* is probably explained by the fact that this species, like most spider crabs, molts infrequently once mature (Hartnoll, 1963). Marine turtles harbor a variety of epifaunal mollusks, including both gastropod and bivalve species (Frazier *et al.*, 1985). The gastropod genus *Crepidula* has been reported to occur on *Limulus* (Hoagland, 1984), and while we found no *Crepidula fornicata* Linné, 1767 on any of the *Limulus* in the sample described here, these gastropods are not uncommon on the ventral surface of *Limulus* from this collection site.

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[1] This is contribution number 282 from the Tallahassee, Sopchoppy and Gulf Coast Marine Biological Association.

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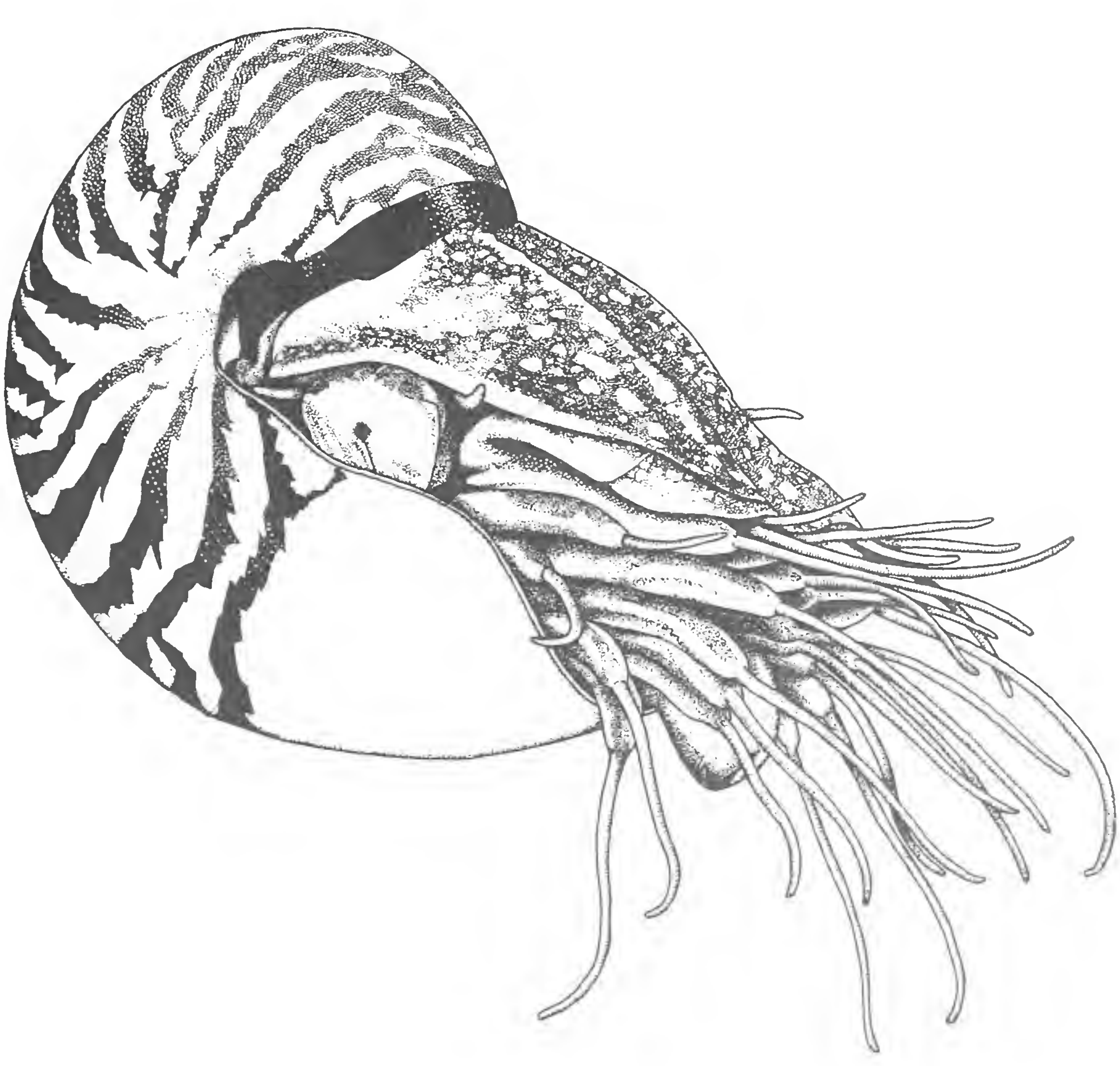

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CONTENTS

Systematic Revision of the Recent Species of *Peasiella* Nevill, 1885 (Gastropoda: Littorinidae), with Notes on the Fossil Species

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ABSTRACT

Peasiella is a genus of the Littorinidae, whose members have minute, trochoidal shells, and are found on rocky shores in the Indo-Pacific region. Six Recent species are recognized herein, one of which is described as new. Shell characters are highly variable, but usually adequate for identification, and provide characters for a key. The reproductive anatomy, paraspermatic nurse cell, egg capsule, head-foot, and radula are described. Distribution maps are provided, and the species can be classified as oceanic, continental, or intermediate, according to their distribution and habitat. Within the subfamily Littorininae the phylogenetic relationships of *Peasiella* are uncertain. Fossils are known from France and New Zealand, the earliest from the Middle Eocene. Four fossil species are briefly described, but the account is probably not complete, because fossils may have been misclassified in other families.

INTRODUCTION

Living species of *Peasiella* are restricted to the Indo-Pacific region. Their shells are minute and trochoidal, quite unlike those of most other littorinids. Consequently, this is one of the most poorly known genera in the family Littorinidae. Nevill (1885) listed seven species, and Tryon (1887), in the first and hitherto only monograph, included eight species. In the present revision six Recent species are recognized, one of which is described as new.

Because of the trochoidal shell and multispiral operculum, it is not surprising that six of the 19 available names for Recent species were first described as members of the Trochidae (Gould, 1849; Adams, 1853; Reeve, 1862; Pease, 1868; Issel, 1869; Turton, 1932). Fossil species have been placed in the non-littorinid genera *Trochus*, *Pseudonina*, *Tornus*, and *Xenophora* (Deshayes, 1824; Morgan, 1915; Cossmann & Peyrot, 1917–19). The littorinid affinities of these shells were first noted by Dunker (1861), who described a species as a *Risella* Gray, 1842 (= *Bembicium* Philippi, 1846; see Reid, 1988). This classification was followed by most later authors, and indeed the name *Peasiella* was first proposed as a subgenus of *Risella* by Nevill (1885). Because the operculum of *Peasiella* is multispiral, while that of *Bembicium* is paucispiral, Kesteven (1903) used it as a full genus, and removed it to the Modulidae, together with the littorinid genus *Echinella* Swainson, 1840 (= *Tectarius* Valenciennes, 1832; see Reid, 1989), which also has a multispiral operculum. The only other authors to indicate a relationship between *Peasiella* and *Tectarius* were Souverbie and Montrouzier (1879), who described a *Peasiella* species as an *Echinella*. *Peasiella* became widely accepted as a full genus through the work of Japanese authors (*e.g.*, Habe, 1956, 1964, 1984; Oyama & Takemura, 1961; Yamamoto & Habe, 1962). Nevertheless, the superficial resemblances between shells of *Peasiella* and *Bembicium* continued to suggest a close relationship, and Rosewater (1970) considered that they should be placed together in a separate subfamily. The status and relationships of all the genera of the Littorinidae have recently been revised, using cladistic analysis of anatomical characters, and it has been shown that while *Bembicium* is a member of the Lacuninae, *Peasiella* belongs in the relatively derived Littorininae (Reid, 1989). However, the relationships of *Peasiella* with other littorinine genera remain uncertain.

An exhaustive survey of the fossil species is beyond the scope of this work, for the material is widely scattered in museum collections, and much of it is probably misclassified in other families.

Peasiella species are often common, but are inconspicuous, so that their ecology is poorly known. The available information is summarized below. Museum collections do provide some information about habitat preferences, and give a relatively complete picture of geographical distribution.

MATERIALS AND METHODS

This account is based on the collections of the following museums: British Museum (Natural History), London (BMNH); Muséum National d'Histoire Naturelle, Paris (MNHNP); National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM); Academy of Natural Sciences of Philadelphia (ANSP); Museum of

Comparative Zoology, Harvard University (MCZ); Los Angeles County Museum of Natural History (LACM); Natal Museum, Pietermaritzburg (NM); National Science Museum, Tokyo (NSMT); Australian Museum, Sydney (AMS); Western Australian Museum, Perth (WAM); New Zealand Geological Survey, Lower Hutt (NZGS). Material has been collected personally (DGR, specimens in BMNH) in Australia, Hong Kong, and Hawaii. In addition, type specimens have been borrowed from the Zoological Survey of India, Calcutta (ZSI); Oxford University Museum (OUM); Museum für Naturkunde, East Berlin (ZMB) and Museo Civico di Storia Naturale 'Giacomo Doria', Genoa (MGD). All type specimens have been examined unless otherwise stated. Lectotypes have only been designated from syntypic series when only a part of the original series was made available for examination.

Shell height was measured parallel to the axis of coiling, and shell diameter perpendicular to this axis. The height/diameter ratio was calculated as an index of shell shape. The number of whorls of the teleoconch was counted from the sinusigera ridge terminating the protoconch, and the number of protoconch whorls counted as described by Reid (1988:94). The numbers of ribs and grooves given in parentheses are the rare extremes of the range.

The amount of preserved material available was not large, but 74 specimens were dissected, as listed in parentheses among the locality records, with the sex indicated. No specimens were found to contain parasitic trematodes. Serial histological sections were cut of three male and two female *P. roepstorffiana*, and one female each of *P. tantilla* and *P. lutulenta*. These were stained with either Masson's trichrome (MT) (Culling, 1963) or by the alcian blue–periodic acid–Schiff (ABPAS) technique for the histochemical differentiation of mucins (Mowry, 1956). Spermatozoa from the seminal vesicle were examined by light microscopy in four *P. roepstorffiana*, three *P. lutulenta* (in each case from whole animals fixed and stored in 10% formalin in seawater), one each of *P. tantilla* and *P. isseli*, and three *P. roepstorffiana* (in these three cases samples from living animals were fixed in 1% formalin in seawater, immediately before examination).

Radulae of 31 specimens were examined, from three to eight for each species. They were treated with boiling 50% potassium hyroxide solution for 15 minutes, rinsed, cleaned ultrasonically for ten seconds, and mounted flat for examination by scanning electron microscopy. Photographs were taken of top and side views, and from the anterior end at 45° to the horizontal; this last was adopted as the standard view for showing cusp shape.

All collections listed in the locality records were examined, and have been used to construct distribution maps.

GENERAL DESCRIPTION

The following descriptions of shell and anatomy of *Peasiella* are brief. A general, comparative account of all the genera of the Littorinidae has been given elsewhere (Reid, 1989).

Shell and protoconch: Shells of *Peasiella* are small (less than 6.6 mm diameter) and almost always umbilicate. The shape is usually trochoidal (conical, with a keeled periphery), but can be rounded at the margin and depressed. The surface is usually sculptured by major spiral grooves and fine spiral microstriae (figure 16). Conspicuous features such as carinate spiral ribs and radial folds show considerable variability within species. The folds may produce undulations of the peripheral keel, or in extreme cases cause it to appear crenulated (scalloped). The high degree of intraspecific variation can be ascribed in part to large-scale geographical variation (see systematic section). In addition, the shells show allometric growth (the apical angle decreasing with size), and a small degree of sexual dimorphism (females being larger and slightly lower-spired than males). Nevertheless, all the six Recent species can be distinguished by their shells. The arrangement of ribs on the shell base is an especially useful character. *Peasiella isseli* and *P. infracostata* may both occasionally show small periostracal bristles on the ribs around the umbilicus (figure 15).

The shell color pattern is basically of spiral rows of dark spots, most prominent at the suture and periphery, which sometimes form oblique or even spiral lines. Again there is much intraspecific variation on a geographical scale, but color patterns are nevertheless useful for identification (figures 1–14).

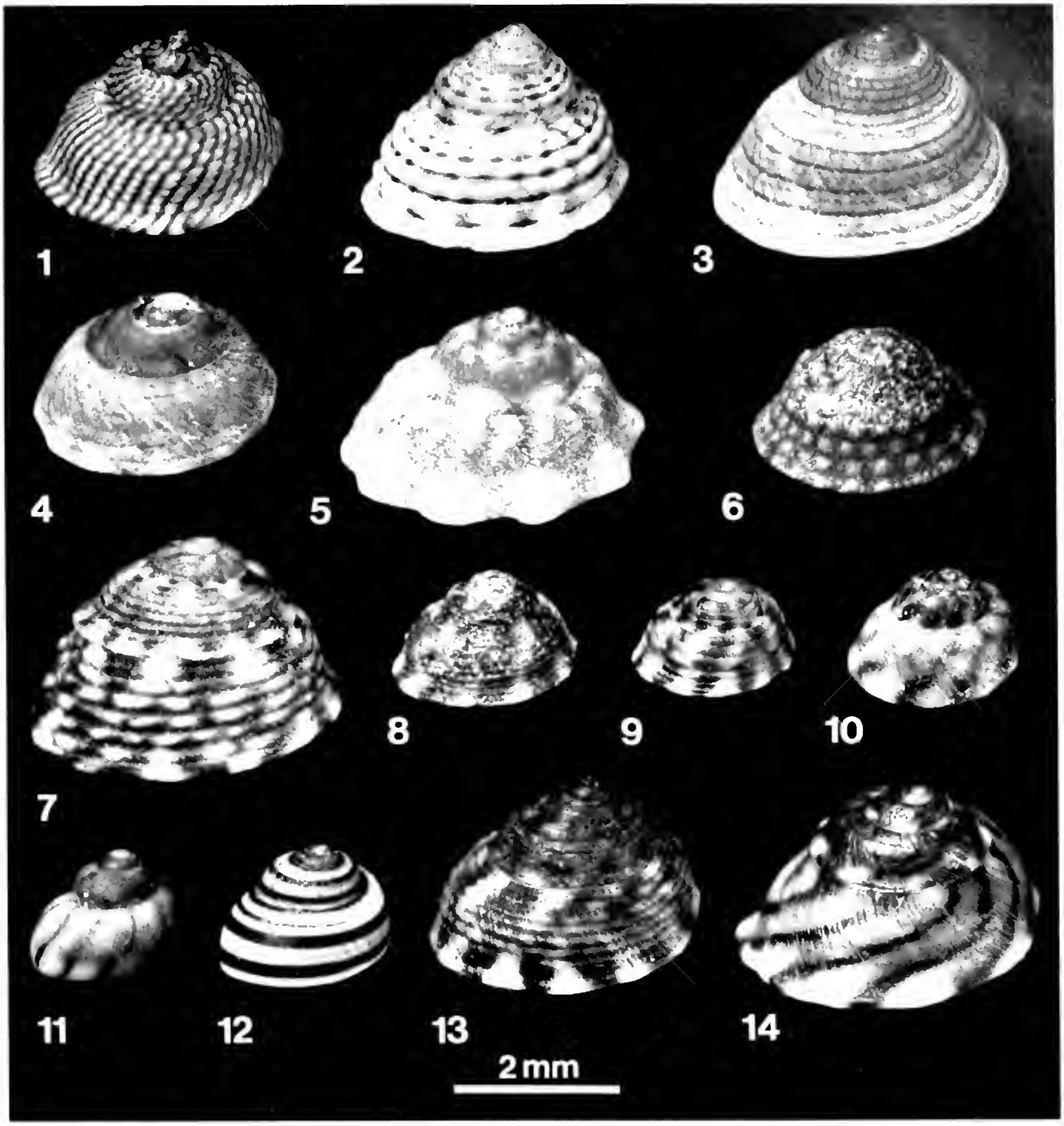
All the species show a small (0.21–0.28 mm diameter), sculptured protoconch, terminated by a sinusigera ridge, indicating planktotrophic development. The protoconch consists of 2.3 to 2.8 whorls, of which the last 1 to 1.5 are sculptured by four or five zigzag or almost straight spiral cords (figures 17, 18). It is only rarely preserved intact in adult shells.

Operculum: The operculum is round, corneous and multispiral, with five to seven revolutions (figure 19). This type is found elsewhere in the Littorinidae only in *Tectarius* (*Echininus*) Clench & Abbott, 1942.

Head-foot: Pigmentation of the head-foot is relatively pale, and frequently there are one to three black bands across the base of the snout. There may be one or two longitudinal black lines on the tentacles (figures 31–50). From the limited amount of preserved material available, it appears that the pigmentation pattern of the head may prove to be a useful taxonomic character in this genus.

There is no evidence of longitudinal division of the foot in preserved specimens, but this requires confirmation in living animals.

Male reproductive system: Both the prostate gland and the anterior vas deferens along the side of the head are open grooves, but the penial vas deferens is superficially closed (*i.e.*, the duct is not surrounded by muscle, but an epithelial connection to the surface remains). The penis is long and usually with a single mamilliform penial



Figures 1–14. Shells of *Peasiella* species, showing color patterns. **1.** *P. tantilla*, Pupukea, Oahu, Hawaiian Is (BMNH). **2.** *P. conoidalis*, New Caledonia (BMNH). **3.** *P. roepstorffiana*, Orpheus I., Queensland (BMNH). **4, 5.** *P. roepstorffiana*, Ping Chau, Hong Kong (BMNH). **6.** *P. roepstorffiana*, Fiji (BMNH). **7.** *P. lutulenta*, Barrow I., Western Australia (BMNH). **8.** *P. lutulenta*, Hoi Sing Wan, Hong Kong (BMNH). **9.** *P. lutulenta*, Rowes Bay, Townsville, Queensland (holotype, AMS C149052). **10.** *P. infracostata*, Japan (BMNH). **11.** *P. infracostata*, Karachi (BMNH). **12.** *P. infracostata*, Cape Ferguson, Queensland (BMNH). **13.** *P. isseli*, Suez (BMNH 82.8.7.316). **14.** *P. isseli*, Grand Bay, Mauritius (possible syntype of *Risella isseli* var. *mauritiana* Viader, 1951, BMNH 1989004).

gland halfway along its length. Histological examination reveals an additional type of penial gland, a small patch of simple, subepithelial glands (not forming a glandular disk, see Reid, 1989), at the base of the mamilliform gland. These two glandular types can be distinguished by their staining reactions. The secretion of the mamilliform gland stains red in MT and magenta in ABPAS, whereas that of the simple gland is colorless or pale blue in MT and stains darker magenta in ABPAS. The secretion passes out through the hollow, raised papilla of the mamilliform gland, but in the simple gland the secretion passes in intercellular extensions through the overlying epithelium to the surface. Goblet cells (staining blue in ABPAS) are abundant in the penial filament (*i.e.*, distal to the mamilliform gland).

In general, penial shape is similar in all *Peasiella* species, and so is not a useful taxonomic character (figures 31–50). *Peasiella roepstorffiana* is unusual, because in parts of its range the mamilliform gland is absent. Penial shape is normally rather constant within littorinid species, and it is possible that two species may be involved here, as discussed in the systematic section.

Spermatozoa: As in all members of the Littorininae, the spermatozoa in the seminal vesicle are dimorphic. The euspermatozoa are filiform and 36 to 50 μm in length. The paraspermatic nurse cells are irregularly rounded or oval and 11 to 23 μm in diameter. They are packed with conspicuous round granules (small and indistinct in *P. roepstorffiana*) and a nucleus is sometimes visible, but they lack rod-shaped inclusions (figures 51–56). In most other littorinines the euspermatozoa are attached in bunches to the nurse cells, to form spermatozeugmata, which may function to prevent premature dispersal of sperm from the largely open male pallial gonoduct (Reid, 1989). However, in the few *Peasiella* that have been examined, the euspermatozoa are not attached to the nurse cells and the two cell types are simply packed together in the seminal vesicle. This condition is also found in *Melarhaphe* Menke, 1828, which, like *Peasiella*, has a superficially closed penial duct. Whether the apparent absence of spermatozeugmata is primitive, or a secondary loss as a consequence of closure of the penial duct, is unknown. The former is more likely, because elsewhere in the Littorininae spermatozeugmata can be found in genera with superficially closed penial ducts (*e.g.*, *Cenchritis* von Martens, 1900, some species of *Littoraria* Griffith & Pidgeon, 1834). As discussed in the systematic section, some specimens of *P. roepstorffiana* lack nurse cells in the seminal vesicle. Neither intraspecific nor intrageneric variation in the presence of nurse cells has been reported in any other littorinids.

Female reproductive system: The general arrangement of the pallial oviduct is the same as in other oviparous members of the Littorininae, with the egg groove passing successively through opaque albumen gland (colorless in MT, magenta in ABPAS), translucent albumen gland (colorless in MT, blue or magenta-purple in ABPAS), opaque capsule gland (red in MT, pale purple in ABPAS), translucent capsule gland (blue in MT, dark purple and magenta in ABPAS), and small jelly gland (colorless in MT, magenta in ABPAS). Differentiation of these glands can sometimes be seen in the whole animal and in gross serial sections; the opaque capsule gland is especially prominent, visible as a chalky white or cream crescent on the lateral side of the pallial oviduct (figures 57–63, 65, 66). The spiral route of the egg groove (figures 58, 66), with a backward loop of albumen gland followed by a larger loop of capsule gland, is unique to the genus, and is the same in all six species.

The histological structure of the glands of the pallial oviduct is unusual, in that there is not a clear separation between a non-glandular epithelial lining of the egg groove and the subepithelial glandular follicles beneath [as found in all other Littorininae except *Melarhaphe* (Reid, 1989)]. The posterior part of the jelly gland and all of the capsule gland clearly show subepithelial glandular tissue, but the albumen gland appears to be largely of epithelial structure. Probably the glandular cells are both epithelial and subepithelial throughout the pallial oviduct.

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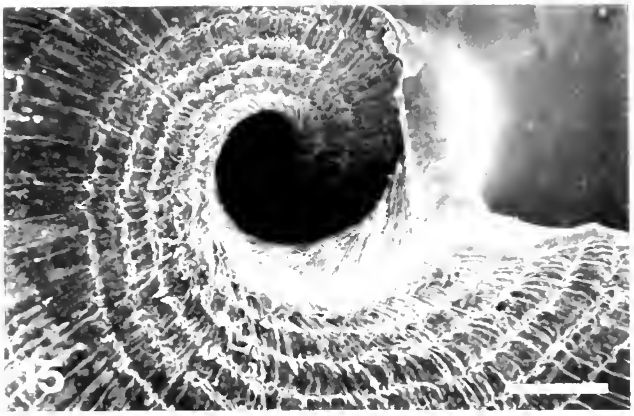
Figures 15–22. Sculptural details, protoconchs, operculum, and radula of *Peasiella* species. Scale bars 15–19 = 0.2 mm; 20–22 = 0.02 mm. **15.** *P. isseli*, detail of umbilicus showing periostracal bristles, Oman (BMNH). **16.** *P. conoidalis*, detail of sculpture on last whorl, Anaa, Tuamotu Is (BMNH). **17.** *P. roepstorffiana*, protoconch, Orpheus I., Queensland (BMNH). **18.** *P. conoidalis*, protoconch, Oneroa, Tuamotu Is (USNM 720753). **19.** *P. roepstorffiana*, operculum, Samar I., Philippines (NSMT 56716). **20–22.** *P. tantilla*, three views (flat, side and anterior from an angle of 45°) of a single radula, Coconut I., Oahu, Hawaiian Is (BMNH).

Figures 23–30. Radulae of *Peasiella* species. 23, 24, and 27 are anterior views from an angle of 45°; others are vertical views of flat radulae. Scale bars = 0.02 mm. **23.** *P. conoidalis*, Dunidu I., Male, Maldive Is (ANSP 305263). **24.** *P. conoidalis*, Anaa, Tuamotu Is (BMNH). **25.** *P. roepstorffiana*, Magnetic I., Queensland (BMNH). **26.** *P. roepstorffiana*, Ping Chau, Hong Kong (BMNH). **27.** *P. lutulenta*, Barrow I., Western Australia (WAM 2347-67). **28.** *P. isseli*, Mahé, Seychelles (BMNH). **29.** *P. infracostata*, Okinawa, Ryukyu Is (AMS C146902). **30.** *P. infracostata*, Cape Ferguson, Queensland (BMNH).

Figures 31–50. Heads and penes of *Peasiella* species. All or part of penial vas deferens and duct of mamilliform gland indicated by dotted lines when visible by transparency. All drawn from fixed material, except 34 and 50, drawn live and relaxed in 7.5% magnesium chloride solution. **31–36.** *P. tantilla*. **31, 32.** Coconut I., Oahu, Hawaiian Is (BMNH). **33–35.** Pupukea, Oahu (BMNH). **36.** Kahuku, Oahu (AMS C144407). **37, 38.** *P. conoidalis*, Otepipi, Anaa, Tuamotu Is (BMNH). **39–42.** *P. roepstorffiana*. **39.** Ping Chau, Hong Kong (BMNH). **40, 41.** Picnic Bay, Magnetic I., Queensland (BMNH). **42.** Marine Biological Center, Phuket I., Thailand (BMNH). **43–46.** *P. lutulenta*. **43.** Shark Point, Barrow I., Western Australia (WAM 2347.67). **44, 45.** Rowes Bay, Townsville, Queensland (BMNH). **46.** Sai Kung, Hong Kong (BMNH). **47, 48.** *P. infracostata*. **47.** Kuchino, Shiznoka Pref., Japan (BMNH). **48.** Hoi Sing Wan, Tolo Channel, Hong Kong (BMNH). **49, 50.** *P. isseli*. **49.** Baie Ternay, Mahé, Seychelles (BMNH). **50.** Eilat, Israel (BMNH).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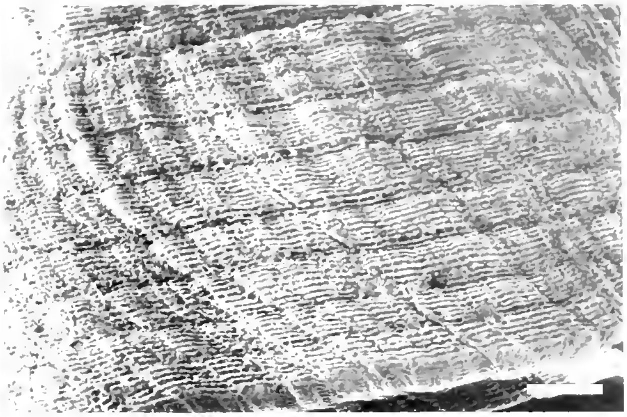

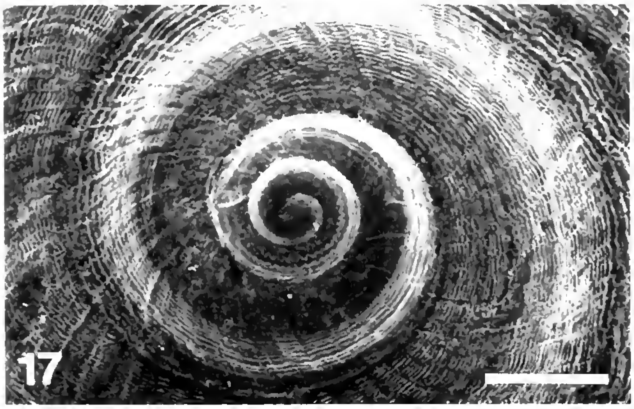
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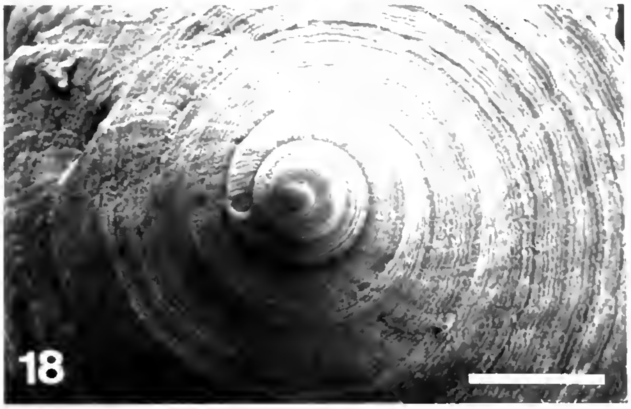
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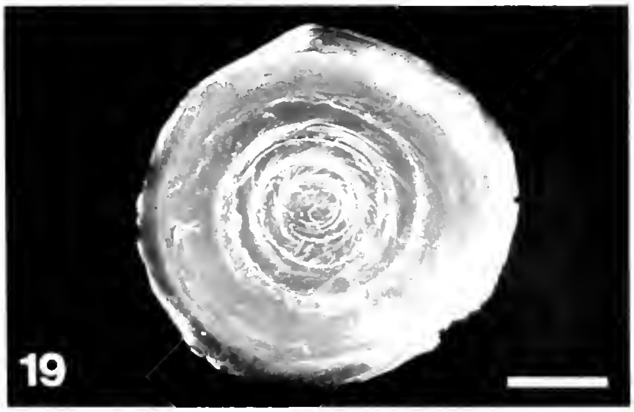
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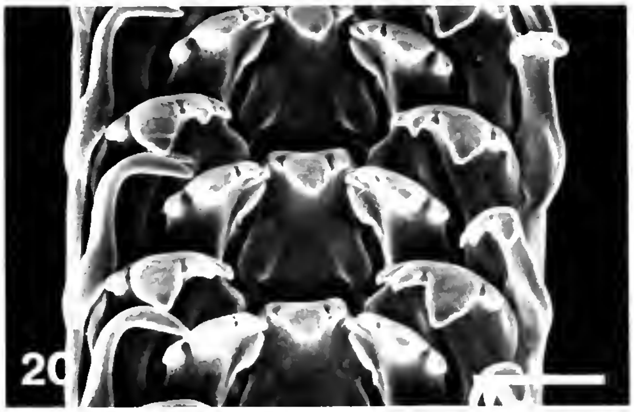
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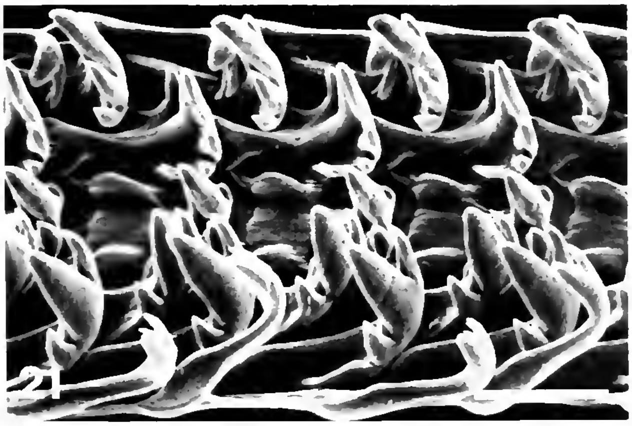
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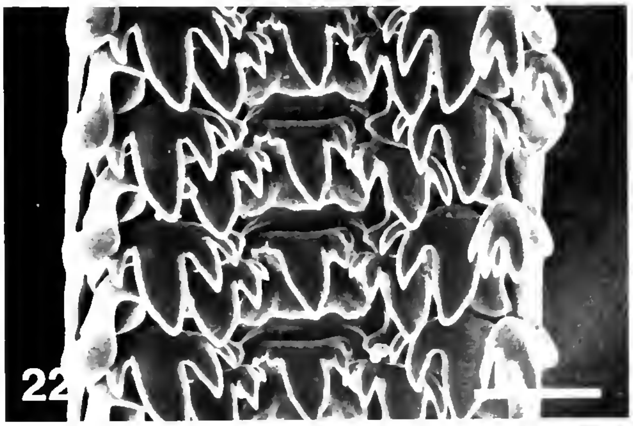
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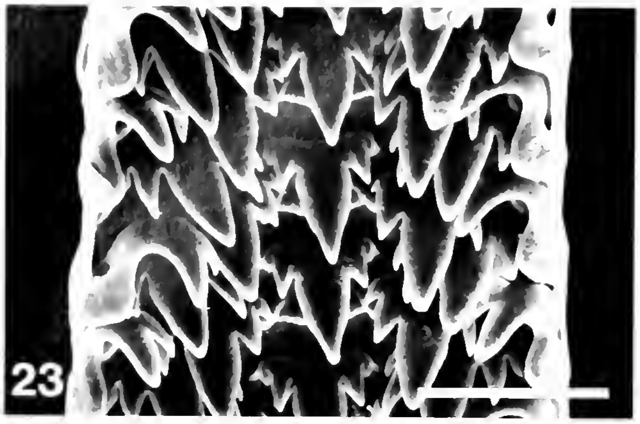
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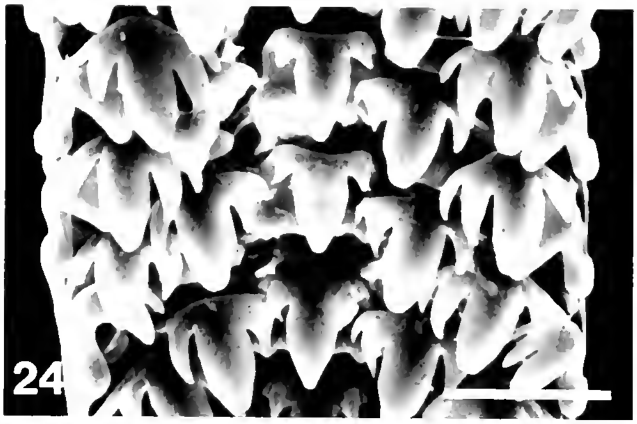
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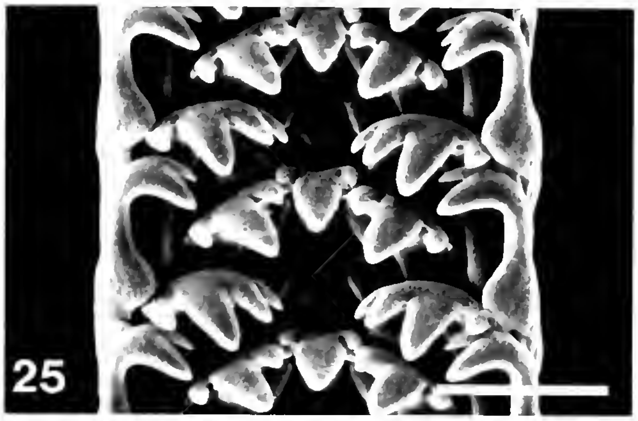
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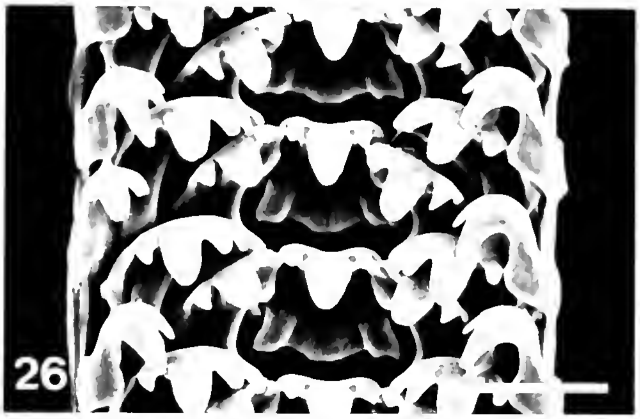
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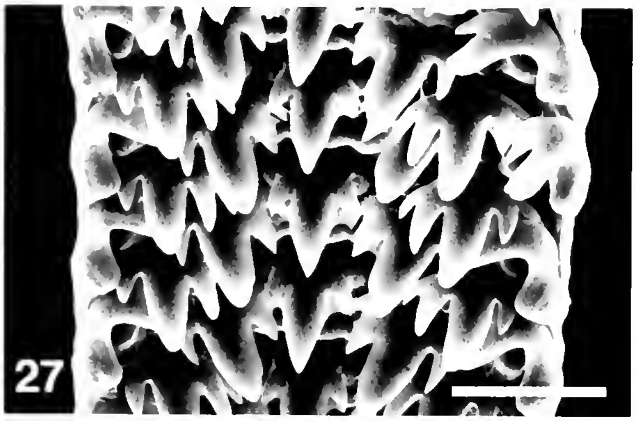
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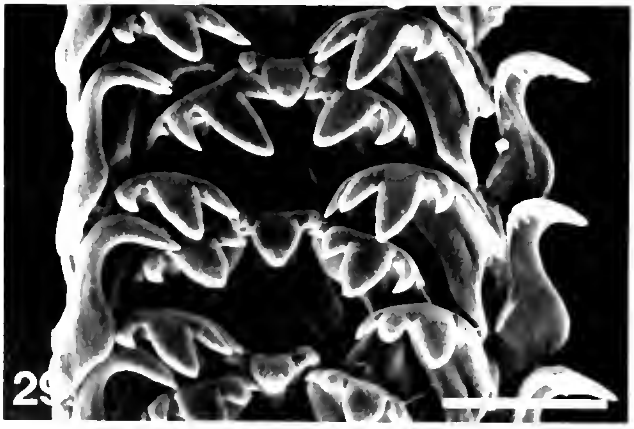
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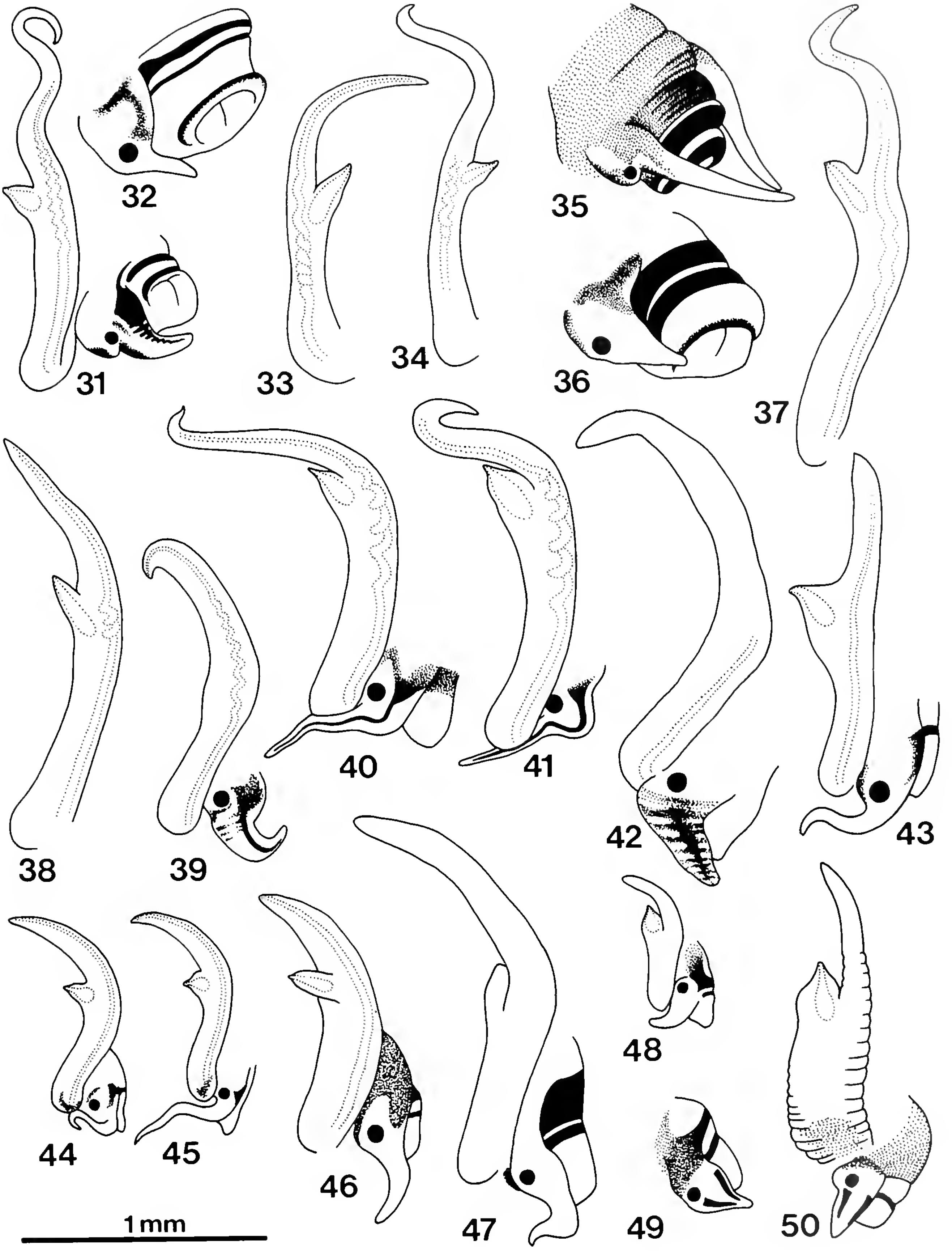
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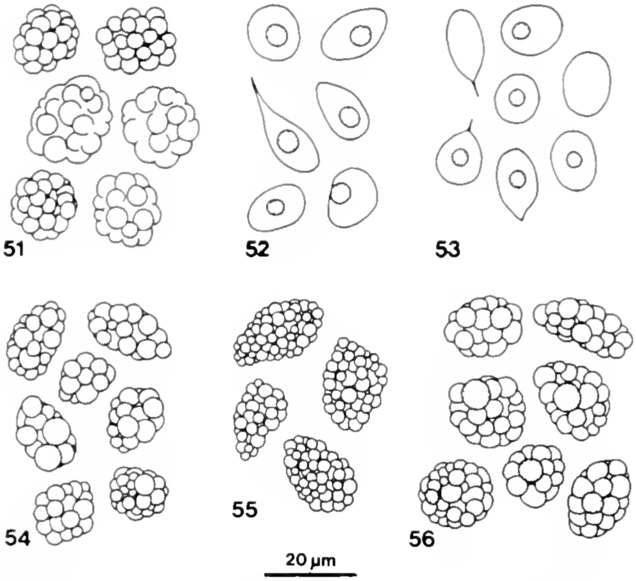


Figures 51–56. Paraspermatic nurse cells of *Peasiella* species. All drawn from living material fixed in 1% solution of formalin in seawater. **51.** *P. tantilla*, Pupukea, Oahu, Hawaiian Is. **52, 53.** *P. roepstorffiana*, Picnic Bay, Magnetic I., Queensland. **54, 55.** *P. lutulenta*, Sai Kung, Hong Kong. **56.** *P. isseli*, Eilat, Israel.

Another unusual feature is that in there species (*P. tantilla, P. conoidalis, P. roepstorffiana*) the bursa copulatrix is rudimentary or absent. In the remaining three species (*P. infracostata, P. isseli, P. lutulenta*) the bursa is large and anterior in position (figure 65). Situated at the back of the spiral part of the pallial oviduct, the seminal receptacle is constricted into two parts, an anterior coiled part and a posterior bulb, both of which store sperm (figures 58, 66). This condition has not been noted in other littorinids.

Egg capsule and development: The egg capsule has been described only for *P. infracostata*. It was first illustrated by Tokioka (1950) (figure 64) as 'Littorinacapsula habei', and subsequently identified by Habe (1956, as *P. roepstorffiana*). The pelagic capsule is 150–200 μm in diameter and contains a single egg 70 μm in diameter. It is of the 'cupola' type, of basically hemispherical shape with the domed surface sculptured by five concentric rings. The capsule has also been illustrated by Amio (1963); this less detailed drawing shows a pill-box shaped capsule with a circumferential flange. All littorinids with pelagic egg capsules undergo planktotrophic development, and this type of development is confirmed by the shape and size of the protoconch of *Peasiella* [see Reid (1989) for a review].

Radula: Characters of the radula are relatively constant within the genus (figures 20–30), and, with one exception, do not provide useful taxonomic characters. The central tooth varies from rectangular to almost square in the group (length/width at mid-point = 1.05–1.57), but does not show consistent intraspecific differences. There are two prominent basal projections and three tooth cusps (sometimes with two extra denticles). All the radular cusps are moderately long, and are pointed or rounded. The cusp patterns of the lateral and inner marginal teeth are similar to each other, and there are four cusps on each. The outer marginal tooth has three cusps in most species (but five to six in *P. infracostata*) and there is no outer projection on the base.

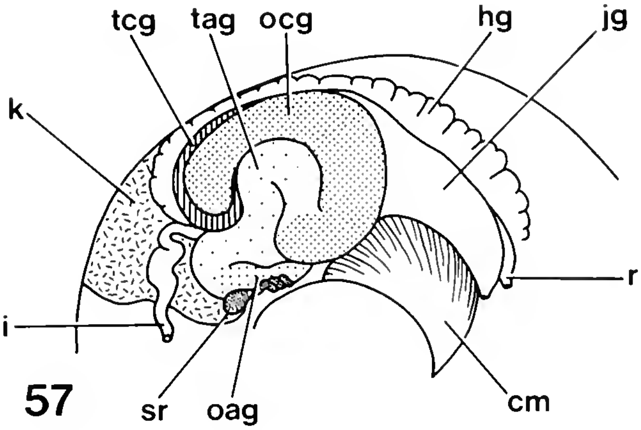
Alimentary system: The ducts of the salivary glands pass through the nerve ring around the anterior esophagus, and there is glandular material both anterior and posterior to the ring.

ECOLOGY

Little is known about the ecology of *Peasiella* species. The available information about their habitats is summarized in the systematic section. All species are apparently predominantly intertidal, occurring most commonly in the mid- to upper eulittoral zone on hard substrates, often in the empty shells of barnacles. They do, however, occur to lower levels on the shore than the littorinids with which they are sympatric, and there are reports of sublittoral occurrences. They can be found on various substrates, including limestone, granite and volcanic rocks, beach rock, coral rubble and mangrove trunks, and occur in a range of conditions of exposure to wave action. Ohgaki (1985) reported that an unidentified *Peasiella* species (probably including both *P. roepstorffiana* and *P. lutulenta*) occurred only on sheltered shores in Hong Kong. As discussed below, distribution records suggest a marked preference by each species for either continental coasts, promontories and high islands, or atolls. *Peasiella* species are usually common where they occur. In Japan, *P. infracostata* reached a density of 5 per 12.5

→

Figures 57–66. Female reproductive tract and egg capsule of *Peasiella* species. Abbreviations: b, bursa, cm, columellar muscle; hg, hypobranchial gland, i, intestine; jg, jelly gland in straight section of pallial oviduct; k, kidney; oag, opaque albumen gland, ocg, opaque capsule gland, r, rectum; ro, renal oviduct; sr, seminal receptacle; tag, translucent albumen gland; tcg, translucent capsule gland. **57–63.** *P. roepstorffiana*, Picnic Bay, Magnetic I., Queensland (BMNH). **57.** Pallial oviduct *in situ*, from right side of body whorl, showing relation to surrounding organs. **58.** Diagram of spiral route of egg groove in figure 57, showing orientation of sections in figures 59–63 (solid line, egg groove; thickened line, portion of egg groove through capsule gland; dashed line, renal oviduct). **59–63.** Sections through pallial oviduct in figure 57 (arrow in figure 63 indicates orientation from which figure 57 is viewed). **64.** Egg capsule of *P. infracostata*, Ago and Tanabe Bays, Japan (after Tokioka, 1950). **65, 66.** *P. lutulenta*, Sai Kung, Hong Kong (BMNH). **65.** Entire pallial oviduct **66.** Diagram of spiral route of egg groove in figure 65 (conventions as in figure 58).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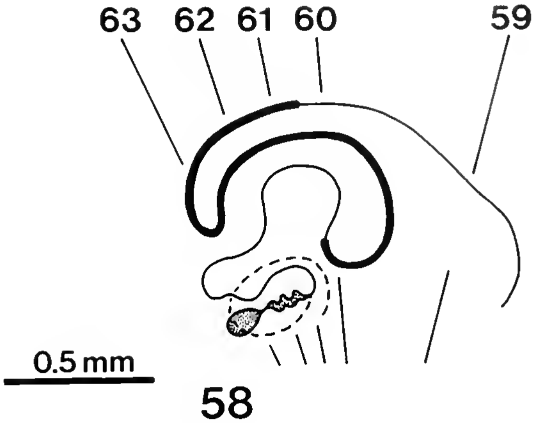
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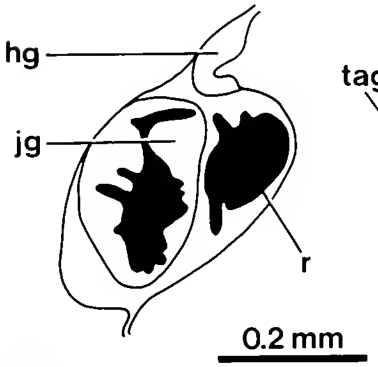
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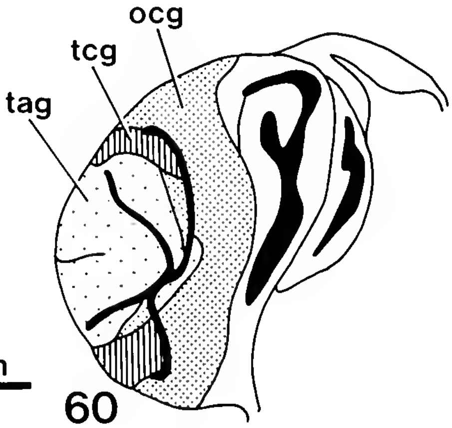
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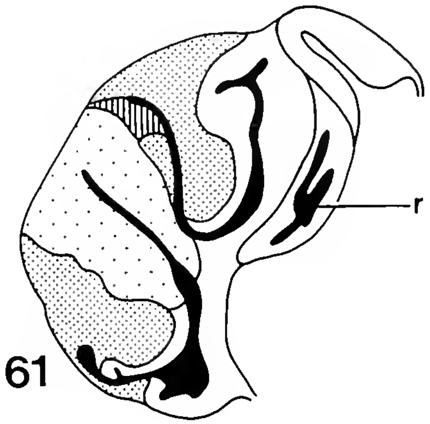
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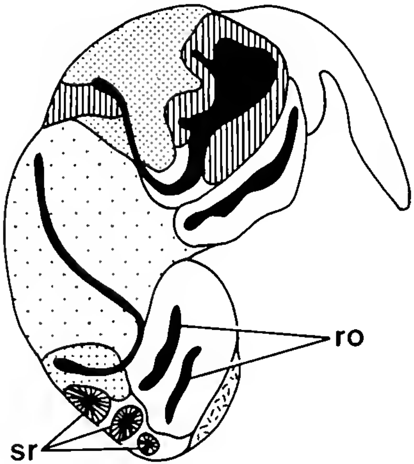
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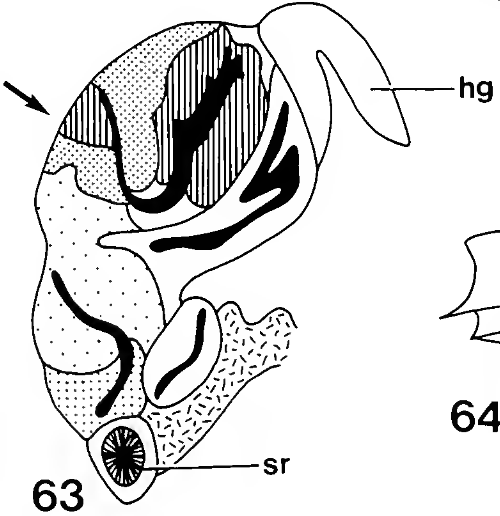
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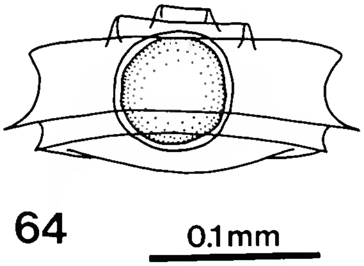
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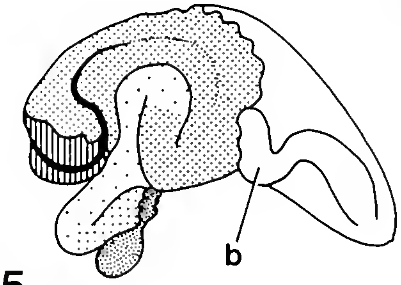
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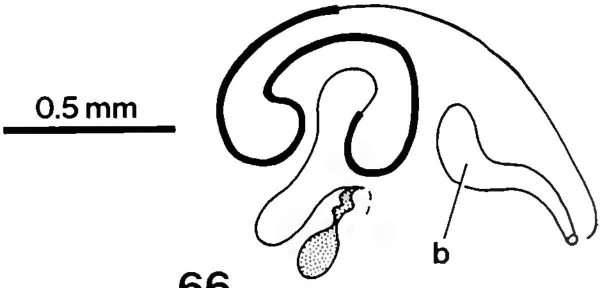
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cm^2 on a moderately exposed shore at Amakusa (Mori *et al.*, 1985, Tanaka *et al.*, 1985), while Habe (1958) recorded up to 4,200 per 25 cm^2 at Tanabe Bay. Taylor (1976) noted that the muricoidean gastropod *Drupella cariosa* included *Peasiella* in its diet.

The spawning season of *P. infracostata* in Japan is from May to September (Kojima, 1960; Amio, 1963; Hirai, 1963; Ohgaki, 1981). The heat resistance of this species has been measured by Fraenkel (1966).

FOSSIL RECORD

Cenozoic fossils of *Peasiella* are not uncommon in France, and at least one species, *P. reyti*, may have lived in a sheltered, perhaps muddy, environment. The oldest are of Middle Eocene age, the youngest from the Upper Miocene. In addition, there is a single specimen known from the Upper Oligocene of New Zealand. Among the material that has been examined, four species have been distinguished, and are described in the systematic section. Two of these have rather long histories, *P. reyti* of about 25 My, *P. roepstorffiana* (if the solitary fossil is correctly determined) of 30 My.

BIOGEOGRAPHY

The Recent species of *Peasiella* are restricted to the Indo-Pacific region and this, together with the European fossil occurrences, suggests an originally Tethyan distribution. Most of the species are exclusively tropical, but *P. infracostata* reaches a latitude of 33°S in South Africa and 41°N in Japan.

There is a close correspondence beween geographical distribution and the environment in which the species occur. *Peasiella lutulenta* inhabits sheltered and somewhat muddy sites, and is found only on continental coasts. *Peasiella roepstorffiana* and *P. isseli* occur in cleaner water, on promontories and high islands, and therefore extend from the continental margins to high oceanic islands in the Pacific and Indian Oceans respectively. *Peasiella tantilla* also belongs in this ecological group, and is endemic to the Hawaiian Islands. *Peasiella infracostata* appears to be intermediate between these two groups; it does not tolerate such turbid conditions as *P. lutulenta*, and occurs on both continental coasts and high islands, but does not extend far into oceanic areas. Only *P. conoidalis* is common on atolls, and has a wide, but disjunct, distribution in the central Pacific and central Indian Oceans. A similar situation occurs in the littorinid genus *Littoraria* and in some other gastropods, in which species within a genus can be classified as 'oceanic' or 'continental' (Reid, 1986), but the species of *Peasiella* suggest a spectrum from one extreme to the other. There is some overlap between *Peasiella* species in these categories of habitat and distribution, and the highest diversity is found in South East Asia and the western Pacific, where *P. roepstorffiana*, *P. lutulenta* and *P. infracostata* occur together on certain continental shores (e.g., Queensland and Hong Kong).

PHYLOGENETIC RELATIONSHIPS OF *PEASIELLA*

In a recent cladistic analysis of all subgenera of the Littorinidae, it was shown that *Peasiella* is a member of the relatively derived subfamily Littorininae, based on the synapomorphies of paraspermatic nurse cells, capsule gland and egg capsules (Reid, 1989). The superficial resemblance of the shell to that of *Bembicium* (a member of the primitive Lacuninae) is therefore a case of convergence. Within the Littorininae, the affinities of *Peasiella* remain uncertain. The trochoidal shell shape and multispiral operculum are synapomorphies with *Tectarius*. However, these may be convergent, in view of the lack of longitudinal division of the foot, the superficially closed penial duct, absence of rods in the paraspermatic nurse cells, and double spiral loop of the pallial oviduct, which are found in *Peasiella* but not in *Tectarius*. There are no important synapomorphies with *Cenchritis* or with *Mainwaringia* Nevill, 1885, two other littorinine genera with uncertain relationships (Reid, 1989). One possible interpretation is that the four characters listed above are plesiomorphic, as they are believed to be in *Melarhaphe* (the most primitive member of the Littorininae). If so, *Peasiella* may be the sister-taxon of all the remaining littorinine genera (excepting *Melarhaphe*). This suggestion is supported by the histology of the glands of the pallial oviduct (which is intermediate between the epithelial state of *Melarhaphe* and the subepithelial state of other littorinines) and by the absence of spermatozeugmata in *Peasiella* and *Melarhaphe* (if this absence is indeed a plesiomorphic character). Clearly further characters are required to test this hypothesis.

Within the genus *Peasiella* the three species *P. tantilla*, *P. conoidalis* and *P. roepstorffiana* share the character state of a vestigial or absent bursa copulatrix. Presence of the bursa is a plesiomorphic character of the Littorinidae, so its absence in these three species is apomorphic. Some similarities in shell shape and color pattern are also shared by this group, which may be a monophyletic one.

SPECIES EXCLUDED FROM *PEASIELLA*

Confusion with the genus *Bembicium* (= *Risella*) has been discussed in the introduction, and the species of *Bembicium* have recently been revised by Reid (1988). The following species have in the past been assigned to *Peasiella*, but are now excluded:

Fossarus caledonicus Crosse, 1874

Classified as *Risella (Peasiella)* by Tryon (1887), this species is a member of the Omphalotropinae (Assimineidae, Truncatelloidea) (W. F. Ponder, personal communication; Reid, 1988).

Tectarius luteus Gould, 1861

Grouped with *Peasiella* species by Smith (1884), this is a *Plesiotrochus* (Cerithioidea) (Yen, 1944; see figure of holotype in Johnson, 1964).

Peasiella roosevelti
Bartsch & Rehder, 1939

Described from the Galapagos Islands, this is a synonym of *Nodilittorina porcata* (Philippi, 1846).

Trochus risella Benoist, 1874
(= *Risella girondica* Benoist, 1874),
Xenophora rhytida Cossmann, 1899

These were erroneously listed as members of *Peasiella* by Reid (1988), and are discussed below.

SYSTEMATIC DESCRIPTIONS

Diagnosis of Genus *Peasiella*

Peasiella Nevill, 1885

Risella (*Peasiella*) Nevill, 1885:159 [type by original designation *Trochus tantillus* Gould, 1849].

Teleoconch small (up to 6.6 mm diameter); usually trochoidal and umbilicate, up to 5 whorls. Protoconch 0.21–0.28 mm diameter, 2.3–2.8 whorls, terminated by sinusigera ridge. Operculum round, corneous, multispiral. Mesopodial sole not longitudinally divided. Male reproductive system: prostate and anterior vas deferens open; penial vas deferens superficially closed; penis long, not bifurcate, some simple subepithelial glandular cells present and usually a single mamilliform penial gland. Paraspermatic nurse cells lacking rods and not forming spermatozeugmata. Female reproductive system: bursa present or absent; egg groove coiled in 2 spiral loops, each of half a whorl; glands of pallial oviduct at least partly subepithelial; capsule gland present. Spawn of pelagic, cupola-type capsules containing single eggs; development planktotrophic. Radula: rachidian tooth rectangular to almost square, 3 main cusps; 4 cusps on lateral and inner marginal; outer marginal lacking basal projection, 3–6 cusps. Salivary glands constricted by nerve ring around oesophagus.

Key to Recent Species of *Peasiella*

The following key employs only shell characters, and because these are variable one species appears twice. The only anatomical characters useful for identification are the lack of the bursa copulatrix in *P. tantilla*, *P. conoidalis* and *P. roepstorffiana*, and the presence of 5–6 cusps on the outer marginal tooth of *P. infracostata*. The distribution maps may also assist with identification.

1. Shell color pattern of 45–55 oblique axial lines on body whorl *P. tantilla*
- Shell color pattern otherwise 2
2. Dorsal surface smooth or with fine spiral microstriae only 3
- Dorsal surface with fine spiral microstriae, major spiral grooves, and sometimes radial folds and carina at shoulder 4
3. Base with 4–5 spiral ribs, extending to edge of umbilicus; dorsal color pattern of 7–13 brown spots at periphery, often joined to suture by oblique lines, or of 2–7 brown spiral lines *P. infracostata*
- Base with 1–6 spiral ribs, on outermost ½–⅔ of basal radius only; dorsal color yellow or orange, sometimes with darker tessellation, or single spiral brown band, or 9–12 peripheral spots only *P. roepstorffiana*
4. Base of columella thickened and angled; basal sculpture of 1–3 ribs near periphery, separated by a gap from up to 3 smaller ribs around umbilicus *P. lutulenta*
- Base of columella not thickened or angled 5
5. Outline equilaterally conical or taller (height/diameter ratio > 0.87); often with radial folds and crenulated margin; base with 5–8 ribs from periphery to umbilicus; color white or cream, sometimes with faint brown dots in spiral grooves *P. conoidalis*
- Outline more depressed 6
6. Base with 1–6 spiral ribs, on outermost ½–⅔ of basal radius only; no shoulder carina; periphery sometimes crenulated *P. roepstorffiana*
- Base with 3–8 spiral ribs, becoming finer and more closely spaced towards umbilicus; usually angled or carinate at shoulder; periphery not crenulated *P. isseli*

Recent Species of *Peasiella*

Peasiella tantilla (Gould, 1849)
(figures 1, 20–22, 31–36, 51, 67–73, 81)

Trochus tantillus Gould, 1849:118 [holotype USNM 5615; 34 paratypes MCZ 169392, not seen; Sandwich Is (= Hawaiian Is)].—Gould, 1852:184–185, 503, pl. 13, figs. 215, 215a, b.

Risella tantilla.—Martens & Langkavel, 1871:41; Smith, 1876: 552.

Risella (*Peasiella*) *tantillus*.—Nevill, 1885:159

Risella (*Peasiella*) *tantilla*.—Tryon, 1887:263, pl. 50, figs. 32–34

Peasiella tantillus.—Kesteven, 1903:633, fig. 1 (radula, operculum).

Peasiella tantilla.—Kay, 1979:74, fig 24A

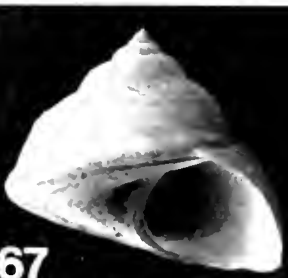
Bembicium tantillum.—Cernohorsky, 1978:43–44, pl 11, fig. 5.

Margarita angulata A. Adams, 1853:190 [type not found, Sandwich Is].

Risella parvula Dunker, 1861 42–43 [5 syntypes ZMB, Sandwich Is].

Trochus diminutivus Reeve, 1862 pl. 11, sp. 57 [type not found, Oahu Is (Hawaiian Is)].

Shell (figures 1, 67–73): *Dimensions:* Adult size range 3.3–6.6 mm diameter, mean height/diameter ratio 0.877 (95% confidence limits ± 0.034, range 0.744–1.093, n = 30 from 13 localities).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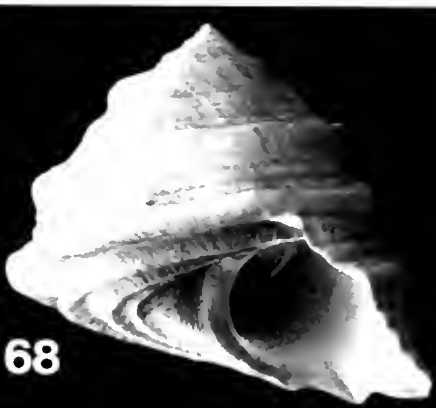
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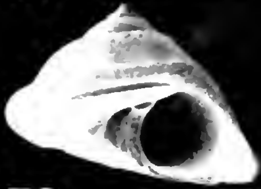
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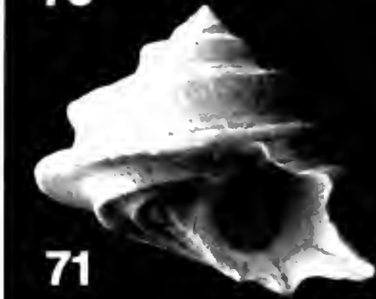
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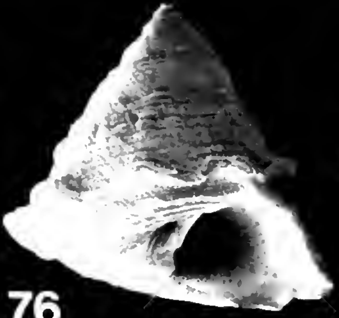
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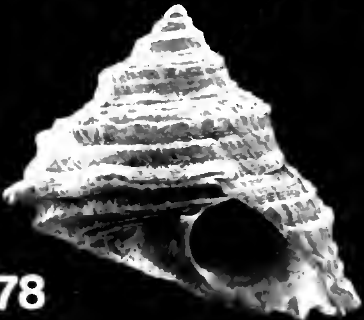
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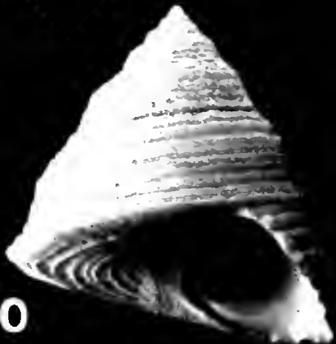
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Shape: Teleoconch 3–5 whorls. Outline equilaterally conical or taller; sides convex; sometimes turreted by carinate rib on shoulder; base flat. Peripheral keel with strong rib; margin not undulating or crenulated; suture indistinct or only slightly impressed. Umbilicus small or closed. Columellar pillar gently concave and rounded at base.

Sculpture: Protoconch 0.24 mm diameter, 2.8 whorls. Teleoconch whorls with 5–10 spiral grooves above periphery, usually rather indistinct; single prominent rib at shoulder in carinate forms. Microsculpture of fine spiral striae over whole surface. Base with (1)2–4 spiral ribs, strong in carinate forms, outermost rib strongest, becoming weaker and more closely spaced towards umbilicus.

Color: Shell whitish, golden yellow or red brown. Pattern of oblique axial lines of red brown or black, 45–55 at periphery of last whorl, but pattern sometimes faint; spiral grooves sometimes darker, giving tessellated pattern. Base white to red brown, alternating white and red brown spots on ribs. Columella whitish, red brown at base. Aperture cream to red brown, exterior pattern showing through.

Animal: *Head-foot (figures 31, 32, 35, 36):* 2–3 black bands across snout; tentacles unpigmented or with 2 longitudinal black lines; sides of foot black or mottled.

Penis (figures 31, 33, 34): Single penial gland; filament slender.

Paraspermatic nurse cells (figure 51): Irregularly rounded, packed with round granules.

Pallial oviduct: Bursa vestigial or absent.

Radula (figures 20–22): Outer marginal with 3 cusps.

Distribution: *Habitat:* Crevices and pools on exposed and sheltered rocky shores, usually in upper eulittoral and supralittoral zones (Kay, 1979; personal observation), also in shallow subtidal zone on corraline algae (S. Kool, personal communication).

Range (figure 81): Hawaiian Is.

Records: Oahu: Waialee (MCZ); Kahuku (AMS, 1♂, 1♀); Coconut I., Kaneohe Bay (DGR, 1♂, 2♀); Kuilima (DGR); Pupukea (BMNH, 3♂, 1♀); Diamond Head (USNM); Maui: Honokowai (USNM); Kauai: Kealia (USNM); Hawaii: Honaunau, Kona (USNM); Hilo (USNM); Laupahoehoe Point (USNM); Punaluu Black Sand Beach (USNM).

Remarks: This is the largest member of the genus, easily distinguished by its color, pattern, commonly carinate sculpture and few, strong basal ribs. It is a common species, endemic to the Hawaiian Islands.

Peasiella conoidalis (Pease, 1868) (figures 2, 16, 18, 23, 24, 37, 38, 74–80, 81)

Trochus conoidalis Pease, 1868:287, pl. 24, fig. 8 [4 syntypes ANSP 18868; Paumotus (= Tuamotu Is); figure 76].
Risella (Peasiella) conoidalis.—Nevill, 1885:160; Tryon, 1887: 263, pl. 50, fig. 38; Couturier, 1907:161; Dautzenberg & Bouge, 1933:359
Risella conoidalis.—Hedley, 1899:424
Risella tantilla.—Smith, 1876:552 [in part, not Gould, 1849].
Echinella gaidei Montrouzier in Souverbie & Montrouzier, 1879: 26–29, pl. 3, figs. 3, 3a, b [17 syntypes MNHNP; Lifou, Loyalty Is, figure 78].
Risella (Peasiella) gaidei.—Tryon, 1887:263, pl. 50, figs. 35–37.
Peasiella gaidei.—Oyama & Takemura, 1961: *Peasiella* and *Littorinopsis* pl., figs. 4–6; Higo, 1973:46; Habe, 1984:11, fig. 2.

Shell (figures 2, 16, 18, 74–80): *Dimensions:* Adult size range 1.9–5.1 mm diameter; mean height/diameter ratio 1.029 (95% confidence limits ± 0.045, range 0.773–1.333, n = 42 from 22 localities).

Shape: Teleoconch 3–6 whorls. Outline equilaterally conical or taller; sides lightly convex; whorls sometimes shouldered; base flat to slightly convex. Periphery strongly keeled, sometimes with straight, undulating, or crenulated flange; suture indistinct except in strongly sculptured and shouldered shells. Umbilicus usually small, sometimes closed in small shells. Columellar pillar gently concave and rounded at base.

Sculpture: Protoconch 0.21–0.22 mm diameter, 2.8 whorls. Teleoconch whorls with (4)6–8 strong, equidistant grooves above periphery, occasionally increasing to 12 on last whorl; short radial plications sometimes present at suture, giving 3 subsutural ribs a beaded appearance; third rib below suture occasionally enlarged, making whorls shouldered. Periphery sometimes with 9–15 short axial folds, crenulating margin. Microsculpture of fine spiral striae over whole surface. Base with (4)5–8 spiral ribs, outermost largest; finer and more closely spaced towards umbilicus.

Color: Shell white, cream or orange yellow; pattern usually indistinct, but spiral grooves sometimes darker or marked by brown dots, and periphery occasionally with orange or brown marks corresponding with axial

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Figures 67–73. *Peasiella tantilla*. **67, 70.** Pupukea, Oahu, Hawaiian Is (BMNH). **68, 69.** Mokuoloe I., Oahu (USNM 346450). **71–73.** Keaukaha, Hilo, Hawaii (USNM 339423). **Figures 74–80.** *P. conoidalis*. **74, 79.** Otepipi, Anaa, Tuamotu Is (BMNH). **75, 80.** Takume, Tuamotu Is (USNM 723721). **76.** Syntype of *Trochus conoidalis* Pease, 1868, Tuamotu Is (ANSP 18868). **77.** Mataira I., Raroia, Tuamotu Is (USNM 698654). **78.** Syntype of *Echinella gaidei* Montrouzier in Souverbie & Montrouzier, 1879, Lifou, Loyalty Is (MNHNP).

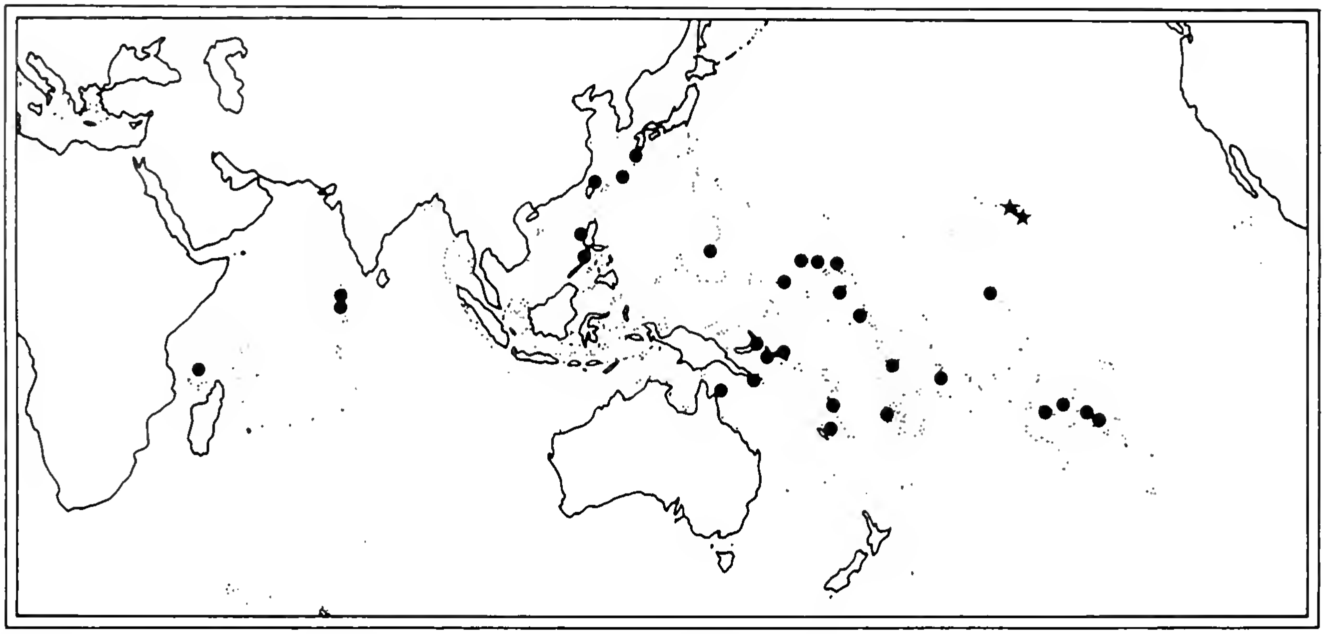

Figure 81. Distributions of *Peasiella tantilla* (asterisks) and *P. conoidalis* (dots).

folds. Base unmarked. Aperture and columella orange yellow.

Animal: *Head-foot:* Unpigmented.

Penis (figures 37, 38): Single penial gland; filament slender.

Pallial oviduct: Bursa apparently absent.

Radula (figures 23, 24): Outer marginal with 3 cusps.

Distribution: *Habitat:* Atolls and oceanic islands. On and under coral rubble or under thin layer of sand, on intertidal reef flats (Viader, 1951; J. Trondle, personal communication); on limestone in high intertidal zone (G. J. Vermeij, personal communication); on beachrock in barnacle zone (J. D. Taylor, personal communication).

Range (figure 81): Maldive Is, Seychelles, southern and western Pacific, from southern Japan to Queensland, Marshall and Tuamotu Is.

Records: Seychelles: Aldabra Atoll (BMNH); Maldive Is: Dunidu I., North Male (ANSP); Fadiffolu (ANSP); Chagos Arch.: Diego Garcia (Viader, 1951); Japan: Yakujima (NSMT); Oku, Okinawa, Ryukyu Is (LACM); Taiwan: Yeh-Liu (ANSP); Philippines: Binanga Port, Luzon (USNM); Corregidor I., Luzon (ANSP); 10 km N of Calavag, Palawan (D. Kadolsky Colln); Mariana Is: Tagachan Point, Guam (G. J. Vermeij Colln); Caroline Is: Ponape (AMS); Marshall Is: Engebi I., Eniwetok (USNM); Bikini (USNM); Busch I., Rongelap (USNM); Enybor I., Jaluit (USNM); Gilbert Is: Tarawa (AMS); Ellice Is: Funafuti (AMS); Australia: Queensland: Lizard I. (ANSP); Papua New Guinea: Rabaul, New Britain (AMS); Bougainville Strait (AMS); Milne Bay (AMS); Solomon Is: NW Sta Isabel I. (LACM); Laulosi I., Malaita I. (AMS); New Hebrides: Malakula I. (AMS); Efate I. (LACM); Loyalty Is: Lifou (AMS, MNHNP); New Caledonia: Panie (Hedley, 1899); Fiji: Deuba (AMS); Samoa: Swains I. (USNM); Line Is: Palmyra (USNM); Society Is: Moorea (LACM); Tahiti (BMNH); Tuamotu Is: Makatéa (USNM); Rangiroa (USNM); Manihi (LACM): Anaa (BMNH, 3♂, 3♀); Marutéa du Sud (AMS); Takume (USNM); Oneroa (USNM); Amanu (USNM).

Remarks: This widely distributed species is distinguished from *P. tantilla* by its pale color, finer and more numerous basal ribs, and frequently crenulated margin. The tall outline, basal sculpture of fine ribs extending right to the umbilicus, and the dorsal color pattern, separate it from *P. roepstorffiana*.

Peasiella roepstorffiana
(Nevill, 1885)
(figures 3–6, 17, 19, 25, 26,
39–42, 52, 53, 57–63, 82–89, 96)

?*Risella* (*Peasiella*) *tantillus* var. *parvula*.—Nevill, 1885:159 [not Dunker, 1861].

Risella (*Peasiella*) *roepstorffiana* Nevill, 1885:161 [1 syntype seen, here designated lectotype, ZSI 1916; Andaman Is; figure 89; 5 possible syntypes BMNH 1989005; S. Andaman].—Tryon, 1887:264, pl. 50, fig. 43

Risella (*Peasiella*) *templiana* Nevill, 1885:161 [1 syntype seen, here designated lectotype, ZSI 1913; Andaman Is; figure 83].

Risella (*Peasiella*) *templiana* var. *nigrofasciata* Nevill, 1885: 161–162 [1 syntype seen, here designated lectotype, 4.8 × 3.2 mm, ZSI M17732/3; Andaman Is].

Risella (*Peasiella*) *templiana* var. *subimbricata* Nevill, 1885: 162 [1 syntype seen, here designated lectotype, ZSI 4.8 × 4.1 mm; Andaman Is].

Risella balteata Preston, 1908:197, pl 14, fig 13 [2 syntypes BMNH 1908.7.2.68–69; Andaman Is]
?*Risella tantilla*.—Hedley, 1910:355 [not Gould, 1849].
Peasiella sp Morton & Morton, 1983:62, figs. 5.3, 5.8.

Shell (figures 3–6, 17, 82–89): *Dimensions:* Adult size range 1.6–5.0 mm diameter; mean height/diameter ratio 0.757 (95% confidence limits ± 0.022, range 0.556–1.000, n = 101 from 55 localities).

Shape: Teleoconch 3.5–5 whorls. Outline varying from rather depressed to equilaterally conical; sides convex or rarely almost straight; whorls usually gently rounded; base flat to slightly convex. Peripheral keel strongly angled, usually a sharp flange, margin usually straight, sometimes undulating or crenulated; suture slightly impressed or indistinct. Umbilicus open. Columellar pillar straight to slightly concave, rounded or slightly angled at base.

Sculpture: Protoconch 0.23 mm diameter, 2.3 whorls. Teleoconch whorls with (3)4–8 approximately equidistant spiral grooves above periphery, sometimes increasing to up to 13 on last whorl, sometimes obsolete. Short, fine, radial plications occasionally developed at suture. Sometimes 9–12 radial folds at periphery of last whorl, producing undulating or crenulated margin. Microsculpture of fine spiral striae over whole surface. Base with (1)3–5(6) approximately equidistant spiral ribs, either innermost or outermost strongest; innermost ⅓–½ of basal radius usually lacking spiral ribs, but rarely showing 1–2 small ribs.

Color: Shell cream, golden yellow or pinkish orange, sometimes with faint tessellated pattern over whole dorsal surface; spiral grooves sometimes brown; peripheral flange occasionally brown, either continuous or broken into spots corresponding with marginal crenulations. Shells occasionally with dark spiral band on lower half or middle of whorls. Base usually unpatterned; underside of peripheral flange sometimes brown or spotted. Interior of aperture golden yellow, exterior pattern showing through; columella yellow to purple brown. Distinctive red brown, tessellated color pattern occurring in Fiji, Samoa, southeastern Papua New Guinea and Philippines (figure 6): red brown and white spots on ribs, 11–24 at periphery of last whorl, making oblique tessellated pattern over whole surface, sometimes darkest on lower half of whorls; base and columella red brown; tessellations showing through in pale band within aperture.

Animal: *Head-foot (figures 39–42):* Black band across base of snout, single longitudinal black line on tentacles; head sometimes entirely unpigmented; foot with faint black speckling or unpigmented.

Penis (figures 39–42): Single penial gland in specimens from Queensland, but this is absent in those from Malaya, Thailand, and Hong Kong.

Paraspermatic nurse cells (figures 52, 53): Rounded to irregularly oval, sometimes with produced tip; finely granular contents with indistinct nucleus; nurse cells absent in specimens from Hong Kong.

Pallial oviduct (figures 57–63): Bursa absent.

Radula (figures 25, 26): Outer marginal with 3(4) cusps.

Distribution: *Habitat:* Islets and promontories on continental coasts; oceanic high islands. High eulittoral zone, on granite and volcanic rock, amongst and above barnacles and oysters. Rare or absent in turbid bays.

Range (figure 96): Central Indo-Pacific, from eastern Bay of Bengal to Hong Kong, Philippines, Palau, Queensland, Fiji and Samoa.

Records: Burma: Arakan (BMNH, USNM); Andaman Is (BMNH); Thailand: Marine Biological Center, Phuket I. (BMNH, 2♂, 1♀); Surin Beach, Phuket I. (BMNH, 1♂); Ko Tao (USNM); Pattaya (J. Le Renard Colln); Malaysia: Langkawi Is (USNM); Port Dickson (ANSP, 1♂); Mersing (BMNH); Vietnam: Baie d'Along (BMNH); Isle de la Table (MNHNP); Hong Kong: Ping Chau, Mirs Bay (BMNH, 3♂, 1♀); Hoi Ha, Mirs Bay (BMNH); Hoi Sing Wan, Tolo Channel (BMNH, 1♂); Lamma I. (AMS, 1♂); Sai Kung (DGR, 3♂, 1♀); Philippines: Binanga Port, Luzon (USNM); Scott's I., Lingayen Gulf, Luzon (LACM); Maricaban I., Luzon (USNM); Samar I. (NSMT); Zamboanga, Mindanao (NSMT); 10 km N of Calavag, Palawan (D. Kadolsky Colln); Caroline Is: Arakapesan, Palau (G. J. Vermeij Colln); Papua New Guinea: Nimoa, Louisiade Arch. (AMS); Milne Bay (AMS); Port Moresby (AMS); Queensland: Somerset (AMS); Lizard I. (AMS); Cooktown (AMS); Low Isles (AMS); Green I. (AMS); Dunk I. (ANSP); Orpheus I. (DGR); Picnic Bay, Magnetic I. (DGR, 5♂, 2♀); Gladstone (AMS); Fiji (BMNH, MCZ, MNHNP, ANSP, USNM); Nadi Bay, Viti Levu (AMS); Samoa: Pago Pago Harbor, Tutuila I. (LACM, AMS).

Remarks: This is a highly variable species, with a distinctive red brown, tessellated color form in the eastern and northeastern part of its range, and a more marked tendency towards marginal crenulation in the northern part. Nevertheless, considerable variation in shape and color also occurs within local populations, and recognition of geographical subspecies appears unnecessary. The unsculptured area around the umbilicus, and common golden yellow color with lines or tessellations, are the most useful diagnostic characters.

Of greater significance is the apparent geographical variation in anatomical characters. The amount of material available for dissection was limited, but the 12 males examined from Hong Kong, Malaya, and Thailand all lacked the mamilliform penial gland, while this was present in the 5 from Queensland. In addition, paraspermatic nurse cells were absent in 4 specimens from Hong Kong, but present in 3 from Queensland. Both nurse cells and the mamilliform gland are uniformly present in other *Peasiella* species. The lack of nurse cells could be simply a developmental abnormality or seasonal variation (although neither has been recorded elsewhere in the family). Penial shape is usually rather constant in


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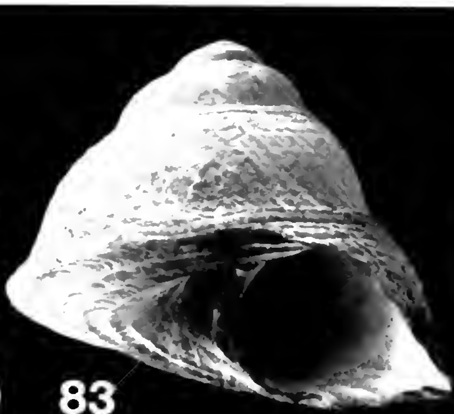
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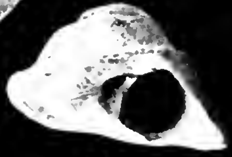
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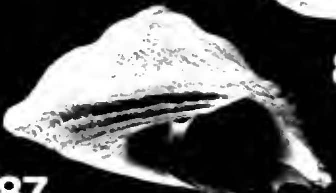
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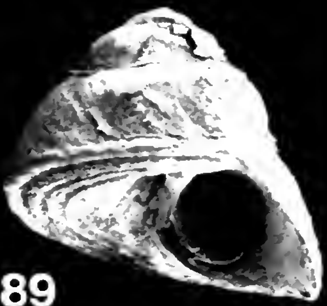
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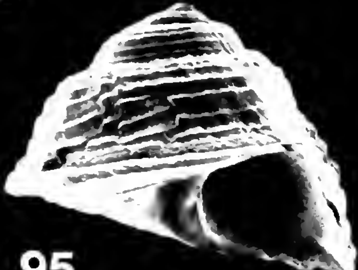
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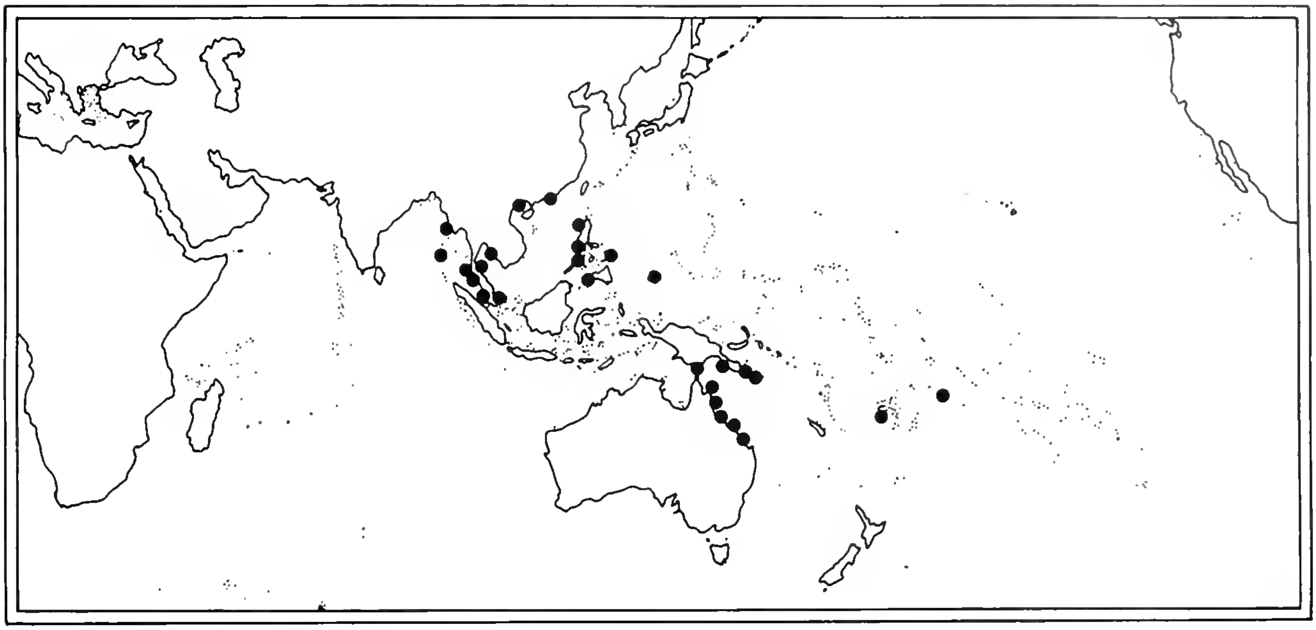

Figure 96. Distribution of *Peasiella roepstorffiana*.

littorinid species, and may differentiate between closely related species, leading to the idea that it serves the function of species recognition (*e.g.*, Reid, 1986). The geographical variation in penis shape in *P. roepstorffiana* could therefore be evidence that two species are involved. However, the number of mamilliform glands does show intraspecific variation, especially in littorinids with many such glands (Reid, 1989). In species of *Nodilittorina* (which normally have a single gland), abnormal animals can be found with two or none. A male *P. infracostata* has been found without a mamilliform gland. For this reason, and because of the absence of any consistently correlated shell characters by which two species could be distinguished in the *P. roepstorffiana* group, a single nominal species is retained here until further information is available.

A single fossil from the Upper Oligocene of New Zealand may be referable to this species (see below).

Peasiella lutulenta new species
(figures 7–9, 27, 43–46, 54, 55,
65, 66, 90–95, 97)

Bembicium sp. Wells & Slack-Smith, 1981:269.
Peasiella lutulenta n. sp. Etymology: Latin lutulenta, muddy, in reference to habitat of species. Types: holotype AMS C149052, Kissing Point, Rowes Bay, Townsville, Queensland (figure 9); 10 paratypes AMS C149053, 16 paratypes BMNH 1988138.

Shell (figures 7–9, 90–95): *Dimensions:* Adult size range 1.7–3.8 mm diameter; mean height/diameter ratio 0.716 (95% confidence limits ± 0.031, range 0.500–0.909, n = 36 from 26 localities).

Shape: Teleoconch 2.5–4 whorls. Outline varying from rather flattened to almost equilaterally conical; sides convex; base flat to slightly convex. Peripheral keel with strong flange, margin not usually undulating or crenulated; suture slightly impressed. Umbilicus open. Columellar pillar straight, with thickened angle at base, forming margin of umbilicus.

Sculpture: Protoconch 0.24–0.27 mm diameter, 2.4 whorls. Teleoconch whorls with (4)5–7(9) strong, approximately equidistant spiral grooves above periphery. Microsculpture of fine spiral striae over whole surface. Peripheral keel usually entire, rarely with 9–11 slight crenulations. Base with 2–6 spiral ribs, outermost 1–3 ribs most prominent, usually separated from smaller ribs around umbilicus by marked gap.

Color: Shell cream to pale horn color; 7–16 brown to black spots at periphery, usually also at suture, the two series connected by fainter irregular axial stripes; occasionally axial stripes complete and conspicuous. Periph-

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Figures 82–89. *Peasiella roepstorffiana*. **82, 85.** Orpheus I., Queensland (BMNH). **83.** Lectotype of *Risella templiana* Nevill, 1885, Andaman Is (ZSI 1913). **84.** Hong Kong (BMNH). **86.** Viti Is (Fiji) (BMNH). **87, 88.** Ping Chau, Hong Kong (BMNH). **89.** Lectotype of *Risella roepstorffiana* Nevill, 1885, Andaman Is (ZSI 1916). **Figures 90–95.** *P. lutulenta*. **90, 94.** Hoi Sing Wan, Hong Kong (BMNH). **91.** Shark Point, Barrow I., Western Australia (BMNH). **92, 93, 95.** Cockle Bay, Magnetic I., Queensland (BMNH).

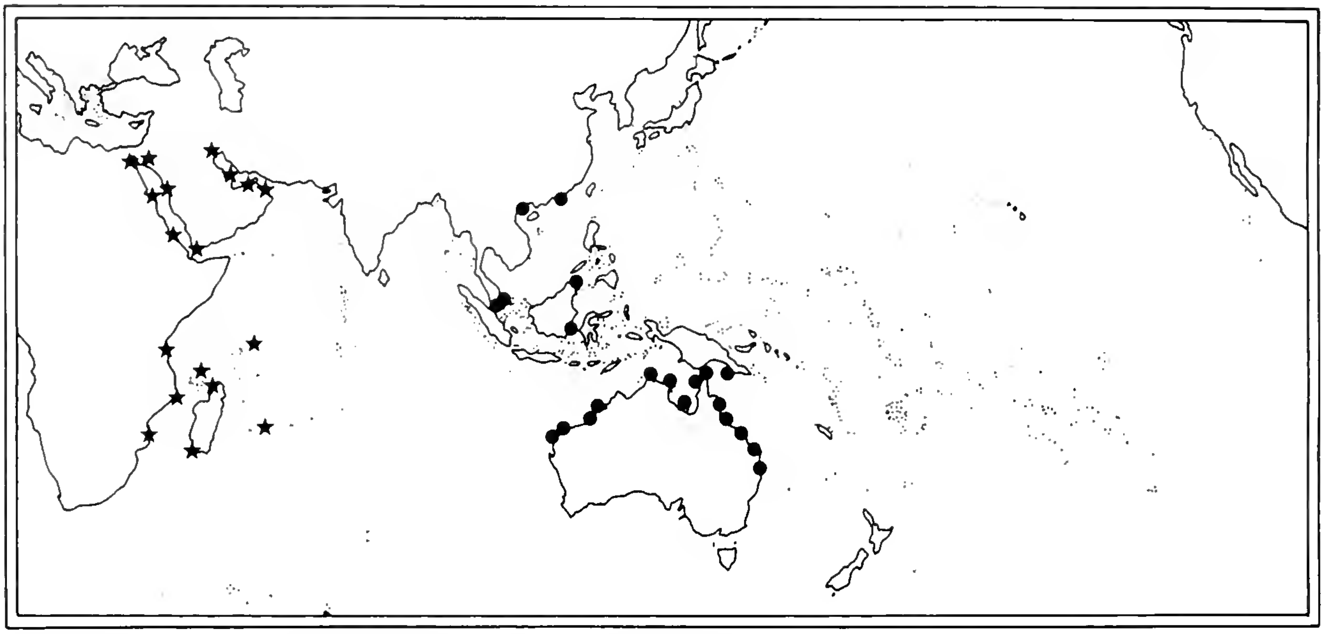


Figure 97. Distributions of *Peasiella isseli* (asterisks) and *P. lutulenta* (dots).

eral spots usually showing through at periphery of base. Columellar pillar whitish, red brown at base. Interior of aperture cream, exterior pattern showing through.

Animal: *Head-foot (figures 43–46):* 0–2 black bands across base of snout; black pigment above and below eye, but tentacles unpigmented; foot unpigmented or black mottled.

Penis (figures 43–46): Single penial gland.

Paraspermatic nurse cells (figures 54, 55): Irregularly oval, packed with round granules.

Pallial oviduct (figures 65, 66): Large anterior bursa present.

Radula (figure 27): Outer marginal with 3 cusps.

Distribution: *Habitat:* Sheltered, often muddy, continental shores. On rocks and outer fringes of mangrove forests, frequently in empty barnacles.

Range (figure 97): Central Indo-Pacific, including Hong Kong, Malaysia, Borneo, and northern Australia.

Records: Hong Kong: Hoi Sing Wan, Tolo Channel (BMNH, 2♂, 2♀); Hoi Ha, Mirs Bay (BMNH); Sai Kung (DGR, 3♂, 3♀); Vietnam: Isle de la Table (MNHNP, MCZ, ANSP); Baie d'Along (BMNH); Malaysia: Mersing (BMNH, 1♀; AMS); Tanjong Tuan (AMS); Port Dickson (ANSP, 1♂); Borneo: Sandakan (USNM); Balikpapan (AMS); Papua New Guinea: Eli Beach, Port Moresby (AMS); Australia: Western Australia: Beagle I., Onslow (AMS); Shark Point, Barrow I. (WAM, 2♂, 1♀); Dampier (AMS); Port Hedland (AMS); La Grange Bay (ANSP); Turtle I., King Sound (AMS); Northern Territory: East Point, Darwin (AMS); Maningrida (AMS); Gove Penin. (DGR); Queensland: Sweers I., Wellesley Is (AMS); Mapoon (AMS); Wednesday I. (AMS); Somerset (AMS); Port Douglas (AMS); Bingil Bay (AMS); Dunk I. (ANSP); Cockle Bay, Magnetic I. (DGR); Rowes Bay, Townsville (DGR, 2♂, 1♀); Bowen (AMS); Island Head Creek, N of Yeppoon (AMS); Gladstone (AMS); Facing I. (AMS); Point Vernon, Hervey Bay (AMS); Moreton Bay (AMS).

Remarks: The thickened columellar base is diagnostic of this species. Other useful characters include the basal sculpture and usually coarse, dark color pattern on the dorsal side (which separate it from *P. roepstorffiana*), the coarse dorsal sculpture (separating it from *P. infracostata*) and the lack of a shoulder keel (separating it from many individuals of *P. isseli*).

Late Pleistocene fossils have been found in Shark Bay, Western Australia (G. W. Kendrick, WAM), but the closest Recent specimens are from Onslow, 500 km to the north.

Peasiella isseli
(Semper in Issel, 1869)
(figures 13–15, 28, 49, 50, 56, 97–105)

Trochus sp. Audouin, 1826:42.

Risella isseli Semper in Issel, 1869:194, 347 [refers to Savigny, 1817, pl. 5, figs. 35.1, 35.2; lectotype here designated MNHNP 1.8 × 1.4 mm, figured by Bouchet & Danrigal, 1982, fig. 65; figures 101, 103 herein; Suez].—Pallary, 1926:84, pl. 5, figs. 35.1, 35.2.

Risella (*Peasiella*) *isseli*.—Nevill, 1885:160–161; Tryon, 1887:263, pl. 50, figs. 39, 40.

Risella isseli var. *carinata* Pallary, 1926:84–85, pl. 5, fig. 36 [reproduced from Savigny, 1817; 1 syntype seen, MNHNP 1.8 × 1.3 mm, Suez]

Risella isseli var. *undata* Pallary, 1926:84, pl. 5, fig. 35.3 [reproduced from Savigny, 1817; type not found; Suez].
Risella isseli var. *mauritiana* Viader, 1951:149, pl. 3, figs. 10, 11 [2 syntypes in Mauritius Institute, not seen; Cannonier's Point and Grand Bay, Mauritius; 3 possible syntypes BMNH 1989004, figure 14].
Trochus sismondae Issel, 1869:225–226, pl. 2, fig. 13 [holotype MGD 4.0 × 4.1 mm, Suez].

Shell (figures 13–15, 98–105): *Dimensions:* Adult size range 1.9–5.6 mm diameter; mean height/diameter ratio 0.758 (95% confidence limits ± 0.044, range 0.545–1.077, n = 45 from 26 localities).

Shape: Teleoconch 2.5–3.5 whorls. Outline varying from depressed to almost equilaterally conical; sides convex, sometimes with strong shoulder carina; base convex. Periphery strongly keeled, sometimes with strong rib or flange; margin usually entire, rarely slightly crenulated; suture slightly impressed. Umbilicus small. Columellar pillar concave, slightly angled at base.

Sculpture: Protoconch 0.26–0.28 mm diameter, 2.3–2.5 whorls. Teleoconch whorls with (6)7–9(12) equidistant or irregularly spaced spiral grooves above periphery, occasionally obsolete; shoulder rib sometimes enlarged or carinate. Microsculpture of fine spiral striae over whole surface. Rarely, periphery and shoulder with 7–12 radial folds, forming slight marginal crenulations. Base with (3)4–6(8) spiral ribs, outermost largest, finer and more closely spaced towards umbilicus; ribs around umbilicus sometimes bearing periostracal bristles.

Color: Shell cream, tan, spire sometimes pink or lilac, or entire shell dark brown or black. Pattern sometimes absent. Patterned shells with (6)8–16 dark brown spots at periphery, sometimes connected to sutural spots by oblique brown lines; others with faint marbled pattern over entire shell; base usually unpatterned. Columella white to brown; aperture cream to brown.

Animal: *Head-foot (figures 49, 50):* Two black lines across base of snout, two longitudinal black lines on tentacles; sides of foot blackish.

Penis (figure 50): Single penial gland.

Paraspermatic nurse cells (figure 56): Round or oval, packed with round granules.

Pallial oviduct: Large anterior bursa present.

Radula (figure 28): Outer marginal with 3–4 cusps.

Distribution: *Habitat:* Continental coasts and oceanic high islands, only rarely on atolls. Upper eulittoral zone of rocky shores.

Range (figure 97): Western Indian Ocean, including Persian Gulf and Red Sea, south to Moçambique and Madagascar.

Records: Egypt: Suez (BMNH); Israel: Eilat (BMNH, 1♂, 2♀; USNM, ANSP); Sudan: Dongonab Bay (BMNH); Port Sudan (ANSP); Ethiopia: Massawa (BMNH, NM); Dehui I., Dahlak Is (BMNH); Saudi Arabia: Jeddah (USNM); Yemen: Aden (BMNH); Oman: Bandar Khayrhan (BMNH); Persian Gulf: Abu Dhabi (BMNH); Qatar (BMNH); Kuwait (BMNH); Tanzania: Zanzibar (BMNH); Moçambique: Moçambique I. (NM); Benguera I., Bazaruto Arch. (NM); Madgascar: Nossi Bé (USNM, ANSP); Tuléar (MNHNP); Mauritius: Grand Bay (BMNH); Seychelles: Baie Ternay, Mahé I. (BMNH, USNM); Northwest Bay, Mahé I. (ANSP, 5♀); Aldabra Atoll (BMNH).

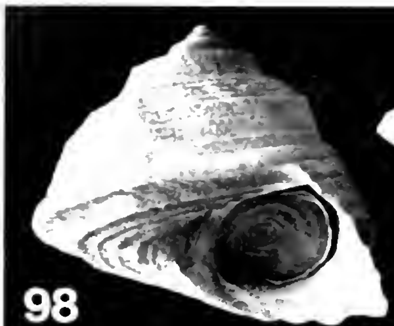
Remarks: This is another species with very variable shell characters. The shoulder is often keeled, but the species is separated from similarly shouldered shells of *P. tantilla* and *P. conoidalis* by the color pattern, a generally more depressed outline and often by the basal sculpture. Specimens without a shoulder keel are separated from *P. lutulenta* by their narrower columellar base, and from most specimens of *P. roepstorffiana* by the basal sculpture. Distinction from *P. infracostata* is discussed below.

Peasiella infracostata
(Issel, 1869)
(figures 10–12, 29, 30, 47, 48,
64, 106–112)

Trochus sp. Audouin, 1826:42.
Risella infracostata Issel, 1869:195–196 [refers to Savigny, 1817: pl. 5, fig. 40; lectotype, here designated, MNHNP 1.5 × 1.2 mm, figured by Bouchet & Danrigal, 1982: fig. 64, Suez; figure 109 herein].—Pallary, 1926:86, pl. 5, fig. 40; Dautzenberg, 1929:496.
Risella (*Peasiella*) *infracostata*.—Nevill, 1885:160; Tryon, 1887: 264, pl. 50, figs. 41, 42.
Risella (*Peasiella*) *tantillus* var. *subinfracostata* Nevill, 1885 160 [1 syntype seen, here designated lectotype, ZSI, 2.3 × 2.2 mm; Nicobar Is].
Cyclostrema fuscopiperata Turton, 1932:198–199, pl. 51, fig 1379 [2 syntypes, OUM; Port Alfred, South Africa].
Peasiella roepstorffiana.—Habe, 1956: fig. A (egg capsule); Oyama & Takemura, 1961: *Peasiella* and *Littorinopsis* pl., figs. 1–3; Yamamoto & Habe, 1962:16, pl. 3, figs. 3, 4, 34, 35; Amio, 1963:303, figs. 22a,b (egg capsule); Habe, 1964:28, pl. 9, fig. 23; Higo, 1973:46; Habe, 1984:11, fig 1 [all not Nevill, 1885].
'Littorina-capsula habei' Tokioka, 1950: fig. 6.1 (egg capsule).

Shell (figures 10–12, 106–111): *Dimensions:* Adult size range 1.1–3.5 mm diameter; mean height/diameter ratio 0.846 (95% confidence limits ± 0.022, range 0.600–1.120, n = 79 from 39 localities).

Shape: Teleoconch 2.5–4 whorls. Shell thin and translucent, or solid. Outline varying from almost equilaterally conical with rounded whorls to depressed globular or almost flat with inflated whorls; in Japan, whorls flat; base flat to convex. Periphery either uniformly rounded, or with weak or strong rib, or (in Japan) with strong flange; margin usually entire, rarely slightly crenulated; suture usually impressed. Umbilicus open, sometimes very small. Columellar pillar straight to uniformly rounded, curved and not thickened at base. Aperture occasionally somewhat patulous.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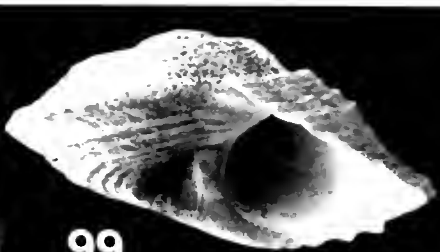
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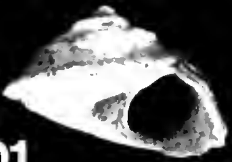
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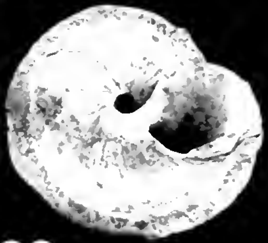
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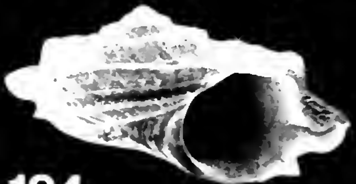
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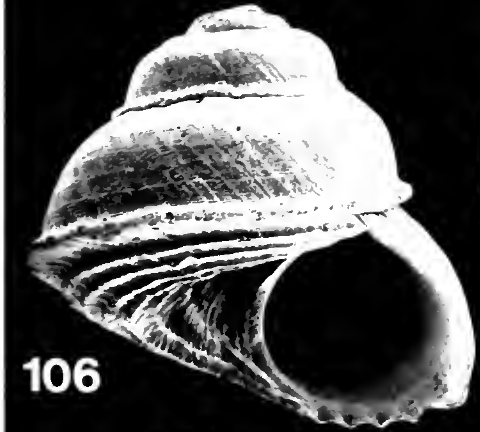
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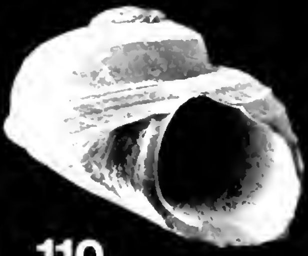
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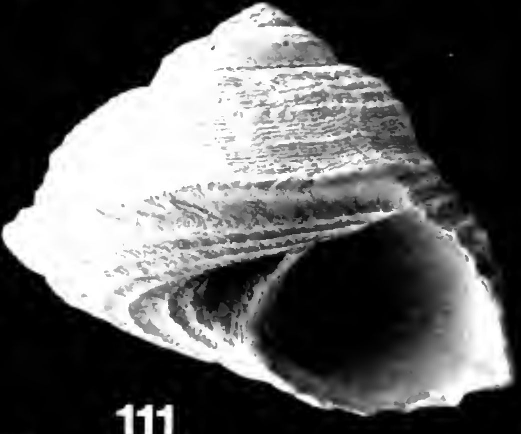
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1 mm

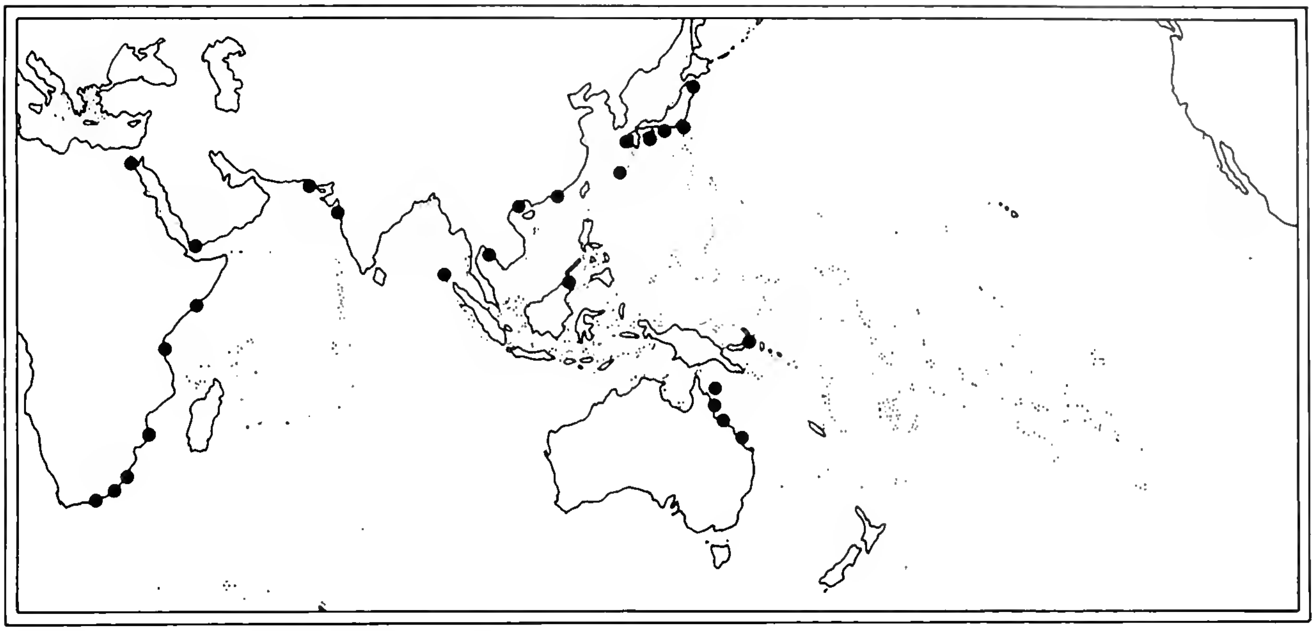

Figure 112. Distribution of *Peasiella infracostata.*

Sculpture: Protoconch not seen, apex usually eroded. Teleoconch whorls commonly smooth above periphery; spiral microstriae sometimes present and (in Japan) 7–10(11) equidistant spiral grooves. Base with (2)4–5 approximately equidistant spiral ribs, becoming a little stronger towards periphery. Basal and peripheral ribs sometimes bearing small periostracal bristles.

Color: Shell white to horn color; spire sometimes dark grey, black or purple brown. Shells from Indian Ocean (figure 11): suture and periphery with alternating brown and opaque white spots (9–13 brown spots at periphery of last whorl); sutural and peripheral spots sometimes connected by oblique brown lines; spiral brown line sometimes placed just above suture on spire whorls; base unmarked or with peripheral brown line. Shells from Pacific Ocean (figure 12): 2–7 brown or black spiral lines or dashes above periphery, with or without brown spots at suture and periphery; 3–4 lines in grooves of base. Shells from Japan (figure 10): black, eroded spire; periphery of last whorl paler, with 7–10 smudged brown spots, sometimes forming oblique stripes or continuous band; base with 7–10 brown spots or band in outermost groove and brown band around umbilicus. Aperture cream with exterior pattern showing through; columella white to purple.

Animal: *Head-foot (figures 47, 48):* Head with 2 black bands across base of snout, posterior one broad; tentacles usually unpigmented, sometimes black pigment above and below eye or single longitudinal black line; sides of foot black, grey or unpigmented.

Penis (figures 47, 48): Single penial gland present, occasionally absent.

Pallial oviduct: Large anterior bursa present.

Egg capsule (figure 64): Cupola type, with 5 concentric rings.

Radula (figures 29, 30): Outer marginal with 5–6 slender cusps.

Distribution: *Habitat:* Usually on continental coasts, sometimes on high islands. On sheltered and moderately exposed shores, from mean high water of spring tides to below mid-tide level, in crevices and empty barnacles, especially on sheltered sides of rocks (Mori *et al.*, 1985).

Range (figure 112): Margins of Indian Ocean, from South Africa to Red Sea, margins of western Pacific Ocean, from Japan to Queensland.

Records: Egypt: Suez (MNHNP); Yemen: Aden (BMNH); Somalia: Mogadiscio (ANSP); Tanzania: Zanzibar (BMNH); Moçambique: Benguera I., Bazaruto Arch. (NM); South Africa: Mapelane, Zululand (NM); Umdhloti, Natal (NM); Mbotyi, Pondoland (NM); East London (NM); Port Alfred (OUM); Pakistan: Karachi (BMNH,

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Figures 98–105. *Peasiella isseli.* **98.** Suez (BMNH 88.10.14). **99.** Baie Ternay, Mahé, Seychelles (BMNH). **100, 102, 104, 105.** Bandar Khayrhan, Oman (BMNH). **101, 103.** Lectotype of *Risella isseli* Semper in Issel, 1869, Suez (MNHNP). **Figures 106–111.** *P. infracostata.* **106–108.** Karachi, Pakistan (BMNH). **109.** Lectotype of *Risella infracostata* Issel, 1869, Suez (MNHNP). **110.** Pattaya, Thailand (J. Le Renard Colln LR99012). **111.** Zanpa Point, Okinawa, Ryukyu Is (AMS C146702).

2♂); 7 km WNW Bulegi Point, Sind Prov. (LACM); India: Mada I., Bombay (ANSP); Nicobar Is (ZSI); Thailand: Pattaya (J. Le Renard Colln); Borneo: Berhala Channel, Sandakan (USNM); Bak-Bak, Kudat (USNM); Vietnam: Isle de la Table, Tonkin (MNHNP); Hong Kong: Hoi Sing Wan, Tolo Channel (BMNH, 1♂); Lok Wo Sha, Tolo Channel (BMNH); Ping Chau, Mirs Bay (BMNH); Hoi Ha, Mirs Bay (BMNH, 2♀); Japan: Zanpa Point, Okinawa, Ryukyu Is (AMS 1♀; USNM, NSMT); Kyushu: Tomioka, Kumamotu Pref. (NSMT); Nagasaki (USNM); Shikoku: Tatsukushi, Kochi Pref. (NSMT, USNM); Honshu: Tanabe Bay, Wakayama Pref. (USNM); Kuchino, Shiznoka Pref. (BMNH, 4♂); Arasaki, Kanagawa Pref. (NSMT, USNM); Kominato, Aomori Pref. (LACM, ANSP); Asamushi, Aomori Pref. (NSMT, USNM); Papua New Guinea: Duke of York I., Rabaul, New Britain (AMS); Australia: Queensland: SW Lizard I. (LACM); Port Douglas (AMS); Green I. (AMS); Halfmoon Bay (AMS); Ellis Beach (AMS); Turtle Bay, Cape Ferguson (BMNH); Facing I., Port Curtis (AMS).

Remarks: This species is the most variable in the genus in its shell form and coloration, with recognizable forms in several areas of its wide geographical range. Shells from the Indian Ocean, South East Asia and Queensland are globular, with inflated whorls lacking grooves or microstriae above the round or slightly angled periphery (figures 106–110), and quite unlike any other members of the genus. The difference between the oblique or spotted color pattern of shells from the Indian Ocean (figure 11) and the spiral lines of shells from the southwestern Pacific (figure 12) is rather consistent. However, it is probably of minor importance, since shells from the Indian Ocean may show a spiral line on the spire, and on the body whorl the oblique lines may become almost perpendicular to the apertural lip. In addition, shells from the Pacific may develop sutural and peripheral spots like those in shells from the Indian Ocean.

Shells from Japan are very different, distinguished by conical shape, peripheral flange, frequent presence of microstriae and grooves above the periphery, and color pattern of a blackish spire and peripheral spots (figures 10, 111). They are, however, connected to the typical form of the species by intermediates from China and Thailand (figure 110), which show the typical globular shape and lined pattern, but with spiral grooves and peripheral keel as seen in Japanese shells. Specimens from Okinawa are especially variable, ranging from smooth to strongly grooved, keeled to globular, and with black or lined spire whorls. Keeled and faintly grooved shells of *P. infracostata* do occasionally occur in the Indian Ocean (figure 106). The basal sculpture is similar in all parts of the range. Radulae have been examined in single specimens from Karachi and Cape Ferguson, Queensland, and in two specimens each from Kuchino and Tomioka, Japan; all show the 5–6 sharp cusps on the outer marginal teeth, which are diagnostic of this species (figures 29, 30).

The Japanese form of *P. infracostata* resembles those shells of *P. isseli* without a shoulder keel. Both species can show a similar color pattern of oblique brown lines. Some collections of juvenile specimens from southern Africa (here doubtfully assigned to *P. infracostata*) contain keeled, shouldered, grooved shells which resemble *P. isseli*. Nevertheless, these two species are considered to be distinct, for the following reasons. Typical forms of both species are present in mixed samples from Zanzibar (BMNH), Aden (BMNH) and the Bazaruto Archipelago (NM). Locality records suggest that *P. infracostata* is a continental species (at least over most of its range in the Indian Ocean), while *P. isseli* is somewhat more oceanic, extending to islands in the western Indian Ocean. *P. infracostata* has not been reliably recorded from the Persian Gulf or Red Sea (the type locality, Suez, is therefore doubtful), where *P. isseli* occurs commonly. In areas where both species occur there are consistent differences in shell shape. In adult *P. infracostata* there is no shoulder keel, grooves are usually absent above the periphery, there are no more than 5 basal ribs, and the periphery is usually rounded. In *P. isseli* the shoulder is frequently keeled, grooves are present above the periphery, basal ribs may number more than 5, and the periphery is sharply keeled. Shell color patterns also differ: in *P. infracostata* the spire whorls often bear a spiral brown line, or may be entirely black; in *P. isseli* both patterns are rare. The most important anatomical difference is the presence of 5–6 narrow cusps on the outer marginal teeth of *P. infracostata* (3–4 in *P. isseli*). A possible difference in coloration of the tentacles requires confirmation in additional specimens.

FOSSIL SPECIES OF *PEASIELLA*

Peasiella minuta (Deshayes, 1824)
(figures 113–115)

Trochus minutus Deshayes, 1824:239–240, pl. 29, figs. 15–18 (Atlas, 1837) [type not seen; Valmondois].—Deshayes, 1864:956.

Risella minuta.—Cossmann, 1888:257–258, Cossmann, 1899:325, pl. 23, fig. 24, Cossmann & Pissarro, 1907–1913: pl. 17, fig. 108.1; Cossmann, 1915:74, pl. 3, figs. 27–29.

Bembicium minutum.—Glibert, 1962:24.

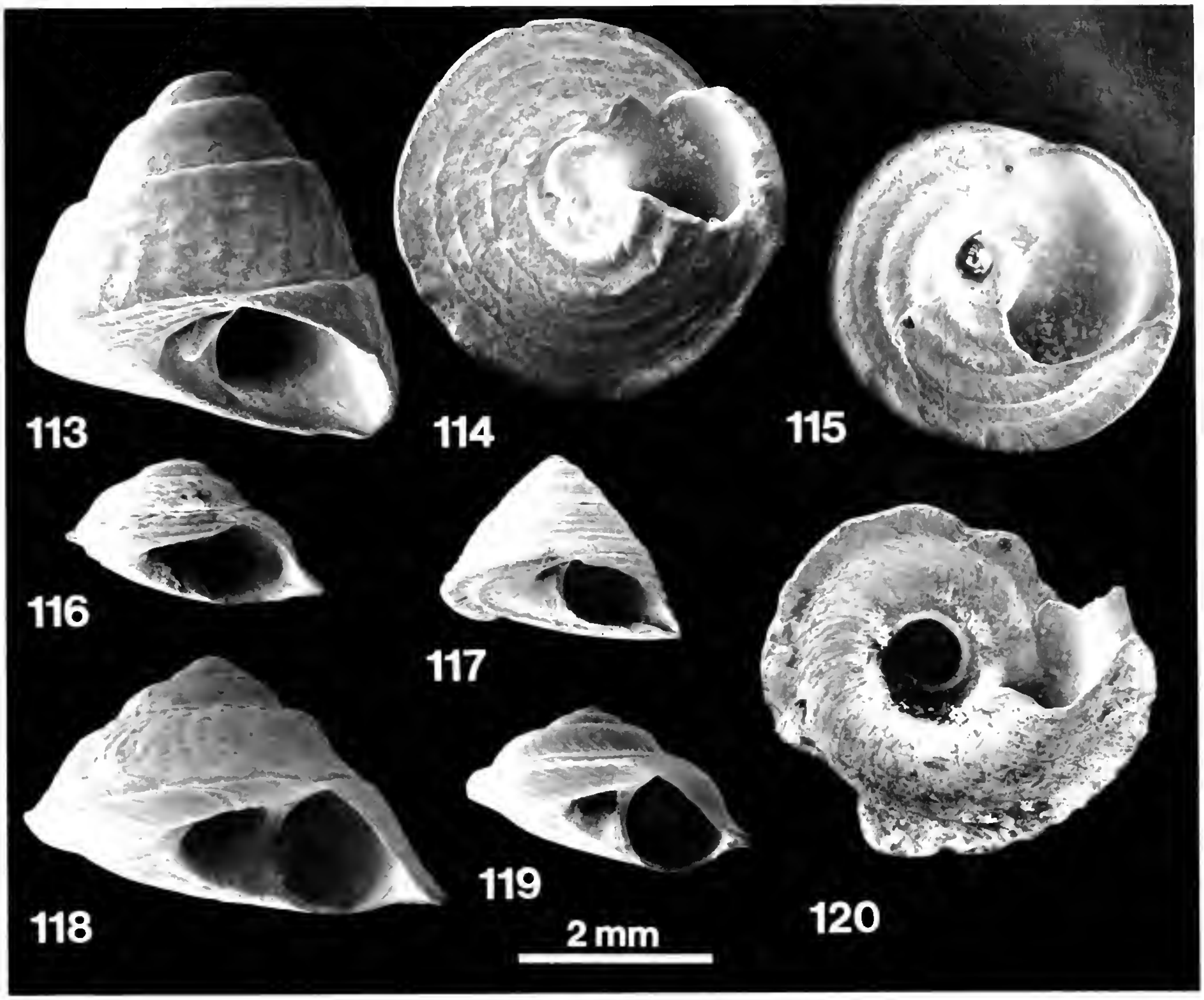
?*Xenophora bouryi* Cossmann, 1888:189, pl. 7, figs. 36–38 [type not seen, Neauphlette, Paris Basin, Eocene].

Shell (figures 113–115): *Dimensions:* Adult size range 3.1–6.6 mm diameter; mean height/diameter ratio 0.810 (95% confidence limits ± 0.074, range 0.545–1.048, n = 17 from 6 localities).

Shape: Outline equilaterally conical or lower; periphery sharply angled or keeled, slight flange in juveniles; margins not crenulated; suture slightly impressed. Umbilicus becoming closed in larger shells.

Sculpture: Teleoconch whorls with 6–9(13) spiral grooves above periphery; sometimes with up to 30 oblique radial folds on last whorl. Base with 2–6(10) ribs, innermost outlining umbilicus, inner 2 often most prominent.

Distribution: *Range:* Paris Basin (Upper Eocene) and Loire (Middle Eocene) of France.



Figures 113–120. Fossil species of *Peasiella*. **113–115.** *P. minuta*. **113, 114.** L'Écaillette, Monneville, Paris Basin, Marinesian (J. Le Renard Colln LR99004). **115.** Ronquerolles, Paris Basin, Auversian (J. Le Renard Colln LR99002). **116.** *P. pontileviensis*, Ferrière-Larçon, Loire, Middle Miocene (MNHNP). **117.** *P* aff *roepstorffiana*, Shell Gully, Chatton, Southland, New Zealand, Duntroonian (NZGS 9806). **118–120.** *P. reyti*. **118, 120.** Le Bois-Gouët, Loire Atlantique, Biarritzian (J. Le Renard Colln LR99010). **119.**B7LSanbotte, Noaillan, Aquitanian (MNHNP).

Records: France: Paris Basin, Le Ruel, Bartonian (MNHNP); Le Ruel, Marinesian; Le Quoniam, Marinesian; L'Écaillette, Monneville, Marinesian; Ronquerolles, Auversian; Baron, Auversian; Barisseuse, Auversian; Méry-sur-Oise, Auversian; Loire: Saint-Lubin-de-la-Haye, Lutetian (all J. Le Renard Colln).

Remarks: This relatively common species shows variation in the development of the peripheral flange, closure of the umbilicus, and number of basal ribs. The combination of conical shape, marked spiral grooves above the periphery, and strong basal ribs extending to the umbilicus, is diagnostic.

The identity of *Xenophora bouryi* is uncertain; the description of radial costules and 3 basal ribs, and apparent lack of a thickened columellar base, resemble *P. minuta*. However, the depressed shape, sinuous marginal flange and apertural form are different, and, taken together, suggest that it may not be a *Peasiella*.

Peasiella reyti
(Cossmann & Peyrot, 1917)
(figures 118–120)

Trochus thorinus —Benoist, 1874b:316 [not Grateloup, 1832, *fide* Cossmann & Peyrot, 1917:63]

Pseudonina reyti Cossmann & Peyrot, 1917:363–365, text fig 30, pl 6, figs 45–48 [type not seen, Mérignac, Aquitaine, Aquitanian]

Peasiella girondica —Lozouet, 1986:229 [not *Risella girondica* Benoist, 1874]

Shell (figures 118–120): *Dimensions:* Adult size range 2.3–5.3 mm diameter; mean height diameter ratio 0.627 (95% confidence limits ± 0.065, range 0.459–0.756, n = 9 from 3 localities).

Shape: Spire relatively low; whorls convex at shoulder, concave towards periphery; suture impressed; base convex, becoming concave around umbilicus. Peripheral keel bearing strong flange, rarely slightly undulating. Umbilicus large (up to 0.3 of basal diameter). Columellar pillar uniformly rounded, thin.

Sculpture: Protoconch 0.30–0.36 mm diameter, 2 to approximately 3 whorls, terminated by sinusigera notch, but sculpture not preserved on specimens examined. Teleoconch whorls usually rather smooth, with growth lines and indistinct spiral microstriae only; sometimes coarser striations forming 11–14 indistinct grooves above periphery; radial sculpture absent, or coarsely rugose at shoulder, sometimes with 6–14 indistinct radial plications producing undulations of marginal flange. Edge of umbilicus a thickened rib, usually outlined by broad, shallow groove; rest of base almost smooth, but with radial growth lines (strongly developed near umbilicus), sometimes up to 10 faint spiral striae.

Color: Sometimes traces of a series of color spots at suture and periphery.

Distribution: *Habitat:* Near Montpellier this species occurred in an assemblage including barnacles, oysters, and the potamidid gastropods *Mesohalina*, *Potamides*, and *Terebralia*, together with driftwood, in a marl free of sand grains, suggesting a sheltered, muddy, possibly slightly brackish, intertidal, or lagoonal environment (D. Kadolsky, personal communication).

Range: Loire (Middle Eocene), Adour (Middle and Upper Oligocene), Languedoc (Upper Oligocene), and Aquitaine (Lower Miocene) of France.

Records: France: Le Bois-Gouët, Loire Atlantique, Biarritzian (J. Le Renard Colln); Gaas, Adour Basin, Middle Oligocene (MNHNP); Peyrère, Adour Basin, Chattian, Upper Oligocene (Lozouet, 1986); La Paillade, near Montpellier, latest Chattian (D. Kadolsky Colln); La Saubotte, Noaillan, Aquitanian (MNHNP).

Remarks: The nomenclature of this species is complex. It was incorrectly listed as *Trochus thorinus* Grateloup by Benoist (1874b), according to Cossmann and Peyrot (1917), who had examined both the Grateloup and Benoist Collections. The original description (Grateloup, 1832) and figure (Grateloup, 1847) of *Trochus thorinus* were both poor, but Cossmann and Peyrot (1917:280–282) examined the holotype and assigned the species (as a synonym of *Trochus biangulatus* Eichwald) to the genus *Gibbula* (Trochidae); furthermore, their figure bears no resemblance to *Peasiella*. The identity of *Trochus helicinus* Grateloup, 1832 (not Gmelin; renamed *subhelicinus* d'Orbigny, 1852) is uncertain; in the absence of type material in the Grateloup Collection, Cossmann and Peyrot (1917) suggested that it was a synonym of *Trochus thorinus*.

From the original description (Benoist, 1874a) it is clear that *Trochus risella* (renamed *Risella girondica* by Benoist, 1874b) is not a *Peasiella*; it was described as 15 mm in diameter, imperforate, with concave whorls and tubercular sculpture. *Xenophora rhytida*, described and figured by Cossmann (1899), bears a superficial resemblance to a *Peasiella*, but the scalloped or spiked margin, projecting at the suture, the dorsal sculpture of 3 faint cords, and the narrow umbilicus, are all unlike the present species, and suggest that it may not be a littorinid.

The specimens examined during the present study bear a close resemblance to the original description and figures of *Pseudonina reyti* by Cossmann and Peyrot (1917), with the exception that the umbilicus is wider in the former, but this character is somewhat variable in living *Peasiella* species.

This species has a long stratigraphic range, from the Middle Eocene to the Lower Miocene, but from the material examined there seems no reason for subdivision. It is compared with *P. pontileviensis* below. In habitat, *P. reyti* may have resembled the Recent *P. lutulenta*.

Peasiella pontileviensis
(Morgan, 1915)
(figure 116)

Xenophora ? (*Haliphaebus*) *pontileviensis* Morgan, 1915:231–232, figs. 14a–d [type not seen; Vallon de Charenton, Pont-Levoy, Falunian].

Circulus pontileviensis.—Glibert, 1949:71, pl. 5, fig. 1.

Tornus orthezensis Cossmann & Peyrot, 1918:27–28, pl. 7, figs. 39–41 [type not seen; Orthez, Aquitaine, Helvetian].

Circulus orthezensis.—Glibert, 1949:71.

Risella girondica.—Cossmann & Peyrot, 1919:437–438, pl. 17, figs. 47, 48, 58 [not Benoist, 1874].

Shell (figure 116): *Dimensions:* 3.1–3.7 mm diameter; height/diameter ratio 0.548–0.568 (n = 3, from 1 locality).

Shape: Depressed; whorls lightly rounded; base convex. Strong flange at periphery, sometimes slightly undulating. Moderate umbilicus. Columellar pillar thickened and angled at base.

Sculpture: Spire whorls of teleoconch smooth; 6–8 spiral grooves and fine microstriae above periphery on last whorl; no radial sculpture. Margin of umbilicus thickened, but not outlined by a groove; 3–4 ribs on outer half radius of base.

Color: Two specimens have 7 brown spots at suture and 12–20 smaller spots at periphery of penultimate whorl, but little color on last whorl. A similar pattern covers the last 2 whorls in fig. 14d of Morgan (1915).

Distribution: *Range:* Loire (Middle Miocene) and Aquitaine (Lower and Upper Miocene) of France.

Records: France: La Brède, Aquitaine, Aquitainian (Cossmann & Peyrot, 1919); Orthez, Aquitaine, Helvetian (Cossmann & Peyrot, 1918); Ferrière-Larçon, Loire, Middle Miocene (MNHNP; Glibert, 1949).

Remarks: This species is similar to *P. reyti*, but appears to differ consistently in the presence of coarser spiral grooves above the periphery on the last whorl (grooves are absent or finer and more numerous in *P. reyti*), in the markedly thickened columellar base and in the presence of ribs on the outer part of the base. Elsewhere in the genus a thickened columellar base is found only in the Recent species *P. lutulenta*, from which *P. pontileviensis* differs in its smooth spire whorls and presence of ribs on the outer part of the base only.

The three specimens examined showed 3 or 4 ribs on the base; in the original description there were said to be 2 (Morgan, 1915), and in *Tornus orthezensis* 5 (Cossmann & Peyrot, 1918). This range of variation is comparable to that of Recent species such as *P. roepstorffiana*. *Tornus orthezensis* was said to lack spiral sculpture on the dorsal surface (Cossmann & Peyrot, 1918), yet as noted by Glibert (1949) the accompanying figure of the holotype apparently shows faint spiral grooves.

This species appears to be generally rare; the authors quoted in the synonymy (with the exception of Morgan, 1915) recorded a total of only 9 specimens. However, Morgan (1915) recorded it as abundant at the type locality.

Peasiella aff. *roepstorffiana*
(Nevill, 1885)
(figure 117)

Shell (figure 117): *Dimensions:* 3.0 mm diameter; height/diameter ratio 0.767 (n = 1).

Shape: Outline slightly convex; whorls almost flat-sided; base slightly concave. Periphery sharply keeled, edge straight; suture indistinct. Umbilicus almost closed. Columellar pillar narrow, concave, rounded at base.

Sculpture: 6 strong, equidistant, spiral grooves above periphery. No radial sculpture. Single strong rib on outer part of base, with trace of another just within.

Distribution: *Record:* Shell Gully, Chatton, Okapua Valley, near Gore, Southland, New Zealand, Duntroonian, Upper Oligocene (NZGS).

Remarks: This single specimen from the Upper Oligocene of New Zealand falls just within the range of variation of the Recent species *P. roepstorffiana*. However, the single strong basal rib and very narrow umbilicus are atypical of that species, and until more specimens are available, identification is tentative.

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A New Species of *Coluzea* (Gastropoda: Turbinellidae) from off Southeastern Africa

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ABSTRACT

Coluzea juliae, a new species of Columbariinae, is described from bathyal depths off northeastern South Africa and southern Mozambique. It appears to be most closely related to *Coluzea liriope* Harasewych, 1986, from Makassar Strait in Indonesia

Key words: Gastropoda; Turbinellidae; Columbariinae; *Coluzea*; Mozambique; South Africa; Indian Ocean.

INTRODUCTION

Although the genus *Coluzea* Allen, 1926 is represented in Middle-Eocene shallow-water fossil beds of Europe, post-Eocene records are restricted to deep water facies of New Zealand. In the Recent fauna it is restricted to bathyal depths along continental margins of the Indian and southwestern Pacific Oceans. The southern coast of Africa contains the richest and most diverse Recent columbariine fauna known to date, to which is added the new species described herein.

Repositories of examined specimens are indicated by the following abbreviations:

DMNH—Delaware Museum of Natural History, Wilmington
NM—Natal Museum, Pietermaritzburg
SAM—South African Museum, Cape Town
USNM—National Museum of Natural History, Smithsonian Institution, Washington, DC

SYSTEMATICS

Genus *Coluzea* Allen, 1926

Coluzea juliae new species
(figures 1–4; table 1)

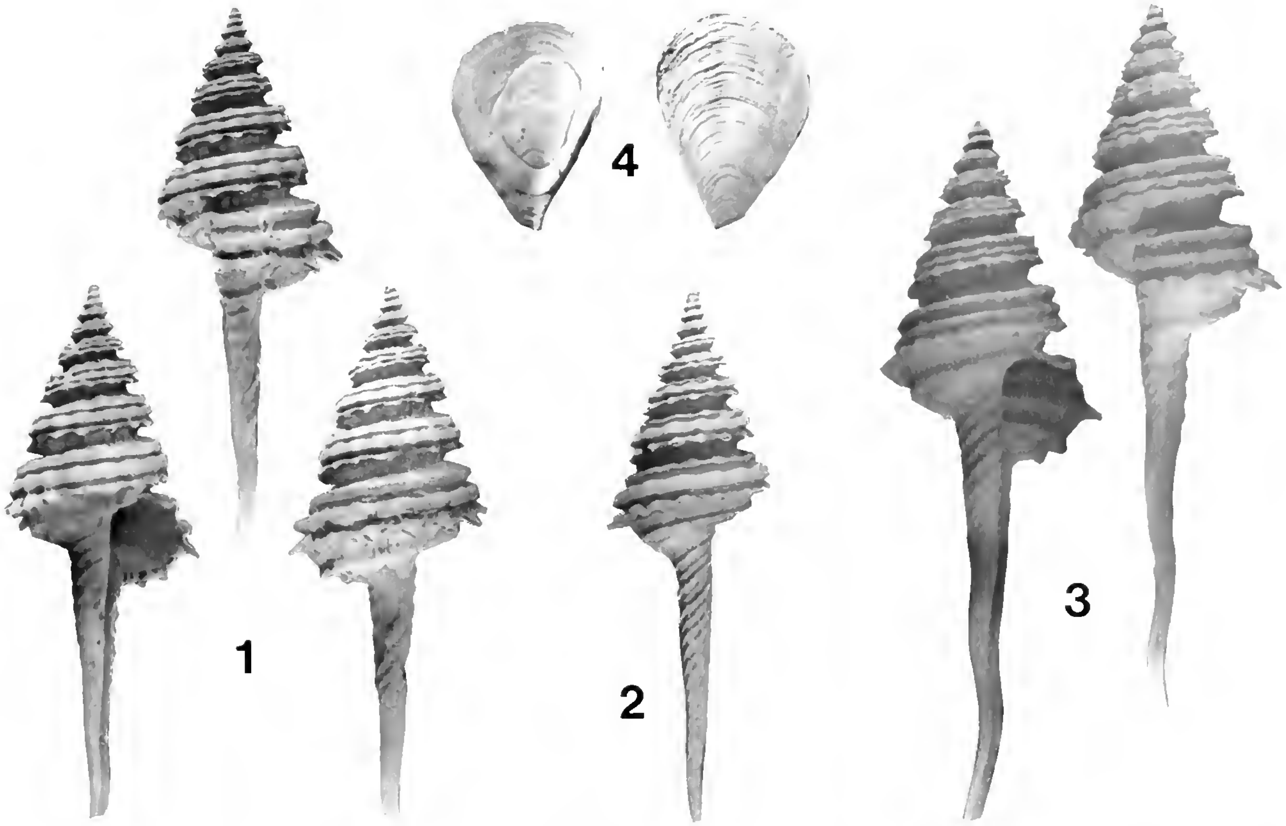
Description: Shell (figures 1–3) large for genus (to 89 mm), thin, fusiform. Spire angle 37.0°–44.5°. Protoconch deviated paucispiral, of 1⅔ smooth, bulbous whorls. Transition to teleoconch gradual, marked by development of peripheral keel and broad axial ribs within ⅓ whorl. Teleoconch with up to 9 whorls. Suture abutting pronounced spiral cord anterior to whorl periphery. Spiral sculpture of 3 equal threads or cords between suture and periphery on early whorls. Cord nearest suture decreasing in prominence or disappearing by fifth post-nuclear whorl; second and usually third spiral cords concomitantly thickening, each forming broad band. Second band sufficiently elevated to form channeled suture. Two strongly pronounced spiral cords between whorl periphery and siphonal canal. Fourteen to 22 spiral cords along proximal ⅔ of siphonal canal, decreasing in prominence distally. Early whorls with 11–13 axial ribs/whorl, each forming tubercle along periphery. Axial ribs becoming less pronounced and tubercles forming short, open, anteriorly-directed spines on third post-nuclear whorl. Body whorl with 15–16 spines. Aperture roughly semi-circular. Outer lip thin, furrowed beneath periphery and major cords. Inner lip smooth due to dissolution of portion of outermost layer from parietal region. Siphonal canal long, stout, axial, occasionally sinuate distally (figure 3). Shell color uniformly white. Periostracum thick, straw-colored to tan, axially-bladed. Operculum (figure 4) corneous, strongly ovate, with two straight sides converging on terminal nucleus. Soft parts unknown.

Etymology: This species is named in honor of my wife Julia, in recognition of her frequent assistance and support of my research.

Type locality: Off Inhaca Island, Mozambique, 26°07′S, 34°11′E, in 600–665 m, Anton Bruun Cruise 8, station 397C, September 29, 1964.

Holotype: USNM 718510, length 67.9 mm.

Paratypes: Paratypes 1–2, USNM 860174, from the type locality; paratype 3, SAM A36257, off northern Natal, South Africa, 27°12.2′S, 32°56.0′E, in 660 m, May 20, 1976; paratypes 4–6, SAM A36256 off northern Natal, South Africa, 27°14.8′S, 32°54.6′E, in 680–700 m, May 20, 1976; paratypes 7–8, DMNH 190068, trawled, deep water off Zululand coast, South Africa, December, 1967; paratypes 9–11, NM 5740, off Natal, South Africa, May, 1970; paratype 12, Gratz collection, off Natal, South Africa, 200–300 fms [366–548 m].



Figures 1–4. *Coluzea juliae* new species. **1.** Holotype, USNM 718510, off Inhaca Island, Mozambique, 26°07'S, 34°11'E, in 600–665 m, Anton Bruun Cruise 8, station 397C, September 29, 1964 (1.0 ×). **2.** Paratype 3, SAM A36257, off northern Natal, South Africa, 27°12.2'S, 32°56.0'E, in 660 m, May 20, 1976 (1.0 ×). **3.** Paratype 9, NM 5740, off Natal, South Africa, May, 1970 (1.0 ×). **4.** Operculum of holotype (2.5 ×).

Distribution: This species is known only from the upper continental slope off southernmost Mozambique and northeastern Republic of South Africa. The confirmed bathymetric range is 548–660 m.

Comparative remarks: *Coluzea juliae* new species most closely resembles *C. liriope* Harasewych, 1986, a species inhabiting similar depths along the Makassar Strait of Indonesia, but differs in having: a periphery that is sharply keeled and lined with long, narrow, open, anteriorly-directed spines rather than a rounded periphery with low nodular spines; two extremely pronounced raised cords between the periphery and siphonal canal, rather that four weaker cords; and a crenulated outer lip rather than one with a rectangular posterior margin. This new species is also similar to *Coluzea eastwoodae* (Kilburn, 1971), with which it overlaps in geographic and bathymetric ranges, but can be readily distinguished on the basis of its characteristic spiral sculpture between the suture and periphery.

Discussion: Of the 13 specimens of *Coluzea juliae* new species examined, 10 had repaired breaks along the proximal portion of the siphonal canal, indicating crab pre-

Table 1. *Coluzea juliae* new species. Measurements of shell characters. Linear measurements in mm (n = 10, except for measurements involving the siphonal canal, where n = 7).

Character	Mean	Range	SD
Shell length (apex to proximal end of siphonal canal)	41.3	33.1–51.3	6.0
Aperture length	13.8	10.6–17.3	2.3
Aperture length/shell length	0.33	0.31–0.36	0.02
Siphonal canal length	34.5	28.2–45.8	6.7
Siphonal canal length/aperture length	2.82	2.44–3.34	0.31
no. whorls teleoconch	8.6	8.0–9.0	0.4
no. axial ribs/spines on body whorl	16.6	14–23	2.7
Spire angle	41.5°	37.0°–44.5°	2.2°

dation. The thick spiral cords characteristic of this species strengthen the shell and increase its resistance to crushing and peeling predators. These expanded cords also result in an altered apertural shape that accommodates a taller, more voluminous mantle cavity, especially in the regions that contain the hypobranchial gland, pallial gonoducts and rectum. Similar modifications of apertural shape occur in *Coluzea liriope* (Harasewych, 1986: pl. 2, figs. 3, 4), and to a lesser extent in *Coluzea cingulata* (Martens, 1901) (see Darragh, 1969: pl. 6, figs. 106, 116) and in the early whorls of *C. distephanotis* (Melvill, 1891) (see Harasewych, 1986: pl. 1, figs. 1–3). The similarities between *Coluzea juliae* new species and *C. liriope* are sufficiently compelling to suggest a close relationship between these two species. The relationships of these species to *C. cingulata* and *C. distephanotis* are less clear. The dorsal expansion of the aperture in the early whorls of *C. distephanotis* occurs anterior to the periphery, and may be a convergent adaptation to increase the volume of the mantle cavity.

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Genetics and Shell Morphology of Hard Clams (Genus *Mercenaria*) from Laguna Madre, Texas*

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ABSTRACT

Texas *Mercenaria* were originally described as a subspecies of *M. campechiensis*, but are now generally regarded as a subspecies of *M. mercenaria*, primarily based on aspects of shell ridging. We used isozyme frequencies at seven loci, six morphometric variables, shell ridging, and nacre color to compare Texas populations to reference populations of *M. campechiensis* and *M. mercenaria*. Texas populations were indeed distinct, but much more similar to the former. Hard clams from Texas should be considered *Mercenaria campechiensis texana* (Dall, 1902).

Key words: Hard clams; Texas; electrophoresis; morphometrics.

INTRODUCTION

Venerid clams of the genus *Mercenaria* (variously known as quahogs, cherrystones, hard clams, etc.) are of such commercial importance that it is surprising their systematic relationships are not better understood. Most authors follow Abbott (1974) in recognizing two North American species, the northern *Mercenaria mercenaria* (Linné, 1758) and southern *Mercenaria campechiensis* (Gmelin, 1791). Three criteria have been used to distinguish the species. *Mercenaria campechiensis* is supposed to have thick concentric ribs, white nacre, and a lunule at least as wide as it is high, while *M. mercenaria* has thin, easily eroded ribs, purple nacre, and a narrower lunule (figure 1).

Abbott (1974:523) noted that *M. campechiensis* hybridizes with *M. mercenaria* in the wild, and "could well be considered a subspecies." It has recently been shown, however, that some reproductive isolation exists between the two species where they occur sympatrically in the Indian River, Florida (Dillon & Manzi, 1989). Thus we consider these species distinct.

Dillon and Manzi (1989) selected one population each from central portions of the ranges of *M. mercenaria* and *M. campechiensis* to serve as "references". These populations appeared to be typical both genetically and morphologically, with no evidence that either contained any hybrid genomes. We found that 100% of the *M. mercenaria* shells had thin, easily eroded concentric ribs, while over 99% of *M. campechiensis* had thick, resistant concentric ribs. Nacre color was also a useful discriminator—80% of the *M. mercenaria* had distinct purple color, while 92% of *M. campechiensis* were completely white. The ratio of lunule width to lunule height proved to be of limited utility. Over 86% of *M. campechiensis* in our sample had ratios less than 1.0, and thus would have been misclassified as *M. mercenaria* using this traditional criterion. We did find, however, that if measures of lunule height and width were combined with overall shell length, width, height, and weight, very accurate morphometric discrimination between the two species was possible (Dillon & Manzi, 1989).

Hard clam populations inhabiting the Texas coast of the Gulf of Mexico were originally described by Dall (1902) as *Venus* (now *Mercenaria*) *campechiensis texana*. Dall viewed the presence of thin, easily eroded concentric ribs in the Texas populations (figure 1) as justification for recognizing the subspecies. The subspecies was transferred to *M. mercenaria* by Abbott (1954), at least partly because the inshore fauna of the Gulf of Mexico is generally Carolinian, rather than Caribbean in affinity (personal communication to Joy Goodsell). Here we show that based on isozyme frequencies and all other shell characteristics besides ridging, *texana* is a subspecies of *M. campechiensis* as originally described, not *M. mercenaria*.

METHODS

We were able to obtain 29 *Mercenaria* of the subspecies *texana* from Laguna Madre, in the vicinity of Corpus Christi, Texas. Samples were taken of both siphon and foot tissue, and electrophoretic analysis performed as described elsewhere (Dillon, 1982, 1985; Dillon & Manzi,

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Figure 1. Left and anterior aspects of the three *Mercenaria* taxa. Left—*M. campechiensis* (Gmelin, 1791), Center—the subspecies *M. campechiensis texana* (Dall, 1902), Right—*M. mercenaria* (Linné, 1758). The scale bar is 50 mm.

Table 1. Allele frequencies at seven enzyme loci for clams of the subspecies *texana* compared to reference populations of *M. mercenaria* and *M. campechiensis* (data of Dillon & Manzi, 1989). Sample sizes were approximately 29 *texana*, 194 *M. campechiensis*, and 224 *M. mercenaria*.

Allele	*M. mercenaria*	*texana*	*M. campechiensis*
GPI 110	0.023	0.0	0.0
105	0.014	0.0	0.0
100	0.901	0.0	0.0
90	0.021	0.0	0.008
85	0.0	0.034	0.023
80	0.002	0.310	0.221
70	0.038	0.414	0.432
65	0.0	0.0	0.013
60	0.0	0.190	0.271
50	0.0	0.052	0.031
LAP 104	0.095	0.063	0.074
100	0.412	0.042	0.127
96	0.463	0.521	0.333
94	0.019	0.354	0.407
90	0.012	0.021	0.059
SOD 100	0.768	0.0	0.018
90	0.232	0.609	0.702
80	0.0	0.391	0.281
6PGD 110	0.030	0.077	0.084
100	0.622	0.481	0.517
95	0.0	0.0	0.011
90	0.348	0.442	0.388
MPI 110	0.0	0.0	0.032
108	0.059	0.370	0.484
105	0.389	0.304	0.267
100	0.300	0.304	0.174
95	0.253	0.022	0.043
PGMS 103	0.012	0.0	0.0
100	0.844	0.060	0.161
97	0.043	0.040	0.078
95	0.0	0.0	0.075
92	0.077	0.860	0.578
87	0.024	0.040	0.056
82	0.0	0.0	0.035
77	0.0	0.0	0.016
PGMF 103	0.148	0.021	0.061
100	0.852	0.417	0.282
97	0.0	0.562	0.636
95	0.0	0.0	0.021

1987). We estimated allele frequencies at the same seven enzyme loci that have been examined previously: glucose phosphate isomerase (GPI), leucine aminopeptidase (LAP), superoxide dismutase (SOD), 6-phosphogluconate dehydrogenase (6PGD), mannose phosphate isomerase (MPI), and phosphoglucomutase (two loci—PGMS and PGMF). Simple Mendelian inheritance of codominant alleles has been demonstrated at GPI, LAP, 6PGD, PGMS, and PGMF by Adamkewicz *et al.* (1984).

Gene frequencies at individual loci were compared using chi-square tests for two independent samples, corrected for continuity in 2 × 2 cases. Alleles with expected frequencies less than 5 were combined with other rare classes if possible, otherwise they were eliminated. The genetic distance over all 7 loci between each pair of populations was calculated using the method of Nei (1972).

Six measurements were made on the shells of most individuals. Maximum shell length, shell height (maximum dimension in the plane of symmetry perpendicular to shell length), shell width (maximum dimension perpendicular to the plane of symmetry), lunule height (along the line separating the valves), and lunule width (the maximum dimension perpendicular to lunule height) were measured with vernier calipers. The weight of both valves combined was recorded to the nearest gram. Nacre color and strength of concentric ridges were also noted. Five whole individuals and two single-valves were lost subsequent to tissue sampling. Thus sample sizes were N = 29 for isozyme frequencies, but only N = 24 for the morphological analyses.

We compared the Texas clams to the reference populations of 224 *M. mercenaria* and 194 *M. campechiensis* analyzed by Dillon and Manzi (1989). The *M. mercenaria* were sampled from a tributary of the Stono River, 15 km south of Charleston, South Carolina. The *M. campechiensis* were collected at Cedar Key, on the north-

Table 2. Results of the principal component analysis of shell morphometric data from *Mercenaria mercenaria*, *M. campechiensis*, and the subspecies *texana*.

Morphological character	Eigenvectors					
	PC1	PC2	PC3	PC4	PC5	PC6
Shell length	0.42	0.16	−0.43	−0.59	0.41	0.32
Shell height	0.44	−0.08	−0.25	−0.15	−0.27	−0.80
Shell width	0.42	−0.33	−0.10	0.10	−0.66	0.50
Lunule width	0.40	−0.05	0.85	−0.30	0.09	−0.02
Lunule height	0.34	0.84	0.05	0.40	−0.10	0.05
Shell weight	0.41	−0.39	−0.06	0.61	0.55	−0.01
Eigenvalue	4.96	0.56	0.25	0.11	0.08	0.03
Cumulative variance	0.83	0.92	0.96	0.98	0.99	1.00

central Gulf coast of Florida. All shells examined in this study have been deposited at the Academy of Natural Sciences of Philadelphia. Catalog numbers are as follows: Texas population 373466, *M. campechiensis* 373467, *M. mercenaria* 373468.

Following Dillon and Manzi (1989), we performed a discriminant analysis on principal component scores extracted from the six measurement variables. First a principal component analysis was performed on the correlation matrix calculated over all 442 individuals (the Princomp procedure, SAS, 1985). We disregarded variance on the first principal component (PC) as a method of factoring out size variance, and used factor scores on the remaining 5 PC's as new variables for nearest-neighbor discriminant analysis (the Neighbor procedure, SAS, 1985). This is a nonparametric discriminant analysis, not involving the calculation of discriminant functions. In our application there were 418 known clams, and only the 24 Texas clams were entered as unknowns. Each clam was classified as *M. mercenaria* if at least 19 of its 20 nearest Euclidean neighbors of known affinity were *M. mercenaria*, *M. campechiensis* if 19 of 20 were *M. campechiensis*, and intermediate if otherwise.

RESULTS

Table 1 compares allele frequencies at seven enzyme loci in the Texas clams to reference frequencies established for *M. mercenaria* and *M. campechiensis* by Dillon and Manzi (1989). The two reference populations are strikingly distinct at GPI, SOD, MPI, and PGMF, and in these four cases, the *texana* sample is not significantly different from *M. campechiensis* by chi-square. The two reference populations are also distinct at the LAP and PGMS loci, but although the *texana* sample is much more similar to *M. campechiensis*, significant differences exist. The frequency of LAP 100 is significantly lower in *texana* (chi-square = 8.01, 2 d.f.), and there seems to have been a significant loss of allelic diversity at the PGMS locus (chi-square = 13.5, 1 d.f.). The Texas population was not significantly different from either reference population at the 6PGD locus.

Calculated over all 7 polymorphic loci, Nei's genetic distance (*D*) between the two reference populations was 0.82. The Texas population showed $D = 0.041$ to *M. campechiensis* but $D = 0.83$ to *M. mercenaria*.

Results of the principal component analysis on shell morphometrics are given in table 2. Factor loadings were somewhat different from those obtained by Dillon and Manzi (1989), since 24 clams of the subspecies *texana* have replaced 170 individuals from the Florida hybrid zone. We discarded PC1, representing 83% of the variance, and used the remaining 17% for discriminant analysis.

Figure 2 shows that the two reference populations are quite distinct on PC2, even though this is not a discriminant function, with *M. campechiensis* scoring lower. Judging from the factor loadings on PC2 (table 2), *M. campechiensis* would seem to have a wider, heavier shell than *M. mercenaria*. In contrast to our previous findings, lunule height loads very strongly on PC2, while the contribution of lunule width is negligible. It would appear that *M. campechiensis* does not have an especially wide lunule for its size, but rather a distinctively short (or "lower") one. Nearest-neighbor discriminant analysis confirmed that the two reference populations are very distinct (table 3). One *M. campechiensis* was misclassified, to 95% confidence, as *M. mercenaria*, but no *M. mercenaria* were misclassified. The reference populations were both about 80% distinct.

Although more similar to *M. campechiensis* than *M. mercenaria*, Texas clams were quite diverse morphometrically (figure 2). The three lowest PC2 scores all belonged to *texana* specimens, suggesting that Texas pop-

Table 3. Classification (to 95% confidence) of clams by nearest-neighbor discriminant analysis on principal component scores, given the two reference populations as knowns and specimens of the subspecies *texana* as unknowns.

	M. mercenaria	Intermediate	*M. campechiensis*
M. mercenaria reference	180	44	0
texana	2	14	8
M. campechiensis reference	1	37	156

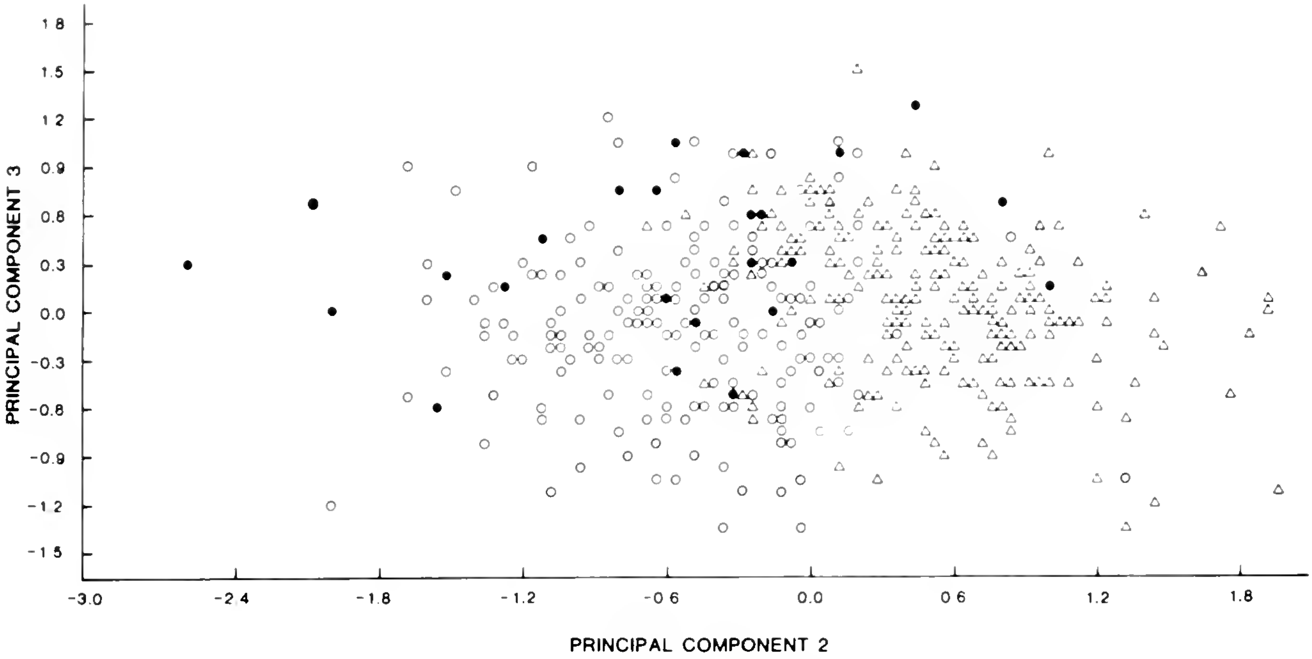

Figure 2. Factor scores on principal components 2 and 3. Triangles are *M. mercenaria* reference, open circles are *M. campechiensis* reference, and closed circles are *M. campechiensis texana*. A total of 51 reference individuals are obscured by overlap.

ulations may be distinguished by greater relative width and weight than reference *M. campechiensis*, and by even shorter lunules. Specimens of the subspecies *texana* also tended to be distinct on PC3, showing wider lunules and shorter shells overall. Table 3 shows that most shells from the Texas population could not be identified, to 95% confidence, as coming from either reference population. Among classifiable shells, however, those indistinguishable from *M. campechiensis* outnumbered those from *M. mercenaria* by a ratio of 4 to 1.

All individuals from the Texas population showed the typical *M. campechiensis* trait of purely white nacre. But the striking feature of the *texana* shells was the presence of thin, easily eroded concentric ridges or ribs. Ribs were eroded to leave bald patches on all 24 individuals examined, even though over 99% of the reference *M. campechiensis* population had strong, resistant ribs.

DISCUSSION

Isozyme frequencies clearly show that the Texas populations are much more similar to *M. campechiensis* than *M. mercenaria*. Considering overall genetic distance, it was in fact the reference *M. campechiensis* population that was intermediate, not the Texas population. It is difficult to compare our values of D to those collected from other taxa, since monomorphic loci were excluded from this study. But it appears that isozyme divergence between both species and subspecies of *Mercenaria* is unusually low (Avise, 1976).

It might be argued that the geographic distance between Texas and South Carolina populations makes a comparison of isozyme frequencies unfair. But extensive dispersal is apparently possible during *Mercenaria*'s veliger stage. Dillon and Manzi (1987) reported only a single significant difference at these seven loci in a comparison of Massachusetts and Virginia *M. mercenaria*. Only two significant differences were apparent between Virginia and South Carolina, and the approximately 20 clams from the Atlantic coast of Florida identified as pure *M. mercenaria* were not strikingly different from South Carolina populations (Dillon & Manzi, 1989). It seems unlikely that a difference of the magnitude reported here between the reference *M. mercenaria* and the Texas clams could be due to distance alone. The minor differences shown at two loci between the Texas population and the reference *M. campechiensis* population from northern Gulf Florida are of the magnitude we have observed from isolation by distance.

The reference populations were quite distinct in shell morphometrics, and again individuals of the *texana* subspecies tended to sort out with *M. campechiensis*. The nacre color of the Texas clams also clearly places them with *M. campechiensis*. But the presence of some peculiarities of shell shape, together with thin, easily eroded concentric ridges, makes Texas populations so distinct that they do warrant recognition as a subspecies, *Mercenaria campechiensis texana* (Dall, 1902).

Preliminary results from hybridization studies between standard *M. mercenaria* and *M. campechiensis* conducted in our facilities suggest that shell ridge thickness is primarily, perhaps entirely, under genetic control. The ridge thickness of F_1 hybrids (measured by mechanical filing) is intermediate between that of pure offspring from the two species spawned at the same time and reared in the same environment. The thinner, finer ribs shared by *M. mercenaria* and *M. campechiensis texana* may be an adaptation for burrowing in the fine, terrigenous silt and mud found in the estuaries of the American Atlantic and northern Gulf coasts. The thicker, heavier ribs of typical *M. campechiensis* may be an adaptation for the coarser, carbonate sands offshore, in peninsular Florida, and the Caribbean Sea. Thin ridges are probably ancestral, with thicker ridges evolving after the divergence of *M. mercenaria* and *M. campechiensis*. Otherwise, one would need to postulate that thin ridges evolved separately in *M. mercenaria* and *M. campechiensis texana*.

Some attention has focused on *M. campechiensis texana* as a candidate for mariculture, especially in the Texas environment to which it is adapted (Craig *et al.*, 1988). Another possible source of commercial interest is in the hybridization of Texas populations to *M. mercenaria* as a method of increasing genetic variability (review by Dillon & Manzi, 1988). Recently Goodsell (1989) has made all reciprocal crosses between *M. mercenaria*, *M. campechiensis*, and *M. campechiensis texana*, demonstrating the feasibility of this approach. In any such future studies, the genetic relationships among these three taxa should be kept in mind.

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Variation in Size Demography of Lotic Populations of *Corbicula fluminea* (Müller)

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ABSTRACT

Patterns of size demography among 14 lotic populations of the Asiatic clam, *Corbicula fluminea*, in the state of Mississippi were compared based on samples collected between May 24 and June 22, 1984. Individuals greater than 20 mm in shell length (SL) and greater than 1 year old comprised a substantial fraction (13–64%) of only six populations. These populations had distinct multiple cohorts. Four of the six populations occurred among longer-lived native unionids, suggesting that streambed stability is crucial to the establishment of lotic populations of *C. fluminea* with complex size (and age) structure. Individuals greater than 20 mm SL comprised a small fraction (0–5%) of the other eight populations; these populations were characterized by a heavily dominant, single cohort of small clams. Unusually high stream discharge throughout the state from December, 1982 through May, 1983 and again in December, 1983 exaggerated ordinarily high winter and spring flows. The simple size demography of the eight populations with few large individuals probably reflected recolonization of flood-decimated assemblages by small individuals transported downstream from more stable upstream sites.

Key words: Corbicula fluminea; unionids; size demography; lotic habitats; flood scour; streambed stability.

INTRODUCTION

The Asiatic clam, *Corbicula fluminea*, is clearly adapted to well-oxygenated sand and gravel shoals of lotic habitats and is intolerant of reducing sand, mud, or silt (McMahon, 1983 and references within). Sand and gravel shoals are often shifted by flood flows in lotic habitats. As reviewed by McMahon (1983), *C. fluminea* shows several adaptations to unstable substrata, including: a massive and concentrically ridged shell to resist abrasion and anchor individuals in substrata exposed to swift flow; extensive mantle fusion, narrow pedal gape, a foramen around the posterior adductor muscle, and highly developed statocysts providing for rapid locomotion and burrowing; and hermaphroditism plus production of crawling pediveliger larvae (also capable of byssal thread attachment) allowing rapid establishment of dense populations by just a few colonists. Despite larval adaptations to enhance local recruitment, *C. fluminea* is passively transported downstream in large numbers. Pediveligers (*e.g.*, Sickel, 1979) and post-larval juveniles less than 2 mm SL (Williams & McMahon, 1986) drift on water currents. Furthermore, small individuals (up to 15 mm but mostly less than 5 mm SL) are passively transported downstream in large numbers, evidently by tumbling along the bottom (Williams & McMahon, 1986). Passive transport of individuals from viable upstream populations allows rapid recovery of downstream populations that have been severely reduced in size or destroyed (*e.g.*, Cherry *et al.*, 1980; McMahon & Williams, 1986).

Despite extensive information on biological adaptations of *C. fluminea* to lotic habitats, only one study has been published detailing the life history of *C. fluminea* in a lotic habitat in the southern United States (Sickel, 1979). Most detailed information about population dynamics of this species comes from studies of lentic populations (McMahon, 1983 and references within). *Corbicula* populations in lotic habitats are likely to be affected by seasonal patterns of stream discharge affecting stability of sand and gravel shoals. The purpose of this paper is to describe interpopulation variation in size demography of *C. fluminea* at 14 lotic sites in Mississippi representing a range of substrata stability conditions.

MATERIALS AND METHODS

A large number of individuals, ranging from 98 to 413, were collected from 14 lotic populations at locations throughout Mississippi (table 1). All samples were taken by scooping or pushing substrate into a dip net with a mesh size of 4.0 mm. The maximum shell length (SL, the greatest anterior–posterior dimension across the valves) of each individual was measured to the nearest 0.1 mm using a Vernier caliper, and SL frequency histograms were plotted for each population. All samples except one were collected within an 18 day period in

Table 1. Description of samples and habitats of 14 lotic populations of *C. fluminea* sampled in Mississippi during late spring and early summer of 1984

Site	Stream	Date	Sample size	Density[1]	Flow[2]	Substrate
BYP	Bayou Pierre	5 Jun	136	L	L	Along stumps and snags; with unionids
TAN	Tangipahoa R.	5 Jun	129	M	M	Sandy gravel along snags and macropytes; with unionids
PAS	Pascagoula R	21 Jun	202	H	N	Mud, sand, and silt; with unionids
LEA	Leaf R	21 Jun	196	M	L	Muddy sand; with unionids
CHU	Chunky R.	18 Jun	119	M	L	Mud over bedrock; with pisidiids
YOC	Yockanookany R.	7 Jun	136	M	M	Gravel where stabilized by stumps and snags
NOX	Noxubee R	18 Jun	280	L	M	Unconsolidated riffles of mud, sand, gravel, and chalk flakes
PRL	Pearl R.	7 Jun	213	L	L	Detritus and sand among roots of cypress trees
BBL	Big Black R.	19 Jun	98	L	L	Sand bar in association with snags, limbs, and sticks
STR	Strong R.	24 May	145	L	H	Pockets of detritus and sand in scour holes in bedrock
BUT	Buttahatchie R	18 Jun	102	L	M	Gravel shoals
CHI	Chickasawhay R	21 Jun	413	H	N	Mud, sand, and broken clay at end of long run
TAL	Tallahala Cr.	21 Jun	192	M	M	Sand and gravel stabilized by snags
FMC	Fourteen Mile Cr.	22 Jun	141	L	N	Thick silt over sand and some gravel

[1] Density was estimated as high (H; >300 individuals/m^2), moderate (M; 50–300 ind/m^2), or low (L; <50 ind/m^2).

[2] Flow velocity was estimated, during relatively low discharge at all sites, as high (H; >0.5 m/sec), moderate (M, 0.2–0.5 m/sec), low (L; detectable but <0.2 m/sec), or neglible (N).

late spring (June 5–22, 1984) to minimize the influence of different dates of sampling on intersite variation in size demography. One sample was collected slightly earlier, on May 24. All samples were collected during relatively low flow conditions.

Stream discharge in Mississippi responds to seasonal patterns of rainfall, and is typically high in winter and early spring and low during summer and early fall (figure 1, US Geological Survey, 1981; Tate *et al.*, 1982, 1983; Tharpe *et al.*, 1984). Winter and spring discharge was unusually high throughout the state from December, 1982 through mid-May, 1983 and in December, 1983. High flows in 1983 broke historic records at two of the 14 sites (BBL and BYP) and approached record levels at several other locations (Tate *et al.*, 1983). Ratios of maximum-to-minimum daily discharge averaged 1,535 from October, 1982 through September, 1983 for gage sites near our sampling locations (Tate *et al.*, 1983), reflecting the extreme shifts in hydrologic conditions characteristic of these lotic habitats.

RESULTS

Individuals greater than 20 mm SL comprised a substantial fraction of six populations (figure 2). The percent abundance of individuals greater than 20 mm SL equaled 12.5, 13.8, 13.9, 19.5, 46.5, and 63.9 at TAL, BYP, PAS, LEA, TAN, and CHU, respectively. Two distinct cohorts were evident at TAL, and the other five populations included three or more cohorts (figure 2). Both the abundance of individuals greater than 20 mm SL and the complex size demography indicated longevity of 2 to 3 years for a substantial fraction of each population. These age estimates are based on Sickel's (1979) detailed study of a single southern lotic population in the Althahama River in Georgia. Individuals in the Altahama River grew to modal SL's of 14 and 22 mm in the first and second year of life, respectively. The largest individual collected (38 mm SL) was from the LEA population, and the CHU, TAN, and PAS populations also included individuals greater than 30 mm SL.

Four of the six populations that included a substantial number of 2 and 3 year old individuals (TAN, PAS, LEA, and BYP) occurred with adult unionacean bivalves (table 1). The most common unionids were *Quadrula pustulosa* (Lea), *Fusconaia flava* (Rafinesque), and *Pluerobema beadleanum* (Lea) at TAN and BYP. Unionids at PAS were dominated by *Lampsilis teres* (Rafinesque) and *Q. pustulosa*. Dominant species at LEA were *Toxolasma texasensis* (Lea) and *L. teres*.

Eight populations were heavily dominated by a single cohort of individuals (1983 recruits) less than 20 mm SL (figure 3). The percent abundance of *C. fluminea* greater than 20 mm SL among these eight populations was significantly less ($t = 3.53$; $p < 0.01$) than among the other six populations. No individuals greater than 20 mm SL were collected at YOC or NOX. Percent abundance of clams greater than 20 mm SL equaled 0.2, 0.5, 2.0, 2.1, 2.8, and 4.9 at CHI, PRL, BBL, STR, FMC, and BUT, respectively. The paucity of large individuals in these eight populations did not allow cohorts other than the 1983 generation to be clearly distinguished (figure 3). The average SL of the dominant 1983 generation ranged among the eight populations from 8.8 mm at YOC to 15.9 mm at FMC. This wide range reflected intersite differences in timing of recruitment and/or SL growth rates. The dominant cohort of the FMC population was considerably larger than the main cohort of the other eight populations. This population was from a small stream in a drainage of mostly agricultural land, while all other populations were in larger streams or rivers that drain primarily forested land. Thus, the FMC site was

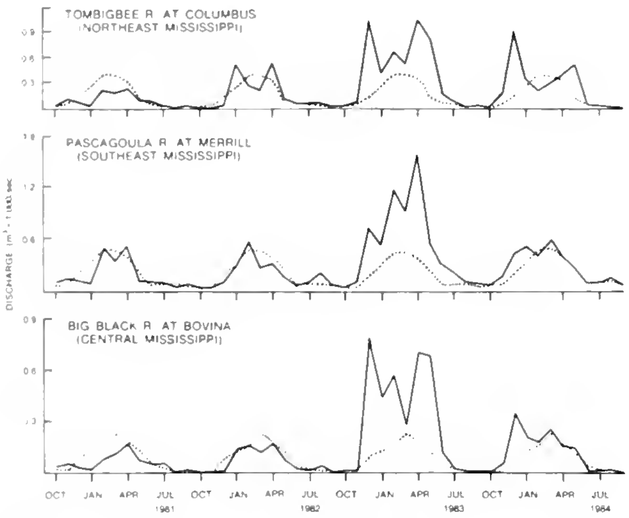

Figure 1. Median monthly discharge recorded from October, 1980 through September, 1984 at three representative gage stations in Mississippi (based on data in Tharpe *et al.* (1984), Tate *et al.* (1982, 1983), and US Geological Survey (1981). The dotted line shows the median monthly discharge averaged for the period 1951–80.

a comparatively eutrophic habitat with sustained periods of warm water temperature during winter (due to increased solar insolation and smaller stream size). These different habitat conditions at FMC probably accounted for the higher than average SL growth of clams at this site.

DISCUSSION

The general lack of large clams greater than 1 year in age in Mississippi stream populations of *C. fluminea* is unusual. Most populations of *C. fluminea* (studied mainly in lentic habitats) have multiple cohorts, including a substantial number of larger individuals ranging in SL from 20 to 40 mm (Britton *et al.*, 1979; McMahon, 1983). In our samples, four of the six *C. fluminea* populations with complex age structure and relatively abundant large individuals occurred with native unionacean clams. These native unionids require long-term substratum stability to establish populations due to their long lifespans and low recolonization capability (Kraemer, 1979; McMahon, 1983; Miller *et al.*, 1986; Payne & Miller, 1989).

Thus, the greater abundance of large *C. fluminea* at TAN, PAS, LEA, and BYP relative to most of the other Mississippi populations is probably due to greater stability of the stream bottom at these four sites. Diamond (1982) reported that the complexity of age structure in lotic populations of the pluerocerid snail, *Juga plicefera*, in the Pacific Northwest was inversely related to the likelihood of scour by flood flows. In addition, Sickel's study of a single population of *C. fluminea* in the Altahama River (1979) revealed differences in size demography of samples taken on opposite sides of the river at sites only 2,250 m apart, suggesting that variation in SL distributions is important even within closely adjacent assemblages in a lotic population. Sand and gravel shoals of Mississippi streams and rivers are typically unconsolidated, and the distribution of unionids in the state is limited to portions of streams with stable substratum (Hartfield & Rummel, 1981; Hartfield & Ebert, 1986). The effects of stream bottom stability on bivalve distribution were especially evident during sampling at TAN and BYP, where *C. fluminea* was most dense and unionids were restricted to gravelly sand (TAN) or sand (BYP) shoals that were stabilized by trunks of fallen trees or stands of the submersed macrophyte *Vallisneria* sp.

Spring and fall peaks in production of pediveliger

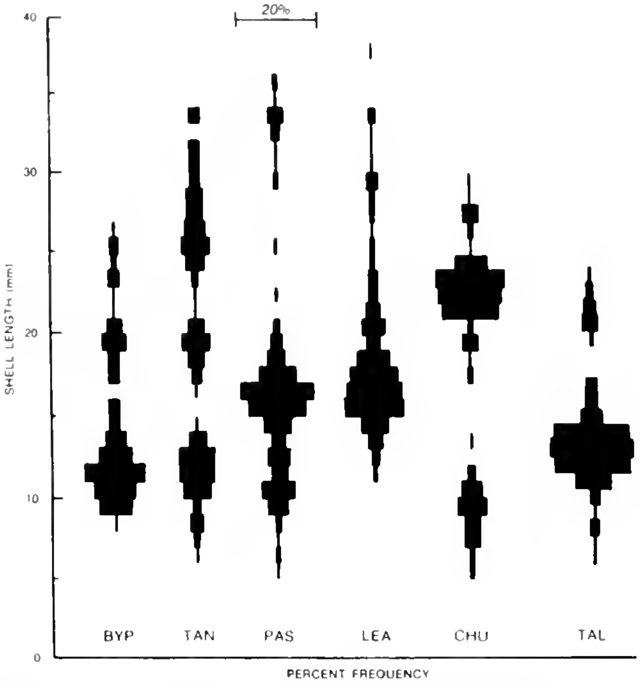

Figure 2. Shell length (SL) frequency histograms for six Mississippi populations of *Corbicula* with a substantial number of individuals greater than 20 mm SL and distinct multiple cohorts.

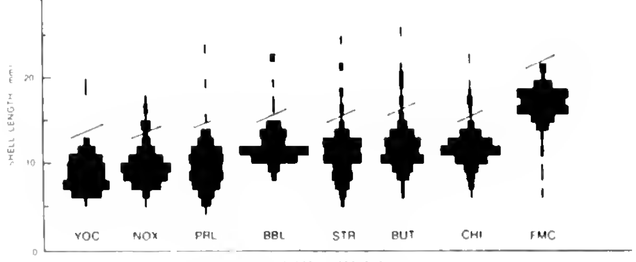

Figure 3. Shell length (SL) frequency histograms for eight Mississippi *Corbicula* populations dominated by individuals less than 20 mm SL that comprise an essentially single cohort of 1983 recruits. The slanted line through each histogram separates 1983 recruits from older individuals.

larvae by *C. fluminea* have been observed in several populations that have been repetitively sampled throughout the year (reviewed by Britton *et al.*, 1979; McMahon, 1983). In most lotic habitats in North America, spring release of pediveligers during high flows would lead to extensive downstream drift and little local recruitment. Late summer and fall release of pediveligers during low flow would be more likely to lead to local settlement near the site of the adult population. Sickel (1979) observed a major peak in density of drifting larvae in early May in the Altahama River. However, major recruitment of juvenile clams was not evident in his samples until mid-July and these recruits attained a modal SL of only 4 mm by late October. These results suggest that the main recruitment period occurred substantially later and during lower flows than the late spring period of maximum larval drift. Patterns of pediveliger release, transport, and recruitment need to be studied in lotic habitats in relation to both stream hydraulics and season. In addition, downstream transport and recruitment of juvenile and small adult clams should be considered in studies of *C. fluminea* population dynamics in lotic systems.

The ubiquity of *C. fluminea* populations almost exclusively comprised of small individuals (figure 3) during the late spring of 1984 may reflect recent decimation of those populations by flood flows during December, 1982 through mid-May, 1983 and December, 1983. Certainly, the eight populations portrayed in figure 3 were comprised mainly of clams small enough to have been passively transported downstream from more stable upstream populations. Several investigations have shown that larvae and young specimens (the latter with SL up to 5.0 mm but generally less than 2.0 mm) of *C. fluminea* are transported downstream in large numbers on water currents (Sinclair, 1964; Goss & Cain, 1977; Sickel, 1979; Williams & McMahon, 1986). McMahon and Williams (1986) showed that populations decimated by thermal stress in a lotic channel receiving heated effluent from an electricity-generating plant in Texas were quickly reestablished by downstream transport of both juveniles (average SL = 3.5) and small adults (average SL = 9.0 mm SL). Large juveniles and small adults were evidently rolled along the bottom by water currents, because no individuals greater than 2.0 mm SL were recovered in water column samples of drift (Williams & McMahon, 1986). Similarly, populations of *C. fluminea* killed during winter by low water temperature in the New River, Virginia rapidly reestablished the next spring by passive transport of juveniles from a viable upstream population (Cherry *et al.*, 1980). Removal by downstream transport of entire *C. fluminea* populations was noted by one of us (RFM) after severe floods of the San Gabriel River in Texas.

Ecological studies of intersite variation in life history of North American *C. fluminea* populations are especially valuable because interpopulation genetic variation is low for this introduced species (Smith *et al.*, 1979; McLeod, 1986). Thus, comparative studies of *C. fluminea* life history offer an opportunity to evaluate the influence of environmental factors on manifestation of life history features in a relatively invariant genetic stock. Lotic populations should be a major component of these comparative studies, because *C. fluminea* is adapted to such habitats (Britton & Morton, 1979; McMahon, 1983). Our single but nearly simultaneous samples of 14 lotic populations provide strong circumstantial evidence that stream discharge and substratum stability are among the most important environmental factors affecting *C. fluminea* population dynamics in lotic habitats. Comprehensive studies of the life history of this species in lotic systems must focus on hydraulic ecology (see Statzner *et al.*, 1988) and include multiple stream locations as well as frequent and long-term sampling programs.

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The Nomenclatural Status and Phylogenetic Affinities of *Syrinx aruanus* Linné 1758 (Prosbranchia: Turbinellidae)

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The largest gastropod ever to have lived inhabits shallow waters along the northern coast of Australia and adjacent islands. Although this species, which reaches nearly a meter in length (Anonymous, 1982), was known to pre-Linnean authors (Buonanni, 1681: fig. 101; Rumphius, 1705: pl. 28, fig. A), its nomenclatural status and phylogenetic affinities have remained unclear during the intervening centuries.

In erecting the taxon *Murex aruanus*, Linné (1758: 753) included references to two figures. The first, that of Rumphius (1705: pl. 28, fig. A), represents a specimen from the Aru Islands [between New Guinea and Australia] that Rumphius had called "Buccinum aruanum". The second figure (Gualtieri, 1742: pl. 47, fig. B) depicts a smaller, unrelated species endemic to the eastern coast of the United States. Linné apparently never realized that his taxon encompassed two species, as he repeated the same figure references in his catalogue of the Museum Ulricae (Linné, 1764:641), which contained a specimen of the western Atlantic species (Hollister, 1958:75–78). In a later work (Linné, 1767:1222), he added a third figure reference (Buonanni, 1681: fig. 101) that illustrates the species from New Guinea and Australia. In all his references to *Murex aruanus*, Linné listed the habitat as New Guinea. There was no specimen of either species in Linné's collection at the time the species was described that could be regarded as the holotype (Hanley, 1855: 302).

The failure of Linné to differentiate between the two disparate species included in his description has resulted in the application of the taxon *aruanus* predominantly to the Australian species [usually as *Syrinx aruanus*], and less frequently to the western Atlantic species [as *Fulgur* or *Busycon aruanus*]. The nomenclature was further complicated when Hollister (1958:78) invalidly designated as lectotype of *Murex aruanus* Linné, 1758, the specimen of the western Atlantic species from the Museum Ulricae collection that Linné examined and referred to in his 1764 work. This specimen was not available for lectotype designation as it was not referred to by Linné in the original description (Linné, 1758:753) and thus could not be considered part of the type series as defined by ICZN article 72(b)(i). Nor was a lectotype designation necessary, as the species had been effectively restricted by previous revisers.

Born (1778:314–315), the first to refer to *Murex aruanus* Linné, cited the Buonanni and Rumphius, but not the Gualtieri figures, and added a reference to figures from Chemnitz [as "Martini"] (1780: table 138, figs. 1295 and 1296) [both are *Neptunea antiquata* (Linné, 1758)]. In 1780, Born repeated these references, but omitted figure 1296. Schröter (1783:520) cited the Buonanni and Rumphius figures, added a figure from Chemnitz (1780: 143, vignette 36, fig. D) that depicts the same species, gave the correct locality, and specifically excluded the Gualtieri figure from synonymy. It could be argued, and was indeed accepted by some authors, that Born had effectively restricted the specific name *aruanus* to the species from new Guinea and Australia. However, by specifically excluding the Gualtieri figure, Schröter unquestionably restricted the species concept to include only the Australian species. His action clearly meets the first reviser provision of the International Code of Zoological nomenclature (ICZN article 24b).

As Röding's (1798:121) erection of the genus *Syrinx* (type species: *Murex aruanus* Linné, 1758, by subsequent designation of Winckworth, 1945:144) remained little known until the twentieth century (Dall, 1915), this species appears in earlier literature predominantly as "*Fusus*" *proboscidiferus* Lamarck, 1816, or as *Megalatractus proboscidiferus* (Lamarck, 1816). The family assignment of *Syrinx aruanus* has generally followed that of the western Pacific species of *Hemifusus*, based on their superficial conchological similarity. Thus, in most twentieth century literature (e.g., Thiele, 1929:321; Wenz, 1943: 1217), this species is referred to the family Melongenidae.

Published observations on the anatomy of this species have been few (Kesteven, 1904), yet the data presented clearly indicate that *Syrinx aruanus* is referable to the family Turbinellidae. The radula of *S. aruanus* (Kesteven, 1904: pl. 42, fig. 3) is nearly identical to that of *Turbinella pyrum* (Dall, 1885: pl. 19, fig. 1; Harasewych, 1987: fig. 21), but differs from the radulae of all melongenids in having monocuspid lateral teeth. *Syrinx aruanus* also has a long thin proboscis that folds into a non-evaginable proboscis sheath (Kesteven, 1904:424, pl. 42, fig. 2), a turbinellid character, and lacks the long snout formed of fused tentacle bases that is diagnostic of melongenines. The protoconch, operculum and egg cases of *Syrinx* are also most similar to those of *Turbinella angulata*. As noted by Kesteven (1904:448) the figures of the alimentary system of "*Fusus proboscideus*" published by Haller (1888) do not accurately represent *Syrinx aruanus*, and may represent an unrelated species.

In summary, the taxon *Murex aruanus* Linné, 1758 has been clearly restricted to the northern Australian species figured in Buonanni, Rumphius, and Chemnitz by Schröter (1783) who may be regarded as the first reviser. This species serves as the type of the genus *Syrinx* Röding, 1798 [*Syrinx* Bohadsch, 1761 having been declared nonbinomial, ICZN Opinion 185]. Based on the structure of its radula, proboscis, proboscis sheath, protoconch, operculum and egg case, *Syrinx* is regarded as a monotypic genus in the subfamily Turbinellinae of the Turbinellidae.

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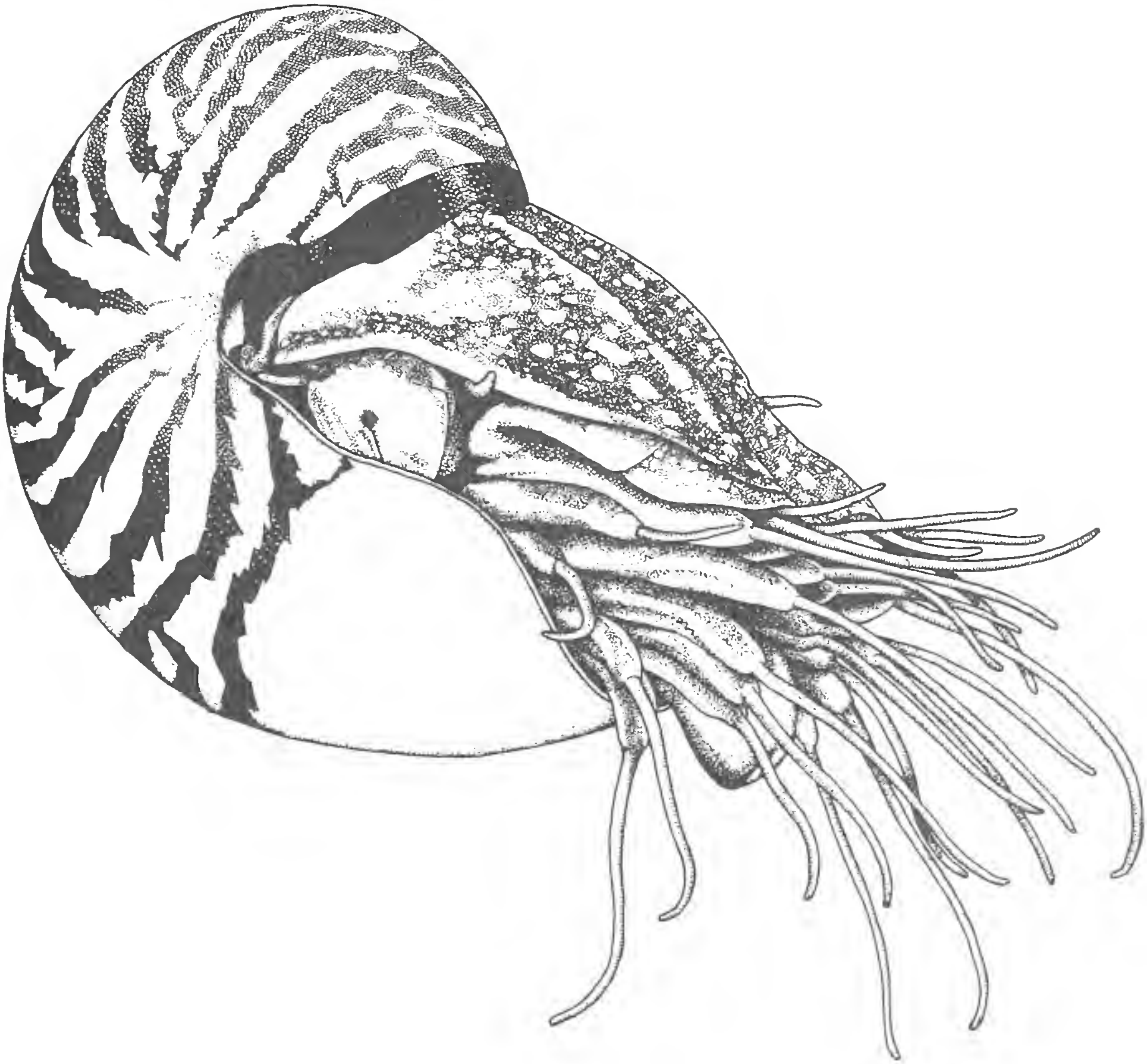

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Effects of Pagurid Density and Size on the Behavior of *Crepidula convexa* Say

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ABSTRACT

The calyptraeid gastropod *Crepidula convexa* Say is commonly found on shells occupied by hermit crabs. Although this facultative association is more common on small shells occupied by *Pagurus longicarpus* Say than on large shells occupied by *P. pollicaris* Say, field experiments clearly show that *C. convexa* does colonize shells occupied by the latter hermit crab and that densities of *C. convexa* can be maintained on such shells at low pagurid density (Shenk, 1986). In this contribution, we report the results of a field experiment that illustrates the negative effect of a high density of *P. pollicaris* on *C. convexa*. In the laboratory, we attempt to determine whether the decline in numbers of *C. convexa* at a high density of *P. pollicaris* is a behavioral response to the hermit crabs or the result of mortality. We also examine the movement of *C. convexa* onto alternative shell substrates and the effect of the size of *P. pollicaris* on these movements. Our results indicate that movements of *C. convexa* are significantly affected by pagurid density and size. We infer that this relatively motile calyptraeid probably escapes mortality in the field by moving off of shells occupied by large *P. pollicaris* and that shells occupied by *P. longicarpus* provide a favorable substrate which may represent a refuge from predation

Key words: Escapes, refuges, predation, hosts, phoresis, epizoism; *Crepidula; Pagurus*.

INTRODUCTION

Along the east coast of the United States, the calyptraeid gastropod *Crepidula convexa* occurs on a wide variety of hard substrates. In addition to living on inanimate objects, this organism can often be found living on shells in facultative associations with other mollusks and two species of hermit crabs (Hendler & Franz, 1971; Hoagland, 1977, 1978, 1979, 1984; Karlson & Cariolou, 1982; Shenk, 1986; Shenk & Karlson, 1986; McGee, 1988). *Crepidula convexa* is a relatively motile, nongregarious species that lacks planktonic larvae (Hoagland, 1978). Juveniles and adult males are not strongly attracted to females (Hoagland, 1978), dispersion patterns are not highly aggregated, and densities are relatively low compared with more gregarious members of this genus (Hoagland, 1978; Shenk, 1986; McGee, 1988).

In spite of not being highly substrate-specific nor strongly attracted by conspecifics, juvenile and adult *Crepidula convexa* can rapidly colonize small shells occupied by the hermit crabs *Pagurus longicarpus* (Karlson & Cariolou, 1982) and *P. pollicaris* (Shenk, 1986; Shenk & Karlson, 1986). *Crepidula convexa* can also colonize large shells occupied by *P. pollicaris*, but densities on these larger substrates have been found to be an order of magnitude less than those on smaller shells (Shenk, 1986; Shenk & Karlson, 1986). In a series of field experiments designed to evaluate several alternative hypotheses explaining *Crepidula* distributions on shells occupied by hermit crabs, Shenk (1986) noted that 1) a relatively high density of *C. convexa*, resulting from colonization of large shells occupied by *P. pollicaris*, could be maintained at low densities of *P. pollicaris*, 2) at high densities of *P. pollicaris*, densities of *C. convexa* on these large shells declined, 3) the density of *C. convexa* on small shells occupied by *P. longicarpus* did not decline even when placed together with high densities of *P. pollicaris*, and 4) the differential response of co-occurring *C. convexa* and its congeners *C. plana* Say and *C. fornicata* (Linné) to high densities of *P. pollicaris* coincided with observed distributional differences; *C. convexa* was most common on small shells, *C. plana* on the inside of large shells, and *C. fornicata* on the outside of large shells (see also Karlson & Shenk, 1983). All three species readily colonized the outside of large shells, but only *C. fornicata* could persist there with high densities of *P. pollicaris*.

After rejecting hypotheses invoking habitat selection and interspecific competition as explanations for observed distributional differences, Shenk (1986) interpreted his experimental results as support for a refuge diversification hypothesis. Under this hypothesis, predation by *P. pollicaris* results in differential exploitation of prey refuges by the congeners; they only coexist at low predator densities. Since predation usually acts to promote species coexistence by reducing prey densities and the intensity of interspecific competition (Paine, 1966), the refuge diversification hypothesis suggests an

Table 1. Mean number of *Crepidula convexa* per shell (± SD) in cages with either one or five *Pagurus pollicaris*. There was one hermit crab per cage in 15 cages and five per cage in 5 cages.

	Number of hermit crabs per cage	
Day of census	1	5
0	1.53 ± 0.93	1.20 ± 0.77
7–8	1.40 ± 1.07	1.00 ± 0.87
10–11	1.27 ± 0.89	0.72 ± 0.80
13–14	1.07 ± 0.55	0.28 ± 0.53***

*** $t = 3.716$, $p < 0.001$

unusual role for predators in this assemblage (Shenk, 1985, 1986).

In this contribution, we focus on the interaction between *Crepidula convexa* and the two hermit crab species. First, we illustrate the density-dependent decline of *C. convexa* from shells occupied by *Pagurus pollicaris*. We then attempt to determine whether this decline is a behavioral response or the result of mortality of *C. convexa* at high densities of *P. pollicaris*. We also examine how *C. convexa* responds to the presence of small shells occupied by *P. longicarpus* and how this response varies with the size of *P. pollicaris*.

METHODS AND RESULTS

Our first experiment was conducted in the field to illustrate the decline in numbers of *Crepidula convexa* in response to a high density of *Pagurus pollicaris* (designated below as the density experiment). We conducted a laboratory experiment in which alternative shell substrates were provided in aquaria with *C. convexa* and a high density of *P. pollicaris* (designated below as the alternative substrate experiment). In another laboratory experiment, we evaluated the effect of the size of *P. pollicaris* on the behavior of *C. convexa* (designated below as the size experiment).

Density experiment: During July 1987, we placed 20 wire cages (80 × 80 × 30 cm) with 0.6 cm galvanized mesh approximately 50 m from shore at a depth of 1.0 m below mean low water at Cape Henlopen, Delaware. We used the small mesh to inhibit colonization of the shells by nonexperimental animals. During low tides over a 5-day period, we used a dipnet to collect hundreds of shells occupied by *Pagurus pollicaris*. Most commonly encountered were the shells of the gastropods *Busycon carica* (Gmelin), *Polinices duplicatus* (Say), and *Natica clausa* Broderip and Sowerby. From these collections, we used 40 hermit crabs in shells with 1–5 *Crepidula convexa* each. We placed a single hermit crab into each of 15, randomly designated cages and five hermit crabs each into the remaining 5 cages; these densities are equivalent to 1.6 and 7.8 hermit crabs m^{2}. We cleaned the cages and inspected all shells for *C. convexa* after the experiment had been in place for 7–8, 10–11, and 13–14 days.

After 13–14 days, there was a significant, density-dependent decline in the number of *Crepidula convexa* per shell (table 1). In response to higher densities of *Pagurus pollicaris*, 77% of the original 30 *C. convexa* disappeared while only 30% of the original 23 disappeared from the shells at low pagurid density. The density-dependent decline in numbers of *C. convexa* is comparable to those reported by Shenk (1986) for predation experiments conducted in Long Island Sound during 1984 and 1985.

Alternative substrate experiment: In this experiment, we placed three *Pagurus pollicaris* into each of 10 aquarium compartments (30 × 20 cm) to achieve a high density equivalent to 50 hermit crabs m^{2}. Such densities occur naturally especially at sites where hermit crabs acquire new shells from dying gastropods (RHK, personal observation). Each hermit crab-occupied shell had 1–4 *Crepidula convexa*. We also placed six *Ilyanassa obsoleta* (Say) shells with no *C. convexa* into each compartment; five randomly selected compartments received *Ilyanassa* shells occupied by *P. longicarpus* and five received shells which had been plugged with non-toxic silicon sealant to prevent occupancy by hermit crabs. These alternative shell substrates were examined for *C. convexa* every 1–2 days for 8 days.

At the end of this experiment, 36% of the original 39 *Crepidula convexa* left their large shell substrates after 8 days (table 2). Comparisons between aquaria receiving plugged *vs.* hermit crab-occupied *Ilyanassa* shells indicate that there was no significant difference in the mean number of *C. convexa* per shell remaining on large shells occupied by *Pagurus pollicaris* ($t = 0.841$, $p > 0.40$, table 2), but the small *Ilyanassa* shells occupied by *P. longicarpus* accumulated significantly more *C. convexa* than did plugged shells ($t = 2.594$, $p < 0.02$, table 2). Of the fourteen individuals that left the large shells over the 8-day period, 10 accumulated on small, hermit crab-occupied shells, one on a small plugged shell, and three were unaccounted for.

Size experiment: After collecting 30 *Pagurus pollicaris* from the field, we divided them into large (18.5 ± 4.3 [SD] mm) and small (9.3 ± 2.1 [SD] mm) size classes based on anterior shield lengths. Maximum anterior shield lengths are reported to be 21.3 mm for *P. pollicaris* and 7.25 mm for *P. longicarpus* (Williams, 1984). We then placed three *P. pollicaris* from a single size class into each of five, randomly selected aquarium compartments for each size class. Each of these hermit crab-occupied shells had one *C. convexa* at the start of the experiment. We also placed six *Ilyanassa* shells occupied by *P. longicarpus* (again with no *C. convexa*) into each compartment to provide *C. convexa* with alternative substrates. In order to monitor net movement of *C. convexa* among substrates, we examined all shells at 1–2 day intervals for 10 days.

Over this 10 day period as many as 12 *Crepidula convexa* had moved onto shells occupied by *Pagurus longicarpus* and, by the end of the experiment, 70% of

Table 2. Mean number of *Crepidula convexa* per shell (± SD) in 10 laboratory aquarium compartments containing three *Pagurus pollicaris* each and either six plugged (PL) *Ilyanassa obsoleta* shells (I) or six shells occupied by *P. longicarpus* (HC). *P. pollicaris* were in *Busycon carica*, *Polinices duplicatus*, or *Natica clausa* shells (B, P, or N).

	Treatment and shell type			
	HC		PL	
Day of census	B, P, or N	I	B, P, or N	I
0	1.40 ± 0.84	0	1.20 ± 0.41	0
1	1.07 ± 0.80	0.20 ± 0.48	1.13 ± 0.35	0
2	1.13 ± 0.91	0.23 ± 0.51	1.00 ± 0.53	0
3	1.10 ± 0.85	0.20 ± 0.48	0.87 ± 0.64	0
4	0.93 ± 0.71	0.20 ± 0.48	0.93 ± 0.60	0.03 ± 0.19
5	0.93 ± 0.71	0.23 ± 0.51	0.73 ± 0.60	0.03 ± 0.19
7	0.87 ± 0.64	0.30 ± 0.54	0.67 ± 0.62	0.03 ± 0.19
8	0.93 ± 0.71	0.33 ± 0.62	0.73 ± 0.60	0.03 ± 0.19

Table 3. Mean number of *Crepidula convexa* per shell (± SD) in the size experiment. Each aquarium compartment contained three *Pagurus pollicaris* in either *Busycon carica*, *Polinices duplicatus*, or *Natica clausa* shells (B, P, or N) and six *Pagurus longicarpus* in *Ilyanassa obsoleta* shells (I).

	P. pollicaris size class and shell type			
	Small		Large	
Day of census	B, P, or N	I	B, P, or N	I
0	1	0	1	0
1	0.67 ± 0.62	0.13 ± 0.35	0.60 ± 0.51	0.07 ± 0.24
2	0.60 ± 0.64	0.13 ± 0.35	0.60 ± 0.51	0.07 ± 0.24
3	0.27 ± 0.60	0.33 ± 0.48	0.47 ± 0.51	0.07 ± 0.24
5	0.40 ± 0.64	0.23 ± 0.43	0.47 ± 0.51	0.07 ± 0.24
6	0.47 ± 0.75	0.20 ± 0.40	0.47 ± 0.64	0.03 ± 0.19
7	0.47 ± 0.64	0.20 ± 0.40	0.47 ± 0.51	0
8	0.58 ± 0.79	0.21 ± 0.40	0.25 ± 0.45	0.12 ± 0.33
9	0.58 ± 0.79	0.21 ± 0.40	0.17 ± 0.38	0.08 ± 0.28
10	0.58 ± 0.79	0.21 ± 0.40	0.17 ± 0.38	0.08 ± 0.28

the original 30 *C. convexa* had left shells occupied by *P. pollicaris* (table 3). However, comparisons of the mean number of *C. convexa* per shell indicate that there were no significant differences between treatments for shells occupied by either *P. pollicaris* ($t = 1.620$, $p > 0.10$) or *P. longicarpus* ($t = 1.304$, $p > 0.10$) after 10 days. Nevertheless, there are some interesting trends in the data. Over the course of the experiment, there was a steady decline in numbers of *C. convexa* on shells occupied by large *P. pollicaris* (from 15 to 2), while several *C. convexa* moved back and forth between shells occupied by small *P. pollicaris* (from 15 to 4 to 7) and those occupied by *P. longicarpus* (from 0 to 10 to 5). Such active movement by *C. convexa* among types of substrates has been noted previously by Hendler & Franz (1971) and Karlson & Cariolou (1982). By the end of the experiment, 16 *C. convexa* were still on shells, 8 had moved to the walls of the aquaria (7 of these were part of the large *P. pollicaris* group), and 6 had died. These deaths occurred in two aquarium compartments (one from each of the two groups) in which hermit crabs had died and fouled the water.

DISCUSSION

The above field and laboratory experiments corroborate earlier reports by Shenk (1986) that the number of *C. convexa* on shells occupied by *P. pollicaris* declines in response to high densities of this hermit crab. In our laboratory experiments, we observed this decline as a total of 38 individuals (out of a possible maximum of 69) moved off their original shells and as many as 23 moved onto shells occupied by *P. longicarpus* (tables 2 and 3). The absence of many deaths in these experiments indicates that the density-dependent decline in numbers of *C. convexa* observed in the field (Shenk, 1986; table 1) was probably not the result of mortality due to predation. Instead, our results are consistent with the hypothesis that the decline in numbers of *C. convexa* is a density-dependent behavior such as an escape response from *P. pollicaris*.

An alternative explanation for why *Crepidula convexa* tend to move off shells occupied by *Pagurus pollicaris* at high, but not low densities of this hermit crab might involve sex ratio biases introduced into the design of these experiments. Since females tend to be less motile during the summer when they brood (Hoagland, 1978), it is possible that disproportionately more females were used in treatments with low densities of *P. pollicaris* by Shenk in 1984 and 1985 (Shenk, 1986) and by ourselves in the density experiment (table 1). Sex determinations were not made in any of these experiments, so we cannot reject this possibility. However, we consider a sex ratio bias to be an unlikely explanation, because density manipulations have yielded consistent field results on three separate occasions.

The movement of *Crepidula convexa* onto small shells occupied by *Pagurus longicarpus* has now been documented in field experiments (Karlson & Cariolou, 1982; Shenk, 1986) and in the laboratory (Karlson & Cariolou, 1982; tables 2 and 3). However, it continues to be unclear why they exhibit this nonrandom behavior. In the field experiment conducted by Karlson and Cariolou (1982) in a shallow subtidal area at Cape Henlopen, *C. convexa* rapidly colonized shells which had been plugged as well as shells occupied by *P. longicarpus*. In the presence of high densities of *P. pollicaris* in the alternative substrate experiment reported above, *C. convexa* appeared to prefer shells occupied by *P. longicarpus* over plugged shells. Alternative explanations for this phenomenon include the notions that 1) these small shells represent refuges from predation (Shenk, 1986), 2) they represent a limited spatial resource in an environment characterized by high sedimentation rates (Karlson & Cariolou, 1982), and 3) these shells are preferred substrates whose selection by *C. convexa* involves cues and sensory adaptations specific to this association. Given the wide variety of substrates utilized by this species, the facultative nature of the associations with hermit crabs, and the field experiment demonstrating no preference for shells occupied by *P. longicarpus* (Karlson & Cariolou, 1982), we consider this last option unlikely. However, additional studies are clearly needed to discriminate among these alternatives.

Our data indicate that the shell-to-shell movement of *Crepidula convexa* is affected by the size of *Pagurus pollicaris*: larger hermit crabs appeared to inhibit the movement of *C. convexa* back onto hermit crab-occupied shells and to favor their movement up the sides of the aquaria. This size-dependent effect on mobility may explain the large effect of shell size on colonization by *C. convexa* (Shenk, 1986; Shenk & Karlson, 1986); in field experiments, they colonized small shells (< 100 cm^2) occupied by *P. pollicaris* at much higher rates than larger shells occupied by larger *P. pollicaris*.

Crepidula convexa is a member of the family Calyptraeidae, a group containing species that are commonly found on the shells of other mollusks. Although the exact nature of most of these associations remains subject to speculation, an escape response and refuge exploitation have been reported for interactions involving *Crepidula adunca* (Sowerby), the host snail *Calliostoma ligatum* (Gould), and the predator *Leptasterias hexactis* (Brandt) (Vermeij *et al.*, 1987). These associations should continue to provide useful models for investigation of the ecological and evolutionary effects of predators on the behavior of their prey and the exploitation of host species as refuges.

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Habitat and Form of *Crepidula grandis* in Japan, with Comments on Habitat Specialization in Calyptraeid Gastropods

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ABSTRACT

Crepidula grandis (Middendorff, 1949) is the only member of the Calyptraeidae in the vicinity of Akkeshi, Hokkaido, Japan. It occupies the full range of substratum types that on many other coastlines are divided among three or more species of Calyptraeidae. *Crepidula grandis* living inside hermit-crab shells are relatively flatter than are individuals on shell exteriors, but they are less flattened than are species such as *C. perforans* (Valenciennes, 1846) or *C. walshi* (Reeve, 1859), which are more or less restricted to the interiors of hermit-crab shells. Great unexplained differences among regions exist in the manner in which calyptraeids have become morphologically specialized to the occupation of gastropod shell substrata.

Key words: *Crepidula*, Calyptraeidae, substratum specialization, hermit crabs, biogeography.

Crepidula grandis (Middendorff, 1849) is an abundant shallow-water calyptraeid gastropod in the cool-temperate waters of the northwestern Pacific. It is the single living member of a distinctive North Pacific group of large-bodied species that during the Miocene, Pliocene, and early Pleistocene occurred in both the western and eastern Pacific Ocean (Hoagland, 1977a; Vermeij, 1989). Despite the fact that *C. grandis* is both biogeographically and ecologically interesting, almost nothing is known of its biology. Habe (1958) pointed out that the species in the vicinity of Akkeshi, Hokkaido (Japan) occurs on the lower valves of the commercial scallop *Mizuhopecten yessoensis* (Jay, 1856), which like *C. grandis* belongs to a lineage that underwent a range restriction to the northwestern Pacific (Masuda, 1971; Kafanov, 1986; Vermeij, 1989). Soviet workers (Golikov & Gulbin, 1978; Golikov & Kussakin, 1978) have summarized the depth distribution of *C. grandis*, which extends from the low intertidal zone to a depth of more than one hundred meters.

During the summer of 1988, I had the opportunity to make some observations on *C. grandis* in the vicinity of the Akkeshi Marine Biological Station on the southeastern coast of Hokkaido. Together with some comments on patterns of substratum specialization among other calyptraeids, these observations are presented in this brief account.

Among cool-temperate northern marine regions with native species of *Crepidula*, the northwestern Pacific is unique in lacking small flat-shelled species that are more or less specialized for life on the inner surfaces of gastropod shells inhabited by hermit crabs. Three species of *Crepidula* have been recorded from the northwestern Pacific: *C. grandis* (which also occurs along the northern and western coasts of Alaska); *C. lingulata* (Gould, 1846), a species also found in the northeastern Pacific; and the endemic *C. derjugini* Golikov and Kussakin, 1962. Nothing is known about the habitats of *C. lingulata* in the northwestern Pacific, but in Puget Sound (Washington) in the northeastern Pacific I have found it on stones and on the inner surfaces of empty pelecypod valves. Golikov and Kussakin (1978) report that *C. derjugini* lives on stones and especially on the outer surfaces of shells of the gastropod *Neptunea*.

Crepidula grandis is the only species of *Crepidula* known from the vicinity of Akkeshi (see also Habe, 1958). In Akkeshi Bay, the species occurs sporadically in the low intertidal zone and is abundant in the shallow sublittoral. It occupies a wide variety of hard substrata, including open rock surfaces, the abandoned cavities of pholad pelecypods, the lower valves of *Mizuhopecten yessoensis*, the outer surfaces of opercula of *Fusitriton oregonensis* (Redfield, 1846), the outer surfaces of shells of living gastropods and hermit crabs, and the inner surfaces of hermit-crab shells. The pattern of occurrence of *C. grandis* on outer and inner surfaces of shells at Akkeshi is shown in Table 1.

Species of *Crepidula* that are usually found inside large shells of hermit crabs are usually concave when seen from above, closely conforming with the curvature of the host shell. Examples include *C. perforans* (Valenciennes, 1846) in the cool-temperate and warm-temperate northeastern Pacific, *C. nivea* (C. B. Adams, 1852) in the tropical eastern Pacific, *C. plana* (Say, 1822) in the western Atlantic, and *C.* (*Siphopatella*) *walshi* (Reeve, 1859) in southeast Asia and northern Australia. When settling on shells, *C. plana* apparently always begins life on the shell exterior and then migrates or becomes restricted to the inside (Shenk & Karlson, 1986). The species also occurs under stones and on the horseshoe crab *Limulus polyphemus* (E. C. Dudley, personal communication).

Although individuals of *C. grandis* taken from the

Table 1. Occurrence of *Crepidula grandis* on exterior and interior surfaces of gastropod shells at Akkeshi, Hokkaido.

Host shell	N_h	N_g	Percentage
Euspira pila (Pilsbury, 1911) hermit crabs, exterior	9	2	22%
E. pila hermit crabs, interior	9	0	0
Buccinum mirandum Smith, 1895, living	67	6	9%
B. mirandum hermit crabs, exterior	22	5	23%
B. mirandum hermit crabs, interior	22	1	5%
Neptunea arthritica Bernardi, 1858, living	9	0	0
N. arthritica hermit crabs, exterior	20	2	10%
N. arthritica hermit crabs, interior	20	5	25%

N_h. Number of host shells.
N_g. Number of *C. grandis*
Percentage number of *C. grandis* divided by number of host shells multiplied by one hundred

inner surfaces of hermit-crab shells at Akkeshi are relatively flatter (mean height : length ratio 0.30 ± 0.025, $n = 18$) than are individuals living on gastropod shell exteriors (mean height : length ratio 0.38 ± 0.047, $n = 20$, $p < 0.001$ by T-test), the former are still convex when seen from above and are therefore much less flattened than are shells of the specialized hermit-crab associated species. In fact, shells of *C. grandis* from the inner surfaces of hermit-crab shells are indistinguishable in profile from shells collected from the lower valves of *Mizuhopecten yessoensis* (mean height : length ratio 0.30 ± 0.022, $n = 8$).

These observations show that *C. grandis* at Akkeshi is a classic habitat generalist, occupying the full range of substrata that on many coastlines are divided among at least three species of *Crepidula*, some of which are specialized with respect to the type of substratum occupied. Interesting regional differences exist in the extent of this specialization. In the vicinity of Puget Sound, *C. adunca* (Sowerby, 1825) is found almost exclusively on exterior surfaces of the shells of living gastropods (Vermeij *et al.*, 1987), whereas *C. perforans* occurs only on shell interiors; *C. lingulata* and *C. nummaria* (Gould, 1846) and the related *Calyptraea fastigiata* (Gould, 1846) are found on stones as well as on empty valves of pelecypods. In the northwestern Atlantic, *C. plana* is usually found on shell interiors; whereas *C. convexa* (Say, 1822) is found on shell exteriors, stones, and eelgrass blades, as well as on the larger stones that are the typical habitat of *C. fornicata* (Linnaeus, 1758) (Franz & Hendler, 1970; Hendler & Franz, 1971; Hoagland, 1977a,b; Shenk & Karlson, 1986). On the Pacific coast of Panama, my observations indicate that *C. incurva* (Broderip, 1834) is a specialist on exterior surfaces of gastropod and hermit-crab shells, *C. nivea* is an interior-surface specialist, and *Calyptraea mammillaris* (Broderip, 1834) is found on interior (rarely on exterior) surfaces of empty pelecypod valves. The larger calyptraeids, such as *Crepidula striolata* (Menke, 1851), *C. lessonii* (Broderip, 1834), *C. onyx* (Sowerby, 1824), *C. aculeata* (Gmelin, 1791), *Crucibulum umbrella* (Deshayes, 1830), *C. spinosum* (Sowerby, 1824), *C. personatum* Keen, 1958, and *C. scetellatum* (Wood, 1828), occur mainly on stones and solid rocks and only occasionally on shells. A division of substrata similar to that in Panama has been qualitatively described by Bandel and Wedler (1987) for the calyptraeids of the Caribbean coast of Colombia. On the west side of the York Peninsula of northern Queensland (Australia), I have found *Crepidula walshi* on the interior surfaces of hermit-crab shells; it was the only calyptraeid species I was able to find locally.

Although there is remarkably little published information about the ecology of calyptraeids except for some of the American species, available information indicates that southeastern Hokkaido is not the only region where there is no substratum specialization by calyptraeids to shells. Several calyptraeids coexist on the temperate west coast of South America, but none of the species appears to be found only on either the exterior or interior surfaces of shells (see *e.g.*, Marincovich, 1973). None of the species is flattened in a way suggesting specialization for life on shell interiors. Only one calypytraeid, *Cheilea equestris* (Linnaeus 1758), occurs on the islands of the tropical western Pacific. Like species of *Cheilea* in tropical America, *C. equestris* is found under rocks and never occurs on shells. The hipponicid *Sabia conica* (Schumacher, 1817) is found only on gastropod and hermit-crab shell exteriors in the tropical Indo-Pacific and in temperate Australia, but no oceanic western Pacific or Indian Ocean gastropod is specialized for life on shell interiors. This situation applies to the shallow waters of the Caribbean islands as well.

These patterns of specialization are puzzling. Although calyptraeids that are specialized for life on shell interiors appear to be restricted to productive waters on the shores of continents and large islands, not all productive shores harbor such species. Hermit-crab specialists occur either sympatrically with many other calyptraeids (as in the eastern Pacific and western Atlantic) or alone (*C. walshi* in Queensland). The absence of hermit-crab associates cannot be attributed to the lack of suitable quantities of large gastropod shells, for the latter are abundant in the tropical western Pacific and West Indies, as well as in northern Japan where *C. grandis* facultatively occupies shell interiors. In the case of *C. grandis*, facultative occupation of shell interiors is accompanied by relative shell flattening in a species with considerable morphological plasticity, but this specialization is much less extreme than in interior specialists, with the result that *C. grandis* is likely to be more intrusive to its hermit-crab hosts.

Northwestern Europe lacked species of *Crepidula* until *C. fornicata* was introduced with oysters from eastern North America (see Hoagland, 1985). It will be interesting to determine whether *C. fornicata* in Europe occupies the interior surfaces of hermit-crab shells, a habitat rarely if ever occupied by *C. fornicata* in its native American range.

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New Species of *Malea* (Gastropoda Tonnidae) from the Pleistocene of Southern Florida

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ABSTRACT

Two new large tonnids of the genus *Malea* Valenciennes, 1832 are described from the early and middle Pleistocene of the Everglades Basin of southern Florida. These are *Malea springi* new species from the Caloosahatchee Formation (Calabrian Pleistocene) along the Miami Canal, Palm Beach County, and *Malea petiti* new species from the Bermont Formation (Aftonian Pleistocene) in extreme southwestern Palm Beach County. With a length of 189 mm (holotype), *Malea springi* is the largest of the known fossil western Atlantic *Malea* species. Due to its stratigraphic position in the middle Pleistocene Bermont Formation, *Malea petiti* may have been the last living North Atlantic *Malea* species.

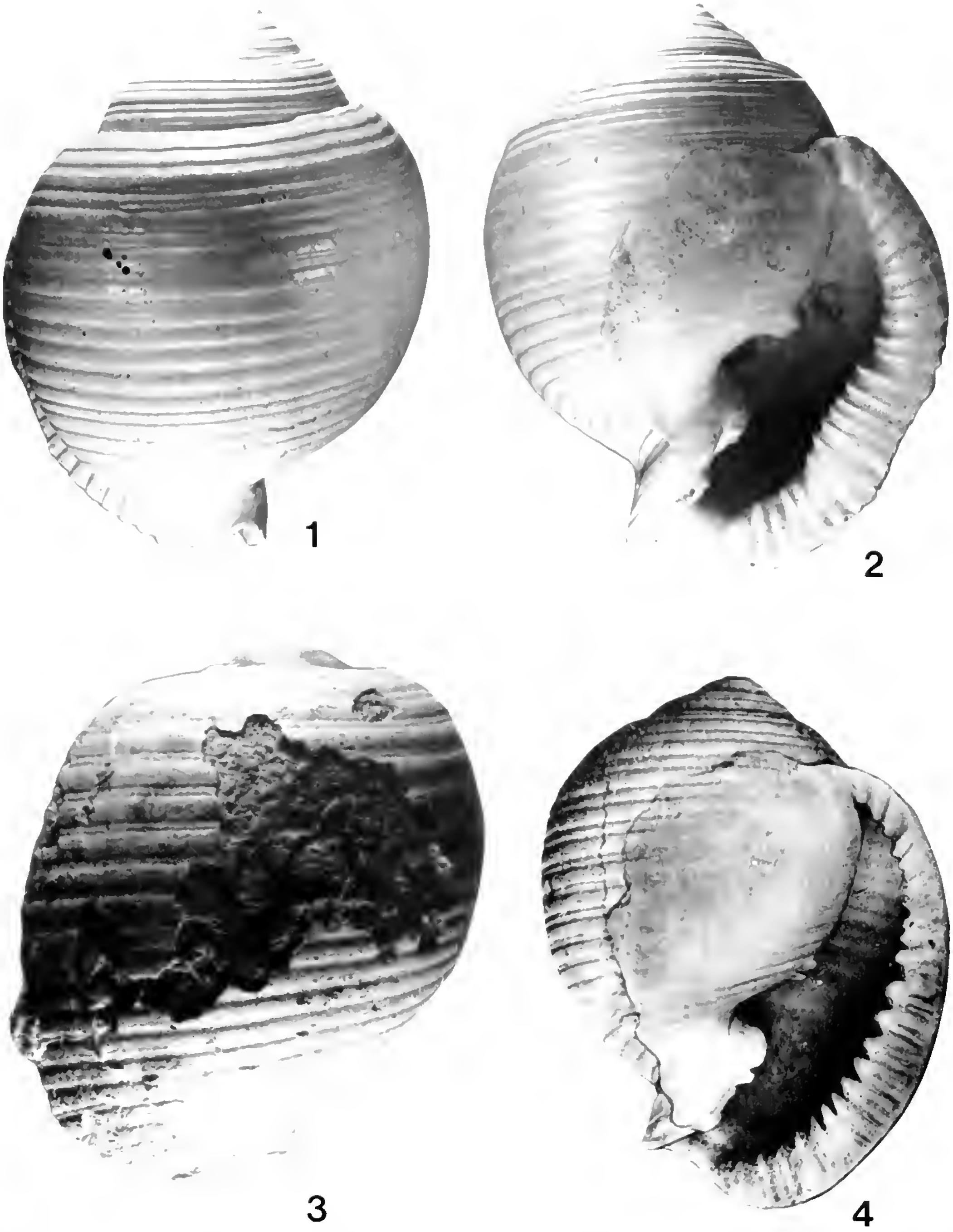
INTRODUCTION

In the Neogene formations of Florida, the tonnid genus *Malea* Valenciennes, 1832 is rarely seen, with only a few complete specimens ever having been collected. The genus was unrecorded from the Floridian Peninsula until 1964, when Olsson and Petit documented the first records of *Malea* species in the Pliocene and early Pleistocene of the Everglades region. The best preserved specimens were collected in the early Pliocene (Zanclian Stage) "Pinecrest Beds" (= Buckingham Formation of Mansfield, 1939; see Petuch, 1986, 1988, for stratigraphic nomenclature and dating) from near Lake Okeechobee, and were assigned to the Pliocene Venezuelan species *Malea densecostata* (Rutsch, 1934) (figure 4). The presence of this characteristic South and Central American index fossil in Florida was used by Olsson and Petit (1964: 554) to correlate the "Pinecrest Beds" with the Punta Gavilan Formation of Venezuela.

Within the same paper (1964:553), Olsson and Petit also mention in passing the occurrence of a second, larger *Malea* species that had been found in dredgings from the early Pleistocene (Calabrian Stage) (see Petuch, 1988 for correlation and dating) Caloosahatchee Formation along the Miami Canal in the central Everglades Basin. This Pleistocene Floridian *Malea*, however, was only collected as tantalizing fragments, and could not be assigned to any known taxon. Olsson and Petit (1964:553) also mention the presence of poorly-preserved internal molds of a possible third Floridian *Malea* species. These were said to be exposed in the limestone of the late Pliocene (Piacenzian Stage) Tamiami Formation, presumably at the stratotype area along the Tamiami Trail in Collier County. In the subsequent literature on Floridian molluscan paleontology, however, little attention has been given to these large and stratigraphically important gastropods.

In 1981, the Miami Canal, particularly in the area just north of the levee at the Broward-Palm Beach County line, was deepened to allow better water flow during times of drought. At that time, several complete specimens of a large new *Malea* species were dredged during the canal deepening, from approximately 20 meters depth below the Everglades surface. This large, un-named tonnid was collected in an undescribed coral reef facies of the Caloosahatchee Formation, along with classic Caloosahatchee index fossils such as *Siphocypraea problematica* Heilprin, 1886, *Hystrivasum horridum* (Heilprin, 1886), and *Turbinella scolymoides* Dall, 1890. Judging from its occurrence in the Caloosahatchee Formation along the Miami Canal, the un-named *Malea* appears to represent the same species that Olsson and Petit had collected as fragmentary specimens in the 1960's. This new reef-associated Caloosahatchee species is the largest *Malea* known from North America and is one of the largest gastropods found in the Caloosahatchee Formation.

Road fill quarries in the central Everglades region, along the Palm Beach-Broward County line, have recently yielded yet another large, un-named *Malea*, in this case from the early middle Pleistocene (Aftonian Stage) Bermont Formation. Unlike the Miami Canal Caloosahatchee specimens, however, the Bermont specimens were all encased in a semifriable limestone and were only partially complete. Within this undescribed indurated member of the Bermont Formation, *Malea* specimens were collected along with classic Bermont index fossils such as *Fasciolaria okeechobeensis* Tucker and Wilson, 1932, *Melongena* (*Rexmela*) *bispinosa* (Philippi, 1844), *Vasum floridanum* McGinty, 1940, *Lindoliva*



Figures 1–4. Fossil *Malea* species from the Pliocene and Pleistocene of southern Florida. **1, 2.** *Malea springi* new species, dorsal and ventral views of holotype, length 189 mm, Caloosahatchee Formation, Calabrian Pleistocene, UF 21455. **3.** *Malea petiti* new species, dorsal view of holotype, length (incomplete) 130 mm, Bermont Formation, Aftonian Pleistocene, UF 21456. **4.** *Malea densecostata* (Rutsch, 1934), ventral view of 109 mm specimen, Buckingham Formation (= Pinecrest Beds) at Indian Prairie Levee, Zanclian Pliocene. Taken from Olsson and Petit (1964, pl. 79, fig. 5).

spengleri Petuch, 1988, and *Strombus* (*Eustrombus*) *mayacensis* Tucker and Wilson, 1933. Fragmentary specimens of this large Bermont *Malea* were also collected at a quarry west of Miami, in Dade County, along with the same molluscan assemblage as that found in the central Everglades rock pits.

In this paper, two new Floridian fossil *Malea* species are described; *Malea petiti* n.sp. from the Bermont Formation and *Malea springi* n.sp. from the Caloosahatchee Formation. These species, along with the Buckingham *Malea densecostata* and the un-named, moldic Tamiami species, show that four different species of *Malea* occurred in southern Florida during Plio-Pleistocene time. The relationship of the new taxa to other Plio-Pleistocene *Malea* species from elsewhere in the western Atlantic are discussed under the respective descriptions. Institutional abbreviations, for the deposition of type material, include: UF (Florida Museum of Natural History, University of Florida, Gainesville, Florida), ANSP (Paleontology collection, Department of Malacology, Academy of Natural Sciences of Philadelphia), and FAU (Paleontology collection, Department of Geology, Florida Atlantic University, Boca Raton, Florida).

SYSTEMATICS

Gastropoda
Prosobranchia
Tonnacea
Tonnidae
Tonninae
Malea Valenciennes, 1832

Malea petiti new species
(figure 3)

Material examined: HOLOTYPE—Length (incomplete) 130 mm, width 98 mm, dredged from approximately 17 m depth in Griffin Brothers road fill pit, 11 km due west of US Highway 27, on Broward County-Palm Beach County line, Florida, lower member of the Bermont Formation, Aftonian Pleistocene, UF 21456; PARATYPES—fragment, length 89 mm, dredged from 20 m depth in Capeletti Brothers pit mine #11, 7 km west of Florida Turnpike, northeastern Dade County, Florida, Bermont Formation, UF 23800; length 56 mm (mold of juvenile), from same locality and depth as holotype, FAU 414.

Description: Shell inflated, subcylindrical, very thin and fragile; sides of body whorl only slightly rounded, giving shell barrel-shaped appearance; shoulder slightly angled, producing flattened subsutural area; spire (of juvenile mold) low, flattened; body whorl (of holotype) ornamented with 22 wide, very flattened ribs; thin, flattened secondary rib present between each pair of wide primary ribs; secondary ribs widest and best developed on posterior half of body whorl, becoming thinner and almost obsolete on anterior half; siphonal canal proportionally small, recurved; because of fragmentary nature of type material, shape and form of outer lip, aperture, parietal shield, and columellar region unknown.

Stratigraphic range: Known only from the lower beds (un-named member?) of the Bermont Formation in the Everglades Basin, Aftonian Stage of the Pleistocene.

Etymology: Named for Mr. Richard E. Petit, of North Myrtle Beach, South Carolina, who, along with the late Dr. A. A. Olsson, documented the first records of *Malea* from southern Florida.

Discussion: Although similar in size to the Caloosahatchee *Malea springi*, *M. petiti* differs in being a more cylindrical shell with straighter sides, and in having a distinctly lower spire and flatter subsutural area above the shoulder. The form of the ribs and rib count also differ between the two species; those of *M. petiti* are wider and less numerous (22 on the holotype), while those of *M. springi* are narrower and more numerous (26 on the holotype). Based on its overall similarity to the older *M. springi*, *M. petiti* is most probably the direct descendant of the finer-ribbed Caloosahatchee species. Taking into account the geologically young age and high stratigraphic position of *M. petiti*, this new species may have been the last-living *Malea* s.s. in North America.

Malea springi new species
(figures 1, 2)

Material examined: HOLOTYPE—Length 189 mm, width 130 mm, dredged from 20 m depth along the Miami Canal, due west of the Talisman Sugar Refinery, 10 km north of the Broward-Palm Beach Levee, southwestern Palm Beach County, Florida, uppermost beds (Ayers Landing Member?) of the Caloosahatchee Formation, Calabrian Pleistocene, UF 21455; PARATYPES—length 178 mm, from same depth and locality as holotype, ANSP 1133; length 170 mm, from same depth and locality as holotype, Spring collection, Stuart, Florida; length 156 mm, from same depth and locality as holotype, collection of author.

Description: Shell inflated, globose, thick and heavy; sides of body whorl distinctly rounded; shoulder and subsutural area rounded; spire whorls elevated, slightly protracted; suture impressed, minutely canaliculate; body whorl ornamented with 26 (on holotype) thin, flattened ribs; small, very thin secondary ribs sometimes present between large primary ribs, especially in midbody region; siphonal canal proportionally well-developed, recurved; parietal region overlaid by wide, thick, smooth shield; columellar notch proportionally large, well-developed, "U"-shaped, deep; edges of notch bordered by large knobby bosses, one on either side, that project into aperture; outer lip very thickened, wide, with 23 (on holotype) thin, elongated denticles along facing edge; medial portion of inner edge of lip wider than rest of lip, projecting into aperture; projecting bosses on either side of columellar notch and wide medial area of lip produce slightly sigmoidal shape within aperture.

Etymology: Named for Mr. Keith Spring, marine biologist at Continental Shelf, Inc., Tequesta, Florida, who collected the holotype along the Miami Canal.

Discussion: *Malea springi* is most similar to the ancestral Pliocene *M. densecostata*, but differs in being a much larger, more inflated shell with a higher, more protracted spire, and in having finer and more numerous ribs. The columellar notch of *M. springi* is proportionally larger than that of *M. densecostata*, being more indented and wider. The knobby bosses on either side of the columellar notch of *M. springi* are also larger and more developed than those of *M. densecostata*, and extend farther into the aperture. The shape of the inner edge of the lip also differs between the two species; with the edge being rounded and arcuate in *M. densecostata*, but subarcuate in *M. springi*, being slightly deformed by the wider medial area that projects inwardly, into the aperture.

The new Caloosahatchee *Malea* also resembles the well known *M. camura* Guppy, 1866, from the late Miocene-Pliocene of the Caribbean Basin (the Bowden Formation of Jamaica, the Gatun Formation of Panama and Costa Rica, and the Cercado and Gurabo Formations of the Dominican Republic), but differs in being a much larger and more inflated shell with more numerous and thinner ribs, and in having a much wider and better developed columellar notch. The 35.8 mm specimen of *M. camura* illustrated by Woodring (1928: pl. 20, figs. 7, 8) is typical of the species, and can be used for comparison with *M. springi*.

Malea springi also resembles *M. mareana* Weisbord, 1962 from the late Pliocene (early Pleistocene?) Mare Formation of Venezuela (Weisbord, 1962). Although similar to *M. springi* in shape and in having an elevated spire, the possibly-contemporaneous *M. mareana* differs in being a much smaller shell (holotype 47 mm), and in having a proportionally smaller and narrower columellar notch. The type of *M. mareana* (illustrated by Weisbord, 1962, pl. 24, figs. 1, 2) also has a sharply-angled, subcarinated shoulder, a feature that is missing in the distinctly round-shouldered *M. springi*.

At 189 mm length, the holotype of *Malea springi* is the largest specimen of any of the known western Atlantic *Malea* species. Previously, this title was held by a specimen of *M. goliath* Pilsbry and Johnson, 1917 from the Gurabo (Cercado?) Formation of the Dominican Republic, which reached a length of 129 mm (holotype). This was followed by the Floridian specimen of *M. densecostata* illustrated by Olsson and Petit (1964), with a length of 109 mm. The Bermont *M. petiti*, with an incomplete holotype of 130 mm, and the Caloosahatchee *M. springi*, then, together probably represent the greatest development in shell size in the fossil American *Malea* species. The "*Malea* sp." that I illustrated previously (Petuch, 1988, pl. 22, figs. 5, 6) is *M. springi*.

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The Influence of Physical Factors on the Distribution and Abundance of Freshwater Mussels (Bivalvia: Unionidae) in the Lower Tennessee River

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ABSTRACT

Sixteen quantitative samples of mussels were taken by SCUBA divers at each of two inshore and two offshore sites from a mussel bed in the lower Tennessee River in July, 1987. Sedimentation (measured with *in situ* sediment traps), sediment type, and current velocity were measured at all sites. *Fusconaia ebena* (Lea, 1831) was the dominant mussel at both the inshore and offshore sites representing 72 and 53% of the community, respectively. Total mussel density, species diversity, and evenness were all greater at the inshore sites. Sedimentation rates were significantly greater and current velocities were approximately half as great (11 and 19 cm/sec, respectively) at the inshore *versus* the offshore sites. We hypothesize that physical factors are the dominant influence structuring this mussel community in the lower Tennessee River

Key words: Mussels; Unionidae; sedimentation; lower Tennessee River

INTRODUCTION

Freshwater mussels (Family Unionidae), being filter-feeders and essentially non-motile, have long been considered intolerant of poor water quality and sedimentation (Hynes, 1960, 1970; Pennak, 1978). Laboratory experiments conducted by Ellis (1933), in which he buried mussels in various types of substrates, provided early evidence on the negative effects of sediment deposition. In addition, Stansbery (1970) considered that sediment from agricultural practices, reservoir construction, maintenance dredging, and pollution eliminated many species of mussels. However, the distribution and abundance of many species of mussels is at least partly dependent upon low water velocities and low to moderate levels of sedimentation for the successful settlement of glochidia.

The objective of this study was to relate community composition and density of the dominant species (*Fusconaia ebena*) at a large mussel bed in the lower Tennessee River to water velocity, sedimentation, and substrate type.

STUDY AREA

Sampling sites were located on the left bank of the Tennessee River (RM 18.6), approximately 6 km below the Kentucky Lock and Dam. Sites 1 and 3 were 61 m apart and 31 m from shore (inshore sites); sites 2 and 4 were 61 m apart and 61 m from the shore (offshore sites). Sites 1 and 2 were located 200 m upstream of sites 3 and 4. Mussels have been collected from this bed, which appears to extend throughout most of the river between RM 18.6 and 11.0 (Sickle, 1985), since 1931 (van der Schalie, 1939). Current velocity at the sediment-water interface was 11.4 cm/sec ($s = 1.1$; $N = 8$) and 19.2 cm/sec ($s = 1.4$; $N = 8$), and water depth was 3–4 m and 5–6 m at the inshore and offshore sites, respectively.

MATERIALS AND METHODS

Sampling was conducted on July 22–23, 1987. Using SCUBA, a diver randomly placed and secured a 16-cell PVC grid (each cell 1 × 1 m) to the substrate at each sampling site. A 0.25 m^2 quadrat was placed in the lower left corner of a cell and all substrate was removed by the diver to a depth of 15 cm. Substrate was returned to the surface in a 20 liter bucket, sieved through a nested screen series (smallest mesh size = 6.4 mm), and all live mussels were removed and identified to species. Sixteen samples were taken from each of the four sites.

Sedimentation rates were measured by anchoring six PVC sediment traps (length:width = 25.4:2.5 cm; two collection pipes/trap) to steel cables. Sediment traps were placed at 3 m intervals along a 21 m transect at each of the four sites. Sediment traps were placed in the river by divers on July 10, 1986 and retrieved on July 23, 1986. In the laboratory, the trapped material was allowed to

Table 1. A summary of the biological and physical data from the lower Tennessee River, 1986. Means in a given row with the same letter (a, b, c) are not significantly different ($p < 0.05$). Densities are expressed as clams m^{-2}.

	Collection site			
	Inshore upstream	Inshore downstream	Offshore upstream	Offshore downstream
Total number of mussels	751	604	319	295
Total number of species	17	15	18	17
Total mussel density	187.7 a	151.0 a	79.7 b	73.7 b
(SD)	(16.3)	(27.4)	(12.6)	(5.6)
Total density of *Fusconaia*	133.3 a	111.0 a	41.0 b	40.0 b
(SD)	(14.5)	(21.1)	(6.9)	(3.9)
Density of *Fusconaia* adults	74.0 a	68.0 a	22.2 b	25.2 b
(SD)	(10.4)	(12.3)	(3.7)	(1.9)
Density of *Fusconaia* juveniles	59.2 a	43.0 b	18.7 c	19.0 c
(SD)	(7.1)	(9.5)	(4.4)	(2.5)
Species diversity (H′)	1.112 a	1.040 a	1.591 b	1.598 b
Evenness (J)	0.392	0.384	0.550	0.564
Sediment deposition (g cm^{-2} day^{-1})	0.055 a	0.060 a	0.031 b	0.033 b
(SD)	(0.003)	(0.003)	(0.002)	(0.002)
Current velocity (cm/sec)	11		19	
[1]% Sand/% gravel at 0–5 cm depth	60/32		35/61	
[1]% Sand/% gravel at 5–10 cm depth	35/20		57/37	

[1] Remaining percentage of substrate was made up of silt

settle for 24 hr, decanted, and the remaining sediment dried for 24 hr at 100 °C and weighed.

Sediment composition was also determined at each of the four sampling sites. Eight 10 × 15 cm cores (Miller and Bingham, 1987) were randomly taken by divers at each site. Cores were brought to the surface and divided into three depth fractions (0–5, 5–10, and 10–15 cm) and subsequently analyzed for particle size distribution.

RESULTS

Total mussel density was significantly greater at the inshore sites, although there was no substantial difference in total number of species between the inshore and offshore sites (table 1). No significant differences in any of the remaining measured parameters were observed between upstream and downstream sites. *Fusconaia ebena* was the dominant mussel at both the inshore and offshore sites representing 72 and 53% of the community, respectively. Total mussel density was two times greater at inshore compared to offshore sites. This was due mainly to *F. ebena*, which was about three times as dense at inshore *versus* offshore sites. The difference in densities of *F. ebena* was significant for both large (≥ 30 mm shell length) and small (< 30 mm shell length) clams (table 1). Species diversity (Shannon-Weaver index, H′; Poole, 1974) and evenness (J; Poole, 1974) was greater at the offshore sites. The greater species diversity and evenness at the offshore sites was the result of a decrease in the densities of *F. ebena* relative to the other species in the community.

Sedimentation and substrate composition differed between the inshore and offshore sites. Sediment deposition over the 2 week period was significantly greater at the inshore sites than at the offshore sites. Particle size analysis of inshore sediments indicated the substrate consisted mainly of medium sand, whereas offshore sediments contained higher percentages of gravel (table 1). Current velocities at the offshore sites were approximately twice those at the inshore sites (table 1).

DISCUSSION

Salmon and Green (1983) reported that there was an increase in the frequency of occurrence of unionids associated with slow moving, shallow water with relatively coarse substrate. Strayer (1983) reported that stream size and surface geology determined the distribution of unionids in streams in southeastern Michigan. Although some unionids appear to be substrate specific, many are tolerant of a wide range of substrate types (Murray & Leonard, 1962; Parmalee, 1967; Strayer, 1981). Green (1971, 1972) found that the distribution of *Anodonta grandis* Say, 1829 and *Lampsilis radiata* (Gmelin, 1791) in 32 lakes was due more to water chemistry and to different geological conditions than to sediment characteristics. Previous workers have indicated that sedimentation negatively affects freshwater mussels (Ellis, 1933; Stansbery, 1970); however, their conclusions apply to abnormally high levels of sedimentation (sufficient to bury mussels) that often result from impoundment, channel modification, or disposal of dredged materials.

The various parameters that affect the distribution and abundance of unionids (suitable fish hosts, current velocity, substrate type, stream geomorphology, water chemistry, etc.) probably have varying levels of importance depending on the specific site studied. These factors are responsible for the lack of statistical correlations between microhabitat use and unionid abundance (Strayer, 1981), but favor statistical correlations between unionid abundance and geological conditions, water chemistry, and substrate type. Our data show that within a mussel bed in the lower Tennessee River, higher densities of mussels (especially the dominant species, *F. ebena*) may be associated with differences in sedimentation rate and water velocity. These physical effects act upon all species in the assemblage, but the resulting changes in community structure are due to a shift in the relative abundance of the dominant species, *F. ebena*. We hypothesize that physical factors are of paramount importance in structuring this mussel community in the lower Tennessee River.

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On the Distribution of *Nautilus pompilius* in the Samoas, Fiji and Tonga

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ABSTRACT

Deep-water trapping off American and Western Samoa, Tonga, and Fiji provides new data on the distribution of *Nautilus* in the southwestern Indo-Pacific. Thirty-nine specimens of *N. pompilius* were trapped at 270–310 m depth in American Samoa, extending the known geographic range of *Nautilus* 1,600 km eastward. The negative results of trapping for *Nautilus* off Western Samoa are inconclusive, but the lack of *Nautilus* in traps containing diverse, commonly associated organisms at 290–500 m off Tonga indicates *Nautilus* does not occur there. Traps set at 220–470 m off Suva, Fiji, yielded 40 *N. pompilius*. Fiji and American Samoa *Nautilus* exhibit some differences in shell morphology, but are similar to other populations of *N. pompilius* in most respects.

INTRODUCTION

The easternmost occurrence of living *Nautilus* has generally been regarded as Fiji, from whence the first documented live specimen was obtained during trawling by the Challenger Expedition (Moseley, 1892), and where a number of studies have been completed in recent years (*e.g.*, Hayasaka, 1985; Zann, 1984; Muntz & Raj, 1984). Until now, in spite of numerous recent reports of *Nautilus* at more westerly locales (see Saunders, 1987, for review), there has been no knowledge of whether this organism occurs further east than Fiji. The present report, based on trapping efforts during 1986 in American Samoa, Western Samoa, Tonga, and Fiji, extends the range of *Nautilus* eastward by more than 1,600 km (figure 1). The find of *Nautilus* in American Samoa suggests that its actual range may prove to be considerably greater than has been surmised on the basis of drifted shells, because in that area there was neither knowledge of the living animal nor of the shells—in fact, there is apparently no Samoan word for *Nautilus*. Nevertheless, animals were trapped outside Pago Pago, literally within sight of the Governor's residence. Subsequent trapping efforts for *Nautilus* in Western Samoa and Tonga yielded no *Nautilus*, but trap yields from south of Suva, Fiji provide new data on depth distribution and on organisms associated with *Nautilus* in that region. In a sense, this report marks the first effort to delimit the geographic range of living *Nautilus*. Following is a brief account of the new occurrence in Samoa, along with observations on morphological differences, ecological conditions and associated organisms at the other sites where deep-water trapping was undertaken.

MATERIALS AND METHODS

Deep-water trapping for *Nautilus* followed procedures developed in Palau (Saunders & Spinosa, 1978). It involved setting funnel-ended, rectangular fish traps (1 × 1 × 2 m) baited with skipjack tuna at bottom forereef sites, with depth and topographic selection determined by echofinder. The traps were marked at the surface with buoys, and were left out for 1–2 nights at depths ranging from 100–500 m. Following is a summary of locations, and yields:

1. American Samoa: Traps were set three times, during July, 1986, along Taema Bank, southeast of Pago Pago Harbor, Tutuila Island (figure 1), for 1–2 nights at depths of 270, 280, and 310 m. Individual trap yields varied from 3–29 specimens of *Nautilus pompilius* plus miscellaneous fishes and invertebrates (table 1). During March, 1987, additional catches totalling 16 specimens of *Nautilus pompilius* were reported by National Marine Fisheries Service personnel, conducting deep-water trapping at 300–400 m in the same area.

2. Western Samoa: Traps were set three times, approximately 6 km north of Apia Harbor, Upolu Island (figure 1). In this region, the bottom descends gradually to a depth of *ca.* 100 m, where it becomes a sheer, vertical face that extends to several thousand meters—well below *Nautilus* depth. This configuration made it impossible to set bottom traps at optimal *Nautilus* depths. Traps set at *ca.* 100 m yielded no *Nautilus*, and only a few specimens of teleosts. Because of the proximity to American Samoa (approximately 130 km eastward), where *Nautilus* appears to be abundant, conclusions regarding the absence of *Nautilus* in Western Samoa based on the present work are premature.

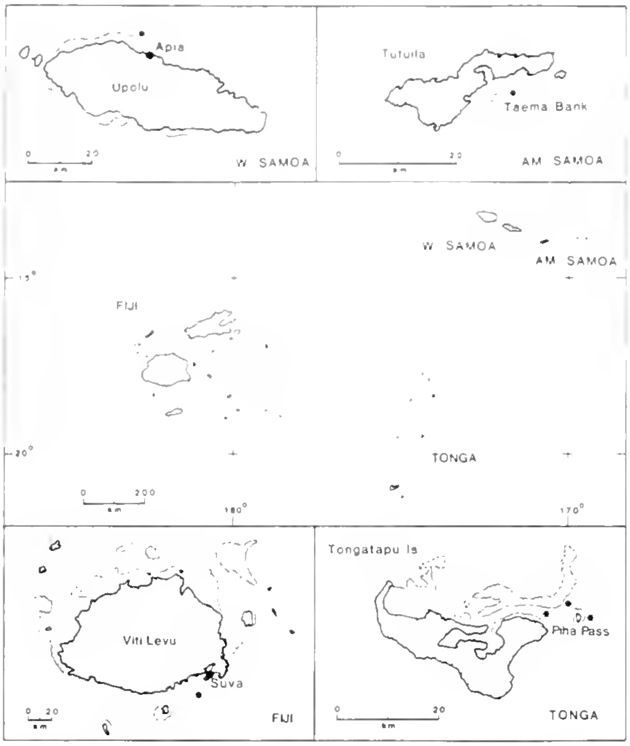

Figure 1. Map showing deep-water trapping sites (asterisks) in American and Western Samoa, Tonga, and Fiji. *Nautilus* was obtained in Fiji and American Samoa.

3. Tonga: Two traps were set overnight six times, in- and just outside Piha Passage, 5–16 km off Nuku'alofa, Tongatapu Island (figure 1), during July, 1986 at 280–500 m depth. Although no *Nautilus* were trapped, a diverse assemblage of organisms was obtained, that are typically found associated with *Nautilus* at other locales (table 1); we conclude that *Nautilus* is not present in this region of Tonga.

4. Fiji: Traps were set overnight five times, 0.8–3.5 km southwest of Suva at depths of 220–470 m. A total of 40 specimens of *N. pompilius* was obtained, along with numerous shrimps and deep water teleosts (table 1).

Reference specimens of *Nautilus*, as well as associated organisms, have been reposited at the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM 816658–816659, 816704–186709); the British Museum (Natural History), London, the J. P. Hayden Museum, Pago Pago (specs. AS 33, 35); and with the Office of Fisheries, Nuku'alofa, Tonga.

RESULTS

The general consensus has been that the genus *Nautilus* is morphologically conservative and exhibits little variation (*e.g.*, Ward, 1984). However, recent multivariate analyses of a large number of morphological characters (Swan & Saunders, 1987) shows that the most common and widespread species, *N. pompilius*, exhibits considerable morphological differentiation in geographically isolated populations. In addition, genetic analyses of the same populations using electrophoretic surveys of protein polymorphisms (Woodruff *et al.*, 1987) show that the species also exhibits a high level of genetic variation. Comparative studies of other living *Nautilus* populations are currently being undertaken that should permit more definite taxonomic assessments in the near future. Following is a summary of some of the differences observed between the Fijian and Samoan populations.

Table 1. Deep-water trap yields of cephalopods, fishes and shrimps in American Samoa, Western Samoa, Tonga and Fiji, based on trapping conducted in 1986. Shrimp identifications follow King (1984).

Assoc. species	Am. Samoa	W. Samoa	Tonga	Fiji
Depth (m)	270–310	~100	280–500	220–470
Cephalopods				
Nautilus pompilius	x (39)	—	—	x (40)
Octopus sp.	—	—	x	—
Fishes				
Conger sp.	x	x	x	—
Muraenesox cinereus	—	—	x	—
Epinephelus sp.	—	—	x	x
Etelis carbunculus	—	—	x	x
Tridon macropterus	—	—	x	—
Pristopimoides multidans	—	—	—	x
Squalus sp.	—	—	—	x
Shrimps				
Heterocarpus ensifer	x	—	x	x
H. gibbosus	—	—	—	x
H. sibogae	—	—	—	x
Parapandalus serratifrons	—	—	x	x
Plesionika longirostris	x	—	x	x
Pl. martia	—	—	—	x

I. *N. pompilius*, American Samoa

Shell size, maturity, and sex ratios: The 39 specimens available range in size from 106.1–180.3 mm shell diameter, but mature specimens range from 163–179.2 mm diameter (figure 2; table 2). This size range is similar to that reported for *N. pompilius* from Tanon Strait, Philippines, and from Papua New Guinea (Saunders & Davis, 1985; Saunders, 1987; Saunders *et al.*, 1987). As in virtually all other populations of *Nautilus* for which data are available, mature males are larger (5%) and heavier (18%) than females (mean diameter for males 174.5 mm; mean weight 861.3 g; females 164.9 mm; 703 g), and males (79.5%) substantially outnumber females (see also Saunders & Spinosa, 1978; Hayasaka, 1983, 1985). Although mature animals typically comprise 75% of *Nautilus* populations, only 28.2% of the Samoan specimens are fully mature; this probably reflects the small sample size.

Distinguishing characteristics: In basic shell form, the Samoan *Nautilus* are indistinguishable from the widely distributed species *N. pompilius*. However, several features of coloration and sculpture are distinctive, and warrant description.

Shell coloration is more prominent than in other populations of this species, in that the stripes are wider and more numerous; *i.e.*, the proportion of striped (brown) dorsal shell is considerably greater than unstriped (white) shell (figures 3–7). In addition, the umbilical area is brown, and the color bands tend to show a zig-zag pattern on the flanks of the shell. Although numerical analysis of these features will be required to evaluate the degree of uniqueness compared to other populations, both stand in contrast to the general trend toward reduced shell coloration, including a white umbilical region, in shells from the southern part of the range of *N. pompilius*—notably in Papua New Guinea and northwestern Australia.

The shells from Samoa also exhibit delicate but distinctive longitudinal (concentric) sculpture (figure 5). This feature is developed more strongly (and was cited as a species characteristic) in *N. belauensis* by Saunders (1981), and it is even more strongly developed in *N. scrobiculatus*, but it is not typical of *N. pompilius*, *N. stenomphalus* or *N. macromphalus*.

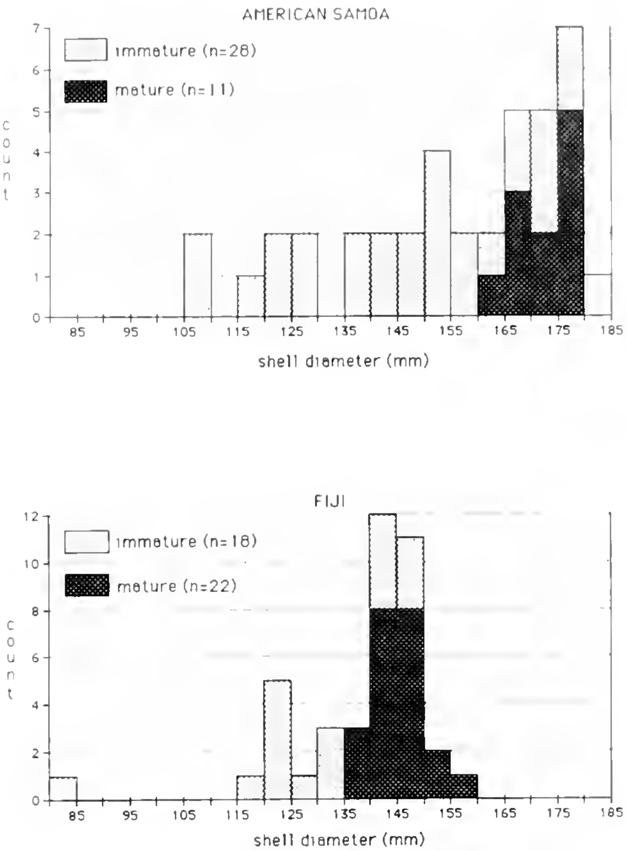

Figure 2. Frequency distribution of live-caught specimens of *N. pompilius* from American Samoa and Fiji, showing size range (maximum shell diameter) and proportion of mature individuals (see Table 2 for additional data).

II. *N. pompilius*, Fiji

Shell size, maturity, and sex ratios: The 40 specimens available range from 80.7–155 mm diameter, but 22

Table 2. Morphologic data from live-caught *N. pompilius s. l.* from American Samoa and Fiji, arranged by sex, showing range in variation in mature animals and sexual dimorphism (shell width measured beneath the ocular sinus; total weight, shell plus body weight in air).

	Shell diameter (mm)			Shell width (mm)			Total weight (g)		
Sex	Range	Mean	SD	Range	Mean	SD	Range	Mean	SD
I *Nautilus pompilius*, American Samoa									
Females (n = 3)	163–166	164.9	1.65	68–72.8	69.8	2.6	680–740	703.3	32.2
Males (n = 8)	168.6–179.2	174.5	4.1	76.7–84.3	81	2.3	800–925	861.3	51.1
Total (n = 11)	163–179.2	171.9	5.7	68–84.3	77.9	5.7	680–925	818.2	86.5
II *Nautilus pompilius*, Fiji									
Females (n = 2)	136.5	136.5	0	58.1–58.2	58.2	1	400–410	405	7.1
Males (n = 20)	138.8–155	146	4.2	60.7–74.1	68	3.1	435–670	528	56
Total (n = 22)	136.5–155	145.1	4.9	58.1–74.1	67.1	4.1	400–670	516.8	64.5

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mature specimens range from 136.5–155 mm diameter (figure 2; table 2). Only two specimens are mature females; they are 136.5 mm diameter, and are smaller (6.5%) than the mature males (mean 146 mm; n = 20), and they weigh 23% less (mean 405 g females *vs.* 528 g males). The proportion of mature animals (55%) is somewhat less than usual for *Nautilus* populations, but the high overall proportion of males (80%) is typical. Considerable additional comparative morphologic data are available for the Fiji *Nautilus*, in published accounts by Ward *et al.* (1977), Ward & Martin (1980), Zann (1984) and Hayasaka (1985).

Distinguishing characteristics: Given the range of variation in size and color patterns that have now been documented in *Nautilus pompilius* (see Saunders & Davis, 1985; Saunders, 1987; Saunders & Swan, 1987) it is not surprising that the Fijian population exhibits some morphologic differences compared to other populations for which data are available. Mature shell size (mean 145.1 mm) is small compared to most populations; mean mature size of Tanon Straits, Philippines, specimens is 165 mm, and mature size for Papua New Guinea populations ranges from 144 mm (Lae) to 169 mm (Kavieng; Saunders & Davis, 1985). In addition, one population of even smaller mature shells (mean 114 mm) is known from the Sulu Sea (Saunders, 1987).

The coloration of the Fiji specimens is generally coarser, (*i.e.*, relatively fewer but broader stripes) than in typical *N. pompilius*, and in many specimens, color bands to not extend to the umbilicus, leaving a white umbilical area (figures 8–10). The latter feature seems also to be more common in southern Papua New Guinea populations and in specimens of *N. pompilius* from the Great Barrier Reef.

An electrophoretic survey has recently been completed on the Fiji populations (Woodruff *et al.*, 1987). The results indicate that the Fiji population is genetically well differentiated from populations of *N. pompilius* in Papua New Guinea and the Great Barrier Reef. This is perhaps not so surprising, given the geographic distances between the samples, and analysis of geographically intermediate populations will be required to evaluate the significance of the genetic differentiation recorded. In this regard, it will be of considerable interest to compare the results of electrophoretic studies (now underway) of the Samoan population, which is even further removed geographically, to the Fiji and other populations.

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The efforts of fisheries officers and personnel in American and Western Samoa, Tonga, and Fiji were instrumental in obtaining the results reported here. In particular, we wish to acknowledge the assistance of Ray Tulafono (Director), Raymond Buckley, and the fisheries staff at Pago Pago, American Samoa. In Western Samoa, Lui Bell, Fisheries Biologist, Apia, provided unlimited assistance. In Tonga, Viliami and Sarah Longi, and Malcolm McGregor assisted immeasurably, along with others at the Office of Fisheries in Nuku'alofa (Semisi Fakahu, Director). Deep-water trapping in Fiji was undertaken with support of Dr. Peter Hunt, Chief Fisheries Officer, Tui Lancala and Malakai Tuilou, also of Fisheries; and we owe particular thanks to Keith Meecham, Programme Director, South Pacific Regional Fisheries Development Program, Suva, and to Robert Gillett, Fisheries Development Advisor.

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Figures 3–10. *Nautilus pompilius* Linné, 1758. **3–7.** Specimens from American Samoa **8–10.** Specimens from Fiji **3.** Living animal (USNM 816658) held in an aquarium (⅓ ×); **4, 6, 7.** Lateral views of mature (4, USNM 816708, 7, USNM 816709) and immature (6, USNM 816707) shells (½ ×); **5.** Detail of shell surface of specimen in figure 7, showing delicate longitudinal sculpture (3.0 ×). **8–10.** Lateral views of immature (8, USNM 816706) and mature shells (9, USNM 816705, 10, USNM 816704) (½ ×)

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Repaired Shell Damage in a Complex of Rissoid Gastropods from the Upper Continental Slope South of New England

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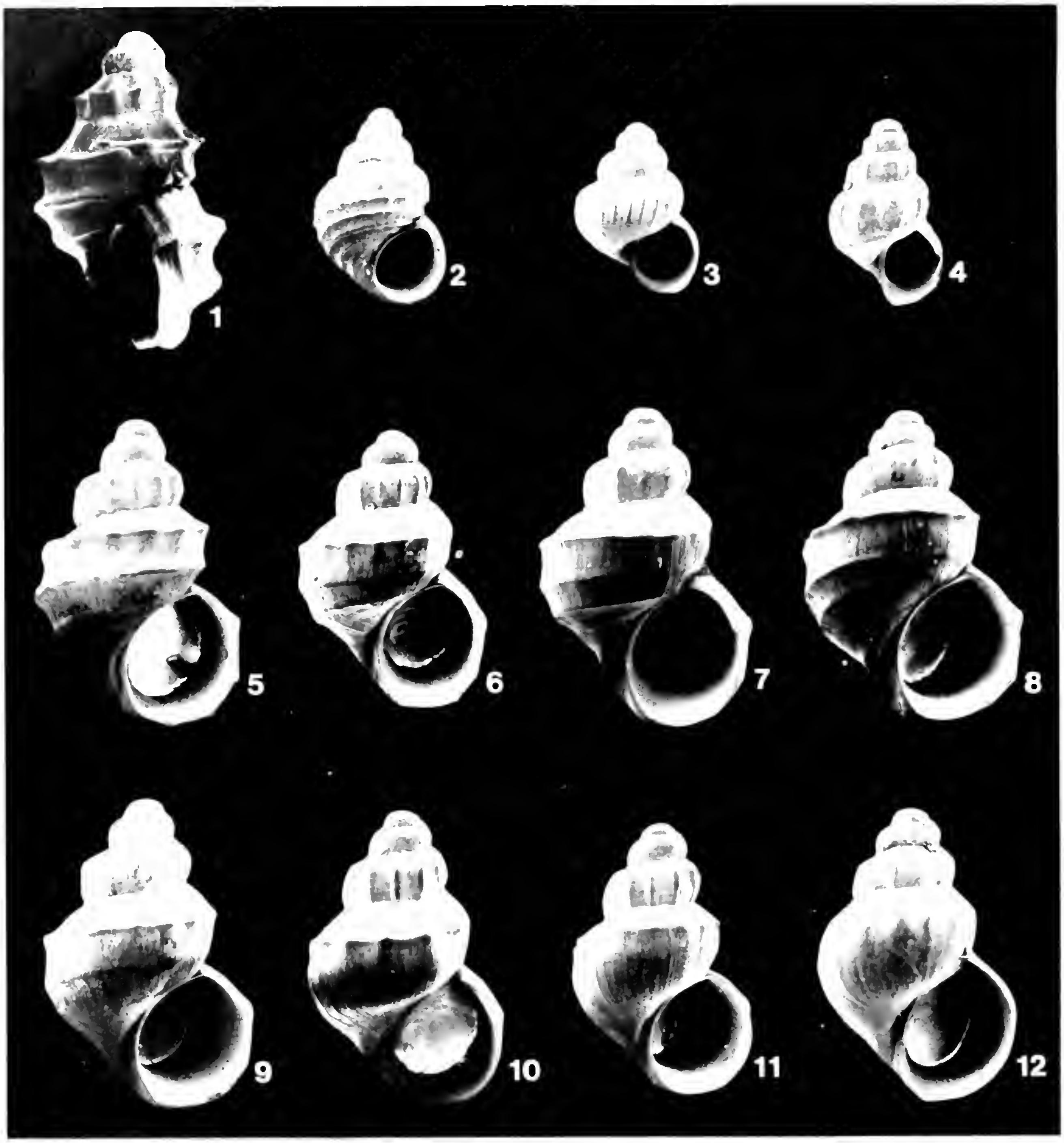
Several theories have invoked predation as a potentially important factor structuring deep-sea benthic communities (reviewed in Jumars and Eckman, 1983; Rex, 1983; Grassle, 1989), but there is little direct evidence for this. In coastal faunas, the incidence of repaired shell damage in snails, when critically and carefully interpreted (Schoener, 1979; Vermeij, 1982a; Schindel *et al.*, 1982), has been a useful measure of the relative importance of predation. In this note we analyze patterns of repaired shell damage in an assemblage of four rissoid gastropods from the upper continental slope south of New England. The four species, *Frigidoalvania brychia* (Verrill, 1884), *Onoba pelagica* (Stimpson, 1851), *Pusillina harpa* (Verrill, 1880), and *Pusillina pseudoareolata* (Warén, 1974), are all deposit feeders with nonplanktotrophic development and similar ventricose shells. Rex *et al.* (1988) recently presented a biometrical analysis of shell form in the assemblage that revealed strong differentiation with depth across the upper slope. Predation was suggested, but not explored further, as a possible cause of this depth-related geographic variation. Our aim here is to test hypotheses that shell-repair frequency corresponds to: 1, depth of sampling and hence the observed depth-related clinal effects, and 2, differences in shell architecture that in coastal species are associated with the relative ability to deter predators.

Station data and species lists for the five samples are provided in table 1 (see Rex *et al.*, 1988, for details of

Table 1. Station data, sample sizes, incidence and statistical analysis of repaired shell damage for rissoid snails from the upper continental slope south of New England (USA). Chi-square tests compare the frequency of repaired damage (using raw data) between *Frigidoalvania brychia* and the other three species combined, and between rugose and smooth forms of *F. brychia* in station 87.

Station number	Latitude (N)	Longitude (W)	Depth (m)	Species	Sample size	Number broken	Frequency broken	Chi-square	Significance
88	39°54.1′	70°37.0′	478	*Onoba pelagica*	3	0	0		
				Pusillina pseudoareolata	6	0	0		
				Pusillina harpa	11	0	0		
				Frigidoalvania brychia	17	2	0.12	0.719	n.s.
96	39°55.2′	70°39.5′	498	*Onoba pelagica*	12	0	0		
				Pusillina pseudoareolata	12	1	0.08		
				Pusillina harpa	79	7	0.09		
				Frigidoalvania brychia	122	16	0.13	1.162	n.s.
105	39°56.6′	71°03.6′	530	*Onoba pelagica*	44	4	0.09		
				Pusillina harpa	84	3	0.04		
				Frigidoalvania brychia	155	33	0.21	13.186	$P < 0.001$
207	39°51.3′	70°54.3′	808	*Onoba pelagica*	3	1	0.33		
				Pusillina pseudoareolata	S100	20	0.20		
				Pusillina harpa	S100	12	0.12		
				Frigidoalvania brychia	S100	27	0.27	4.217	$P < 0.05$
87	39°48.7′	70°40.8′	1,102	*Frigidoalvania brychia*	S200	41	0.21		
				Rugose form	53	8	0.15		
				Smooth form	147	33	0.22	0.881	n.s.

S before sample size indicates that a random subsample (rather than all appropriate shells at that station) was scored



Figures 1–12. Specimens of rissoid gastropods collected from the upper continental slope south of New England (USA). **1.** *Frigidoalvania brychia* showing repaired shell damage at the end of the second whorl (station 105; shell height is 3.5 mm). **2.** *Onoba pelagica* (sta. 207, 2.3 mm). **3.** *Pusillina harpa* (sta. 96, 2.0 mm). **4.** *Pusillina pseudoareolata* (sta. 96, 2.2 mm). **5–8.** Rugose forms of *F. brychia* (sta. 87; 3.6, 3.5, 3.8, 3.7 mm respectively). **9–12.** Smooth forms of *F. brychia* (sta. 87; 3.7, 3.5, 3.2, 3.5 mm respectively). See Table 1 for station data.

sampling and a bathymetric map showing station localities. Individuals were scored for repaired shell damage using the criteria developed by Schindel *et al.* (1982) and Vermeij (1982a). We recorded only what Vale and Rex (1988:65) termed "major" damage: "conspicuous breaks generally resulting in displacement of subsequent growth patterns and interruption of sculpture." An example of such damage in *Frigidoalvania brychia* is shown in figure 1. Essentially the same criteria have been used to identify predator-induced shell breakage in numerous shallow-water snail faunas (see Vale and Rex, 1988, for a review). We scored all individuals with at least a half post-larval whorl, and recorded the number of repaired breaks for the first, second and third whorls (shells of these species seldom have a complete third whorl) to determine whether there was any variation in repaired damage with shell size. If the samples were very large (636–5,318 individuals, see Rex *et al.*, 1988: table 1), we scored 100–200 randomly selected individuals. The incidence of shell repair was calculated as simply the frequency of repaired shells (Raffaelli, 1978). An alternative index is the average number of scars per shell (Vermeij, 1982b). The measures are nearly identical for the rissoid complex because only 5% of the shells that were repaired had more than one break.

The number and frequency of repaired breaks are given in Table 1. We report data for the entire adult shell (i.e., whorls 1–3 combined) because no consistent differences in frequency were associated with shell growth. The median frequency of repaired damage for the whole complex in all 5 samples is 0.11 (0.13 if only large, $N > 40$, samples are used). This value is near the median value obtained for the deep-sea prosobranch fauna as a whole (0.15) by Vale and Rex (1988), and falls within the range of values reported for a wide variety of shallow-water habitats (see Vale and Rex, 1988: table 2).

We used chi-square tests to determine whether there is any association between sampling depths [about 500 m (stations 88, 96, and 105 combined), 800 m, and 1,100 m] and frequency of shell repair. The null hypothesis is that frequencies of repair are equal among snails grouped by depth. The alternative hypothesis is that depth groups differ in frequency of repair. None of the rissoids show a significant difference in the incidence of repaired shell damage among sampling depths (chi-square values range from 2.30–4.38, $0.20 > P > 0.05$, two-tailed test, Siegel, 1956).

We also explored whether the frequency of repaired damage is associated with shell architecture. *Frigidoalvania brychia* exhibits more rugose sculpture than the other three species (figures 1–4). Its heavy shoulder knobs and strong spiral costae are identical to sculptural features that deter predators in shallow-water snails (Palmer, 1979). At the 500 m stations all individuals of *F. brychia* are heavily armored like the individual shown in figure 1, but at greater depths variation increases to include both rugose forms and smoother forms (figures 5–12). Rex *et al.* (1988) interpreted the increased variation in deeper populations of *F. brychia* to be a possible case of competitive release. It was also suggested that heavy sculpture on *F. brychia* might confer greater protection against predation than the less sculptured shells of the other species. *Frigidoalvania brychia* might also be less vulnerable to predation because of its larger size (Rex *et al.*, 1988, table 2, and figures 1–12 herein). To test whether this might be reflected in the frequency of repaired shell damage, we compared the incidence of repair between *F. brychia* and the other three species combined at sites where they are sympatric, and between rugose (figures 5–8) and smooth (figures 9–12) forms of *F. brychia* at the 1,102 m site. The sculptural variation in *F. brychia* at 1,102 m is continuous. Following Rex *et al.* (1988), we used a qualitative scale to score shells as either rugose (in the range of figures 5–8) or smooth (in the range of figures 9–12).

Whether rugose forms should have a higher or lower frequency of shell repair than smooth forms is difficult to predict. The relationship of predation intensity to incidence of repair depends on a complex set of life-history features and population dynamics of both predators and prey, and evolved responses to predator-prey interactions (Schoener, 1979; Schindel *et al.*, 1982; Vermeij, 1982a, 1983). Virtually none of this information is known for either the rissoids or their likely predators, the decapod crustaceans and fishes. We can test only in a general way whether rugose and smooth shell forms experience predation differently. Two-tailed chi-square tests on the frequency of repair between rugose and smooth forms of *Frigidoalvania brychia* and between *F. brychia* and the other rissoids do not reveal a consistent pattern (table 1). Within *F. brychia* there is no significant difference in repair frequency between smooth and rugose forms. Among the species, *F. brychia* generally shows a higher frequency of repair, but the difference is strongly significant in only one of the 500 m stations (sta. 105), and weakly significant at 808 m (sta. 207).

Our results show that the rissoid assemblage is subjected to a comparatively high level of potentially lethal predation. However, there is no clear correspondence of the incidence of repaired shell damage to the depth-related patterns of geographic variation observed by Rex *et al.* (1988). Nor is there convincing evidence that differences in shell size and architecture relate to predation. These findings are consistent with the hypothesis of Vermeij (1978) and Vale and Rex (1988) that, while crushing predation imposes a certain level of mortality on deep-sea snails, relationships between gastropod prey and crushing predators are more generalized and poorly coevolved than they appear to be in their shallow-water counterparts.

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Distribution of *Melampus bidentatus* (Say) and *Succinea wilsoni* (Lea) within a Tidal Marsh in Eastern Connecticut

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Succinea wilsoni Lea 1864 and *Melampus bidentatus* Say 1822 are halophilic plumonate snails which occasionally share the same microhabitat (Fell & Williams, 1985). *Melampus* occurs primarily in the higher salinity regions of salt marshes, its population density being generally low in brackish areas (Parker, 1976; Fell & Williams, 1985). *Succinea* is found in freshwater marshes and the less saline regions of salt marshes (Grimm, 1975). The present report describes the distribution of *Melampus* and *Succinea* within a single marsh system in Connecticut.

MATERIALS AND METHODS

This study was conducted on the Paffard Marsh which is located in Stonington, Connecticut, and is situated north of Route 1 along the upper extent of a tidal creek (Oxecosset Brook) that empties into Fishers Island Sound at the eastern end of Long Island Sound (figure 1). The marsh is cut by a series of mosquito ditches that drain into the creek. Throughout much of the marsh, most of the interditch area is covered by stunted *Spartina alterniflora* Loisel. 1807. Tall *Spartina alterniflora* grows along the banks of the ditches; and a belt of *Spartina patens* (Ait) Muhl 1817 frequently occurs between the ditches and the interditch *Spartina alterniflora*. *Distichlis spicata* (L.) Greene 1887 and *Juncus gerardi* Loisel. 1809 are found in patches within the marsh, being most abundant near the upland border. *Phragmites australis* (Cav.) Trin *ex* Steud. 1820 and *Eleocharis rostellata* Torr. 1843 also occur along the edge of the marsh. At the upper ends of the two major branches of the tidal creek, there are large stands of *Typha angustifolia* L. 1753. During mid-July the salinity at the upper end of the western branch of the tidal creek was 1–2 parts per thousand (ppt) and that of the creek at Route 1 was 27 ppt.

The study was conducted from 6 June through 22 July 1987. The densities of the snails at 55 stations were determined using a 50 cm square wooden frame, 9 cm high, which was tossed onto the marsh in areas chosen for study. The vegetation within the frame was clipped at the surface of the peat and all of the snails were collected and counted. The shell lengths of the snails were measured to the nearest 0.5 mm under a dissecting microscope using a mm ruler. The salinity of the soil water was determined at 44 stations by squeezing water from a piece of peat, filtering the water through Whatman No. 1 filter paper, and measuring the salinity with a Goldberg refractometer.

Spatial overlap between *Melampus bidentatus* and *Succinea wilsoni* was calculated using the equation:

$$C = 1 - \tfrac{1}{2}[\textstyle\sum(PAi - PBi)] \qquad \text{(Schoener, 1970)}$$

Where C is the spatial overlap, PAi is the percentage of the total number of species A (*Succinea wilsoni*) found in a particular microhabitat category (i), and PBi is the percentage of the total number of species B (*Melampus bidentatus*) occurring in the same microhabitat category (i). Each of the 55 quadrats was treated as a separate microhabitat category. A value for C of 0 indicates that there is no spatial overlap between the two species, while a value of 1 indicates that there is complete overlap.

Voucher specimens of *Melampus bidentatus* (USNM #858073) and *Succinea wilsoni* (USNM #858074) collected on the Paffard Marsh have been deposited at the National Museum of Natural History, Smithsonian Institution.

RESULTS

Melampus occurred at greatest densities where the soil water salinity ranged between 20 ppt and 30 ppt (figure 2) and in regions dominated by stunted *Spartina alterniflora* and *Distichlis spicata* (figure 4). The density of *Melampus* was weakly correlated with soil water salinity (r = 0.420). *Succinea* was most abundant at stations where the soil water salinity varied from 15 ppt to 22 ppt (figure 3) and where the vegetation consisted of *Eleocharis* or *Typha* (figure 4). It exhibited the highest densities at the upper ends of the two major branches of the tidal creek

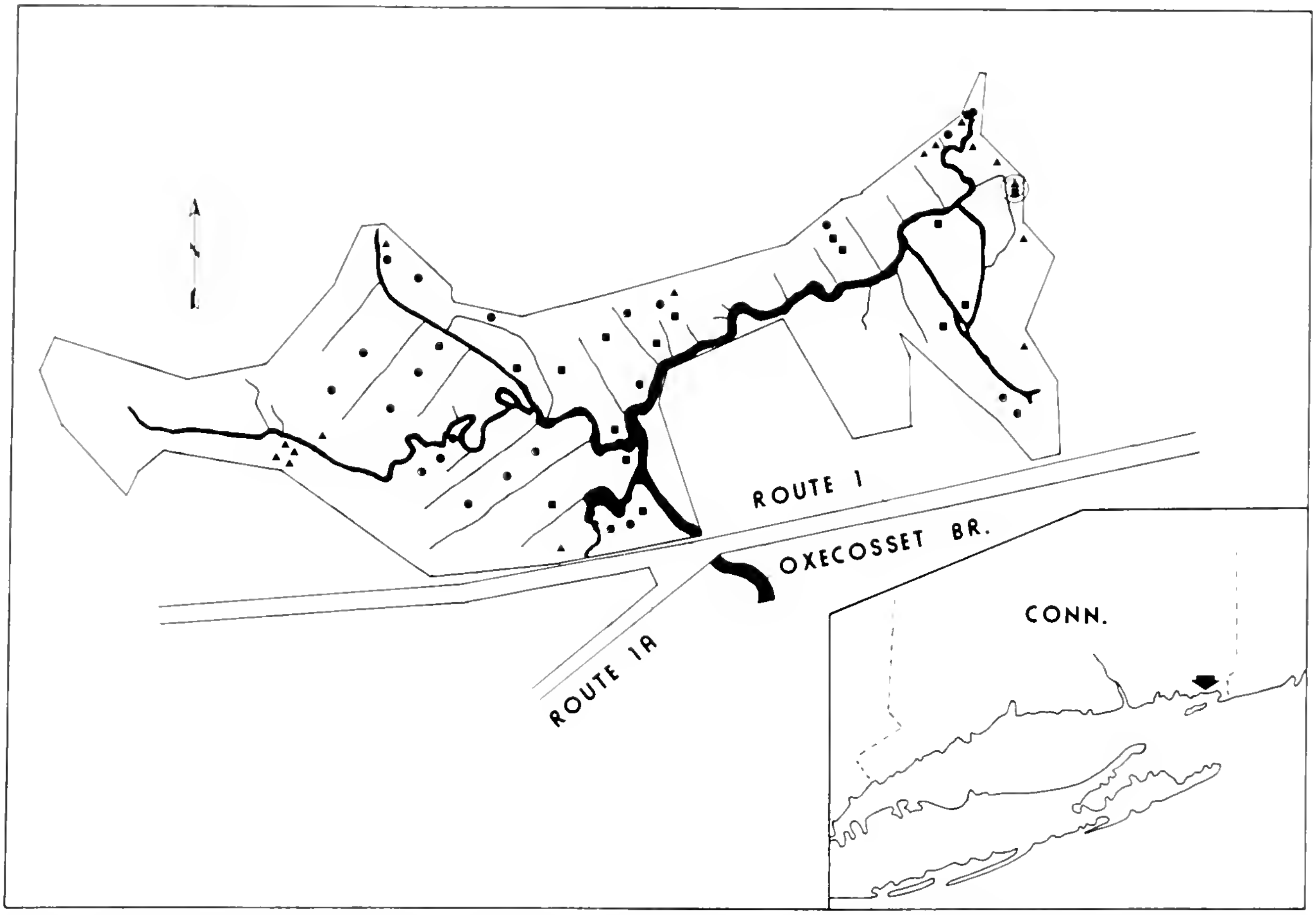

Figure 1. Map of the Paffard Marsh, in Stonington, Connecticut, showing the 55 study sites. Squares represent sites that contained 25 or more *Melampus bidentatus* per 0.25 sq. meter; triangles show sites that contained 25 or more *Succinea wilsoni* per 0.25 sq. meter, and circles represent sites where only a few snails were found. One site contained 25 or more of both species of snail per 0.25 sq. meter. The inset (lower right) shows the location of the Paffard Marsh (arrow) on the Connecticut shore.

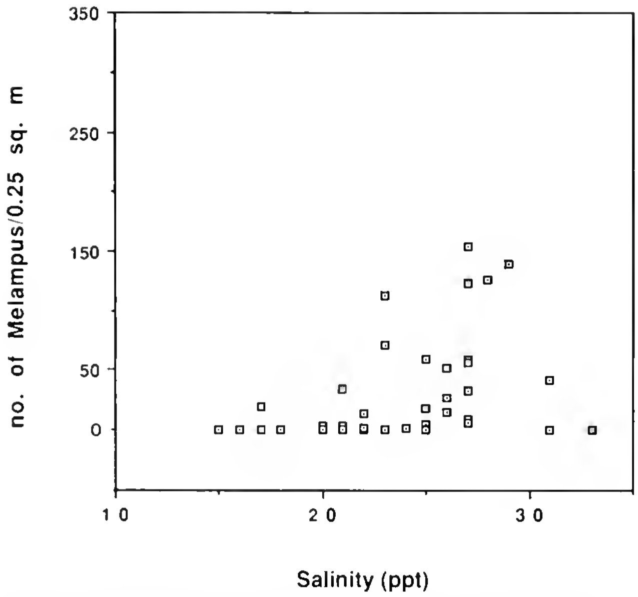

Figure 2. Densities of *Melampus bidentatus* in relation to soil-water salinities on the Paffard Marsh in Stonington, Connecticut.

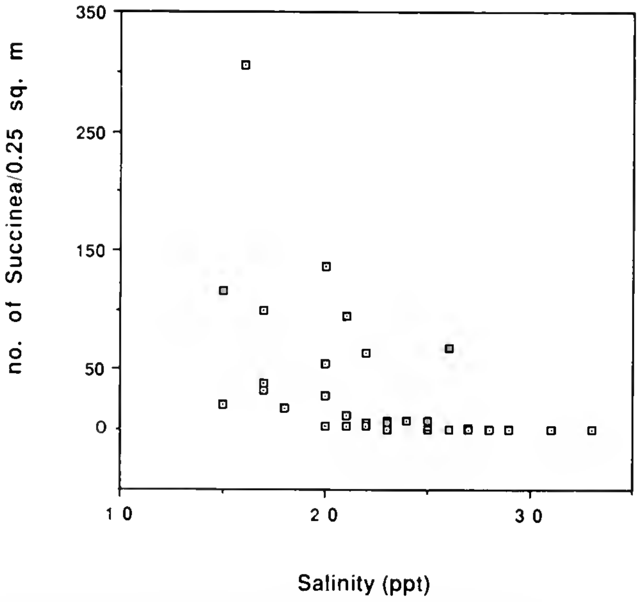

Figure 3. Densities of *Succinea wilsoni* in relation to soil-water salinities on the Paffard Marsh in Stonington, Connecticut.

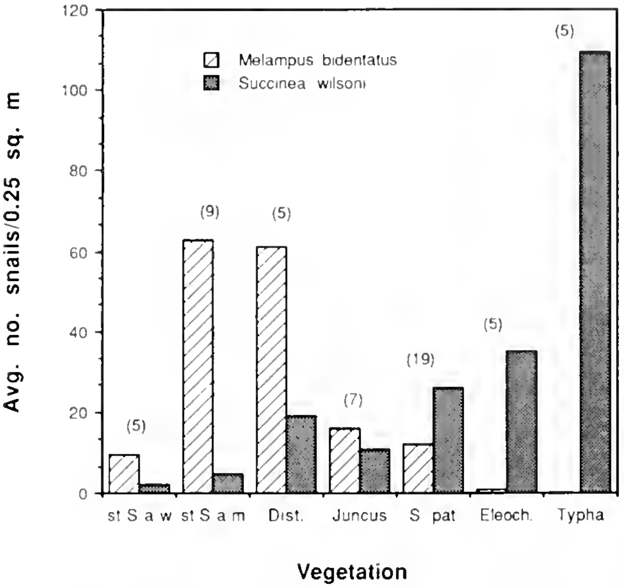

Figure 4. Average densities of *Melampus bidentatus* and *Succinea wilsoni* in different vegetation types on the Paffard Marsh in Stonington, Connecticut. The number of quadrats studied in each vegetation type is indicated in parentheses. st. S.a. w = stunted *Spartina alterniflora* with standing water; st. S.a m = stunted *Spartina alterniflora* with moist soil; Dist. = *Distichlis spicata*, Juncus = *Juncus gerardi*; S. pat. = *Spartina patens*; Eleoch = *Eleocharis rostellata*; Typha = *Typha angustifolia*.

Table 1. Abundance, no. per 0.25 m² (mean ± S.D., range), of *Melampus bidentatus* (Say) and *Succinea wilsoni* (Lea) at 55 sampling sites on the Paffard Marsh in Connecticut

Snail abundance	Number of quadrats
Many *Melampus* (83 ± 44, 33–155) only	10
Many *Melampus* (63 ± 39, 32–126); few *Succinea* (1.4 ± 0.9, 1–3)	5
Many *Succinea* (101 ± 77, 29–306) only	11
Many *Succinea* (40 ± 15, 27–55); few *Melampus* (10 ± 9, 4–20)	3
Few *Melampus* (6 and 15) only	2
Few *Succinea* (9 ± 7, 1–21) only	8
Few *Melampus* (5.4 ± 5.7, 1–18); few *Succinea* (4.5 ± 3.2, 1–12)	13
Many *Melampus* (27); many *Succinea* (69)	1
No snails	2

(figure 1). Density of *Succinea* was negatively correlated with soil water salinity (r = −0.534).

Spatial overlap between *Melampus* and *Succinea* was calculated to be 0.07 indicating little spatial overlap between the two species. *Melampus* and *Succinea* occurred together in 22 of the 55 quadrats that were examined; however, in only one quadrat were both species present in large numbers and in 36% of these quadrats one species or the other predominated (Table 1). The snails tended to occur together in regions of the marsh covered by *Distichlis*, *Juncus* and/or *Spartina patens*.

Succinea ranged in size from 1 mm to 8 mm, but most of the snails were small. The largest size class was 2–3 mm. *Melampus* ranged in size from 4 mm to 12 mm, with 9–10 mm snails constituting the largest size class.

Melampus egg masses were observed occasionally from 6 July through 21 July 1987. The egg masses were found in areas of the marsh covered by stunted *Spartina alterniflora*, *Spartina patens* and *Distichlis* and where soil salinities ranged from 17 ppt to 29 ppt. No *Succinea* eggs were observed in the field. However, adult *Succinea* were kept in the laboratory and observed for egg laying. Beginning on 6 June, ten adult *Succinea* averaging 7 mm in length were kept in a plastic container with wet paper towels and fed iceberg lettuce. Egg laying was observed on 22 June. The eggs occurred singly or in clusters of up to five capsules. They were 1 mm in diameter, with the early embryo being about 0.1 mm in diameter and the remainder of the capsule being filled with albumen. Although no eggs hatched, the embryos developed for up to two weeks. At the end of this period, the young snails had filled the entire egg capsule.

DISCUSSION

The distribution of *Melampus bidentatus* observed in this study is consistent with the pattern described in previous reports (Leathem & Mauer, 1975; Parker, 1976; Fell *et al.*, 1982; Fell & Williams, 1985). This snail, which is restricted to the high marsh, extends far up estuaries into regions of low salinity; but its population density is low where salinities fall below about 10 ppt (Parker, 1976; Fell & Williams, 1985). *Succinea wilsoni* was found primarily in the more brackish regions of the marsh as predicted by earlier studies. Grimm (1975) states that this snail usually occurs in the freshest zone of saltmarshes but that it occasionally may be found in shaded fresh water swamps or in more saline environments. *Melampus* and *Succinea* were found occurring together in 40% of the quadrats examined, but in only one of the quadrats were both of them present in large numbers (>25 per 0.25 sq. meter). Although these snails occupy some of the same microhabitats, they evidently exhibit little spatial overlap. There appears to be only one previous report of the co-occurrence of *Melampus* and *Succinea* in salt marshes (Fell & Williams, 1985). However, such an association of these snails is relatively common in brackish marshes in Connecticut (unpublished observations). Further studies of *Melampus* and *Succinea* in other brackish marshes should provide important information concerning the factors that determine the distributions of these snails.

ACKNOWLEDGEMENTS

We are indebted to the Mashantucket Land Trust for permission to conduct the study in Paffard Marsh. This work was supported by Research Experience for Undergraduates Grant No. BBS-8713347 from the National Science Foundation to Connecticut College.

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The "Gray Catalogues" [Mollusca] of the British Museum

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John Edward Gray (1800–75) was the longtime Keeper of Zoology at the British Museum (Montagu House, Bloomsbury); in 1824 he was appointed as an assistant and became a full keeper in 1840 (following the death of J. C. Children). Gray played an important role in the development of systematic zoology in England, and his research greatly enhanced the value of the zoological collections now housed in the Natural History Museum [formerly known as the "British Museum (Natural History)"; *i.e.*, South Kensington]; further biographical detail is in Gunther (1975, 1980) and Smith (1906).

Gray authored over 1,160 publications on all the major groups of animals of which a tabulation is provided in Gray (1875); this list, however, contains numerous small errors and omissions. Gray edited an extensive series of catalogues of the natural history collections contained in the British Museum. These catalogues covered the whole spectrum of systematic zoology and are of great importance as they contain generic diagnoses and descriptions of new taxa. The first such, the "Synopsis of the Contents of the British Museum" (from 1808 to 1856, in 63 editions), were rather cursory overviews of the entire collection; the more specific "Lists . . ." and "Catalogues . . ." are unquestionably of greater importance today.

Günther (1912) discussed the history, rationale, and limitations (specifically, the few illustrations provided) of these various publications. Needless to say, Gray did not write all of these catalogues, although he did provide prefaces for many of those authored by his colleagues. Sherborn (1926a, 1934) provided a valuable, albeit abbreviated, collation of these publications, with the dates of publication determined by when "they were laid upon the table of the Trustees . . ." (Sherborn, 1926a:271). These dates show some slight variance from those provided in the "Catalogue of Books, Manuscripts, Maps, and Drawings of the British Museum (Natural History)" (Woodward, 1903b).

In the field of systematic malacology, the "Gray Catalogues" are still most useful in providing a guide to the taxa of Gray, Baird, Deshayes, d'Orbigny and Pfeiffer, as well as of the pioneering collections from Cuba, the Canaries, South America and Mazatlán, and of the various molluscan taxa monographed. Nonetheless, it must be admitted that some of the taxa listed were nude names (lacking a description) and were probably subsequently (re-)described by Gray or another author. In particular, many of the generic names tabulated in the various editions of the "Synopsis of the Contents of the British Museum . . ." were not made available until Gray's 1847 "A List of the Genera of Recent Mollusca . . . ," as discussed by Iredale (1913); all of Gray's works should be carefully consulted with respect to these generic names. A number of family-group names were also made available in these catalogues.

Due to the slight variations in previous citations of the dates of publication of these catalogues, some confusion has inevitably arisen over the years. Some authors, apparently unaware of Sherborn's determinations, have based the dates upon those printed on the title page or following the editorial preface. However, the actual date that should be used is, in some cases, the following year. For example, Ruhoff (1980) not only provided several incorrect dates, but also listed Gray as the author when he was merely the editor of a colleague's work.

Herein is presented as complete a collation as possible of the 22 catalogues of the British Museum that contain treatments of the Mollusca. They are listed by author, in chronological order (based on the dates of Sherborn, 1926a, 1934), with the editor (if different) and "date of publication in text" noted at the end of each citation. The publisher is the British Museum; the printer is also given. As some readers may be aware, Carpenter's 1857 "Catalogue of the Collection of Mazatlan Shells . . ." was simultaneously printed under a separate title, on different paper of a larger size. The two printings differ only in their title, prefatory material, and dimensions. All the other British Museum catalogues are approximately 16.0 cm × 10.3 cm; the "Catalogue of the Reigen Collection of Mazatlan Mollusca . . ." is 17.5 cm × 10.2 cm (sizes may vary due to trimming and binding).

LIST OF CATALOGUES

Baird, William. 1850 [12 June]. Nomenclature of Molluscous Animals and Shells in the Collection of the British Museum Part I. Cyclophoridae. Spottiswoodes and Shaw, London. 69 p. [Preface by J. E. Gray, "March, 1850."]

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xii + 552 p. [Some copies have the pagination of introductory material as "i–iv, ix–xvi."]

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News and Notices

MONOGRAPHS OF MARINE MOLLUSCA CHANGES HANDS

The malacological journal *Monographs of Marine Mollusca*, formerly published by American Malacologists, Inc., with Dr. R. Tucker Abbott as editor-in-chief, will be published by Trophon Corporation, which publishes *The Nautilus* (business office: Trophon Corporation, P.O. Box 7279, Silver Spring, MD 20910, USA).

The new editor-in-chief will be Dr. Rüdiger Bieler (editorial office: Delaware Museum of Natural History, P.O. Box 3937, Wilmington, DE 19807, USA). The editorial board will consist of Drs. Abbott and M. G. Harasewych as associate editors and an international panel of consulting editors.

The journal will continue to publish systematic monographs of Recent and fossil marine mollusks. The next number (no. 4) will be a monograph by W. O. Cernohorsky on Mitridae and Vexillidae, with an expected publication date in March of 1990.

AMERICAN MUSEUM OF NATURAL HISTORY FELLOWSHIPS

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Grants—Grants are available to advanced predoctoral candidates and recent postdoctoral researchers. Awards range from $200–$1,000. Deadlines vary according to grant program: *Theodore Roosevelt (N.A. fauna)—February 15, 1990. *Lerner-Gray (marine)—March 15, 1990.

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Sincerely,

Maureen MacLellan
Office of Grants & Fellowships

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THE NAUTILUS publishes papers on all aspects of the biology and systematics of mollusks. Manuscripts describing original, unpublished research as well as review articles will be considered. Brief articles, not exceeding 1000 words, will be published as notes and do not require an abstract. Notices of meetings and other items of interest to malacologists will appear in a news and notices section.

Manuscripts: Each original manuscript and accompanying illustrations should be submitted in triplicate. Text must be typed on one side of 8½ × 11 inch white paper, double spaced throughout (including literature cited, tables and figure captions), with at least 1 inch of margin on all sides. All pages must be numbered consecutively. If printed on a word processor, the right margin should be ragged rather than justified. Authors should follow the recommendations of the *Council of Biology Editors Style Manual*, which is available from the Council of Biology Editors, Inc., 9650 Rockville Pike, Bethesda, MD 20814, U.S.A. The first mention of a scientific name in the text should be accompanied by the taxonomic authority, including year. Latin names and words to be printed in italics must be underlined; leave other indications to the editor. Metric and Celsius units are to be used.

The sequence of sections should be: title page, abstract page, introduction, materials and methods, results, discussion, acknowledgements, literature cited, tables, figure captions, figures. The title page should include the title, author's name(s) and address(es). The abstract page should contain the title and abstract, which should summarize in 250 words or less the scope, main results and conclusions of the paper. The abstract may be followed by a maximum of 8 key words. All references cited in the text must appear in the literature cited section and vice versa. In the literature cited section, all authors must be fully identified and listed alphabetically. Follow a recent issue of THE NAUTILUS for bibliographic style, noting that journal titles must be unabbreviated. Information on plates and figures should be cited only if not included in the pagination. Tables must be numbered and each placed on a separate sheet. A brief legend must accompany each table. Captions for each group of illustrations should be typed on a separate sheet and include a key to all lettered labeling appearing in that group of illustrations.

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Voucher Material: Deposition of type material in a recognized public museum is a requirement for publication of papers in which new species are described. Deposition of representative voucher specimens in such institutions is strongly encouraged for all other types of research papers.

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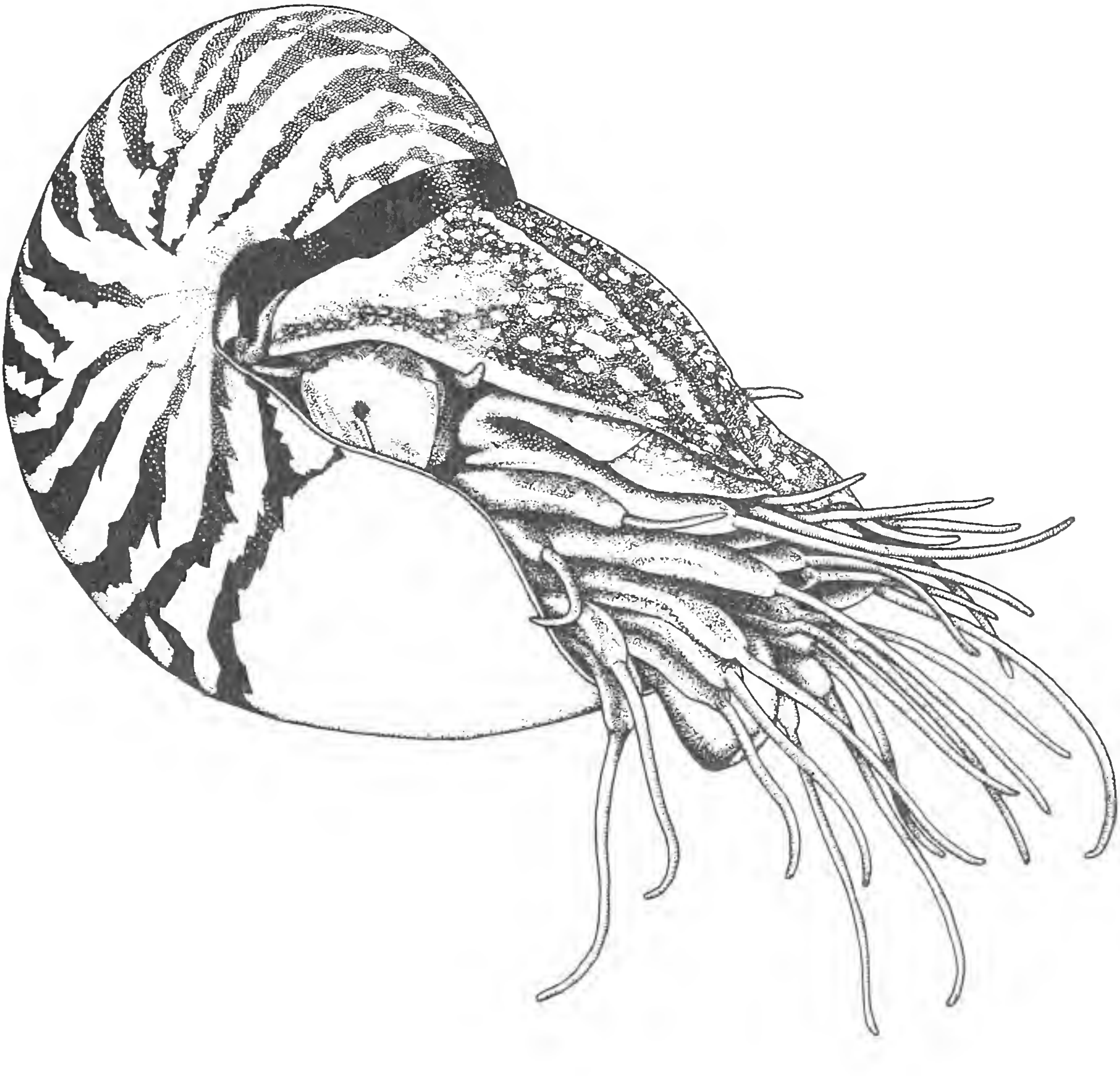

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CONTENTS

Clarification of the Identity of the Snail *Margarites groenlandicus* (Gmelin, 1791) (Gastropoda: Trochidae)

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ABSTRACT

The boreal Atlantic trochid *Margarites groenlandicus* (Gmelin, 1791) is generally regarded as a species ranging from Massachusetts, Scotland and Norway north to polar waters, and varying in sculpture from smooth to strongly lirate. A critical examination of many specimens and of the putative syntypes of *Trochus groenlandicus* Chemnitz, 1781, the basis of Gmelin's name, revealed that two species are involved in what has been known as *Margarites groenlandicus:* (1) the typical *M. groenlandicus*, with a usually larger, smooth, more broadly conical shell, found only in the colder Arctic and polar waters, and (2) *M. striatus* (Leach, 1819), with a smaller, more elevated, spirally lirate shell with a narrower umbilicus, found in northern Europe and Iceland in the eastern Atlantic, and on the western Atlantic coast from southern Massachusetts northward to southern Baffin Land and Disko in western Greenland. Biometric and geographic data are adduced to support the distinctiveness of these two taxa.

INTRODUCTION

In the process of preparing a field guide to North American marine shells, I found that there is confusion over the true identity of *Margarites groenlandicus* (Gmelin, 1791), a species found in the cold waters of the North Atlantic.

In "American Seashells" (Abbott, 1974:36), *Margarites groenlandicus* is described as having "whorls with about a dozen smooth spiral lirations or almost entirely smooth (form *umbilicalis* Broderip and Sowerby, 1829)", and its geographic range is given as "Arctic seas to Massachusetts Bay." Examination of material in the collection of the National Museum of Natural History revealed that two distinct taxa are involved, and that the smooth form occurs no farther south than northernmost Labrador and the southern tip of Greenland. A study of material on which Chemnitz's *Trochus groenlandicus* was probably based shows that this name should be applied to the smooth, broadly umbilicate, Arctic form.

The true taxonomy of *Margarites groenlandicus* and *Margarites striatus* (Leach, 1819), the species with which it has been confused, is reviewed in the following synonymies and discussions.

SYSTEMATICS

Margarites groenlandicus (Gmelin, 1791)
(figures 1–7, 13)

Trochus Grönlandicus umbilicatus anfractibus ... etc.—Chemnitz, 1781 108, pl. 171, fig. 1671 (type locality, northern Greenland). [Non-binomial].

Trochus groenlandicus Gmelin, 1791:3574, Dillwyn, 1817:771

Margarita umbilicalis Broderip and Sowerby, 1829:379; Sowerby, 1838a:26 (type locality, Melville Island); Sowerby, 1838b:pl. 133, fig. 5; Reeve, 1855:393; Sowerby II, 1878: pl. 1, fig. 1; Posselt, 1895:90.

Margarita sulcata Sowerby, 1838a:26 (type locality, Melville Island); Sowerby, 1838b:pl. 132, fig. 1.

Margarita groenlandica, Sowerby, 1838a:25; Sowerby, 1838b: pl. 133, fig. 10; Morch, 1857:89. Sowerby II, 1878:pl. 1, fig 6. Odhner, 1912.56–62 (in part), pl 4, figs. 15, 16, 18, 19; Thorson, 1944 15–20.

Margarita undulata laevior Möller, 1842.81 (type locality, Greenland).

Trochus umbilicalis, Philippi, 1852:245, pl 37, fig. 2, Jeffreys, 1877·237.

Trochus gronlandicus, Philippi, 1852 247, pl. 337, fig 5

Trochus rossi, Philippi, 1852·288, pl. 43, fig 9 [new name for *Margarita sulcata* Sowerby, 1838a, not *Trochus sulcatus* Lamarck, 1804, etc.].

Margarites umbilicalis, Pilsbry, 1890:288, pl. 3, figs. 61, 62, 64, pl 64, figs. 39–41; Baker, 1919:503-504; Johnson, 1934 72.

Margarites umbilicalis spiralis, Baker, 1919.503–504 (type locality, Etah, Greenland).

Margarites groenlandicus umbilicus, Odhner, 1915 149; Abbott, 1954 108, fig. 31d; Galkin, 1955 82–83, fig 25; Abbott, 1974.36, fig 215

Margarita groenlandica, var. *laevigata* Odhner, 1915 149 (type locality, Isfjorden, West Spitsbergen)

Diagnosis: Shell reaching 24.85 mm in width, 16.85 mm in height, glossy, broadly conical, occasionally some-

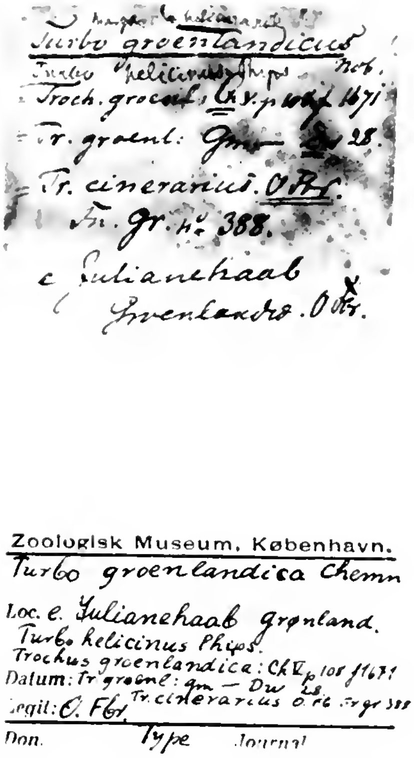
Figure 1. Lectotype of *Margarites groenlandicus* (Gmelin, 1791). Diameter 13.75 mm. Zoologisk Museum, Copenhagen, Denmark.

what depressed; suture deeply impressed; color light olive gray to light grayish brown (Kelly & Judd, 1965); early whorls usually strongly and spirally lirate, but may be weakly lirate, with shallow grooves, or smooth; later whorls smooth or with fine, impressed, spiral lines; umbilicus rather broad, deep; rarely are specimens found that are dull and strongly lirate on all whorls, but otherwise typical in form and umbilical characters.

Discussion: Chemnitz (1781:109) described a species he called "Der Gronlandische Krausel, *Trochus Gronlandicus umbilicatus, anfractibus rotundatis, intus margaritaceus*". It is figured rather poorly on plate 171, figure 1671.

Chemnitz described the shell as thin, pearly under a thin, flesh-colored layer, the six rounded whorls with very delicate spiral lines, and with a broad, deep umbilicus. The figure depicts a shell about 17mm wide, broadly conical and rather elevated, with numerous fine, interrupted spiral lines on the rounded whorls. The locality is given as "from the most distant shores of cold, raw Greenland", and the specimens are designated as "*ex museo nostro*". The brief description and poor figure have led to a misunderstanding of the identity of Chemnitz's species.

Chemnitz was never in Greenland, and according to J. Knudsen (in litt.) he probably received these specimens from Otto Fabricius, a missionary in Greenland from 1768 to 1773, and from 1774 to 1779 a pastor in southern Norway, a country at that time united with Denmark. He returned to Denmark and in 1783 received a post in Copenhagen, where he spent the rest of his life. While residing in Norway Fabricius worked on his "Fauna Groenlandica", published in 1781, and it seems very likely that during this time he was in correspondence with Chemnitz, a relationship that undoubtedly became closer when he returned to Copenhagen.



Turbo groenlandicus
Turbo helicinus Phips. Nob.
Troch. groenl.: Ch. V. p. 108 f. 1671
Tr. groenl.: Gm. — Dw. 28.
Tr. cinerarius. O Fr.
Fn. Gr. no. 388.
e Julianehaab
Groenlandiae. O Fr.

Zoologisk Museum, København.
Turbo groenlandica Chemn
Loc. e. Julianehaab grønland.
Turbo helicinus Phips.
Trochus groenlandica: Ch V p 108 f 1671
Datum: Tr groenl: gm — Dw 28
Legit: O. Fbr. Tr. cinerarius O. Fb. Fn gr 388
Don. Type Journal

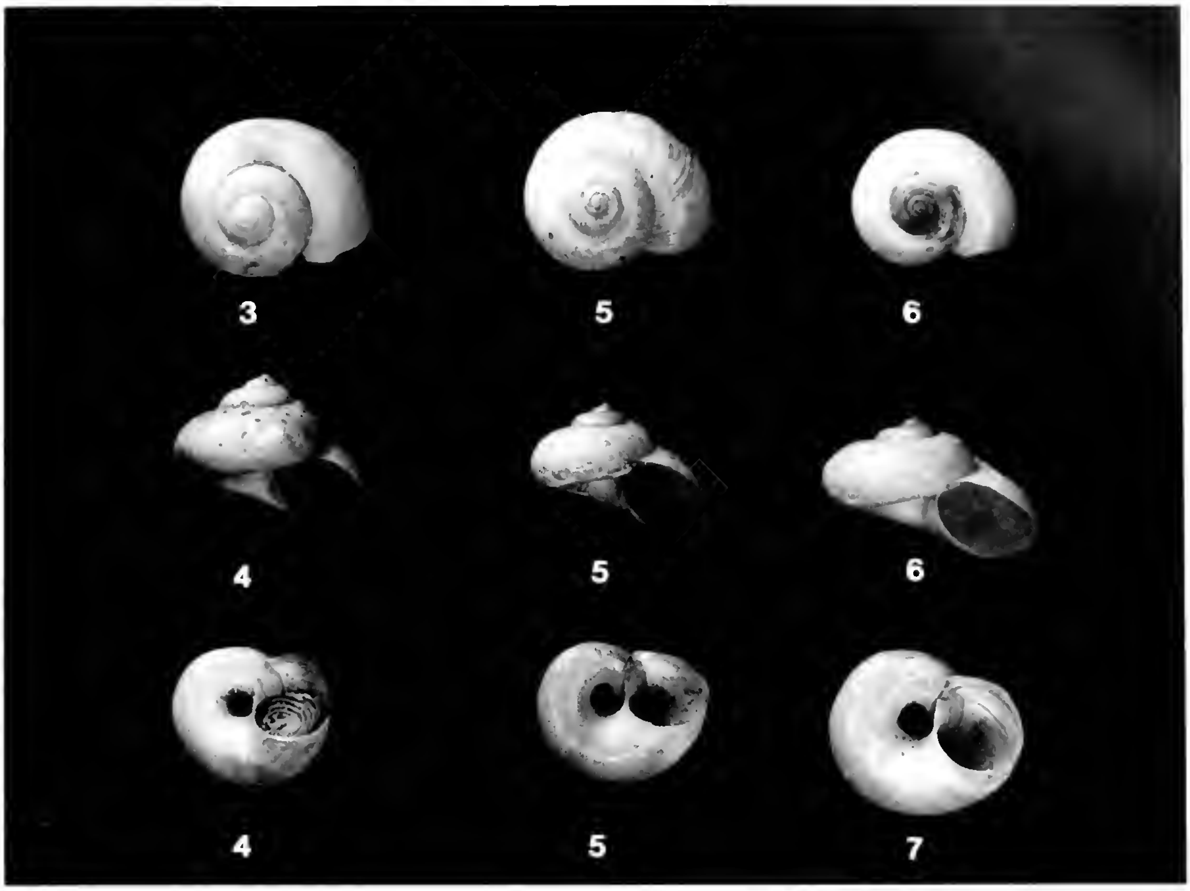
Figure 2. Labels present with syntypes of *Margarites groenlandicus* (Gmelin). Label in handwriting of O. A. Mörch.

Chemnitz's name was validated by Gmelin as *Trochus groenlandicus*, and listed under this name by Dillwyn in his "Descriptive Catalogue" (1817). Neither Chemnitz nor Gmelin gave any measurements but Dillwyn gives the dimensions as "about seven lines long and eight broad". This is equivalent to 14.8 mm height and 17 mm width, almost exactly the dimensions of Chemnitz's figure.

Through the kindness of Dr. Jörgen Knudsen I was able to examine two lots of specimens labeled *Trochus groenlandicus* and *Turbo groenlandicus* from the collections of the Zoologisk Museum in Copenhagen. One lot, comprising ten specimens, has a label written, according to Knudsen, about 40 years ago which has the word "type" on it. Accompanying it is an older label, written by Mörch, which states that the specimens came from Fabricius. Near the top of the label is the name "*Turbo groenlandicus* nob." in a slightly different handwriting, and below it is a reference to Chemnitz's description and figure (figure 2).

Since this lot appears to consist of specimens received from Fabricius, and may very well have been seen by Chemnitz, I feel justified in selecting one of these specimens (figure 1) as the lectotype.

Examination of this material shows that *Margarites groenlandicus* (Gmelin) is the earliest valid name for the species called *Margarites umbilicalis* Broderip & Sow-



Figures 3–7. Shells of *Margarites groenlandicus* (Gmelin), showing apertural, dorsal, and ventral views. 1.5 × **3.** Sabine Id., E. Greenland (USNM 219180). **4.** Clavering Id., E. Greenland (USNM 406156). **5.** Cumberland Gulf, Baffin Land (USNM 219181). **6.** Coburg Id., S of Ellesmere Land (USNM 466586). **7.** Cape Sabine, Ellesmere Land (USNM 126754).

erby by Pilsbry and *Margarites groenlandicus* form *umbilicalis* by Abbott (1974).

This species is restricted to the cold Arctic waters from Victoria Island, northern Canada, eastward to Franz Joseph Land and south to the northern tip of Labrador and to the southern point of Greenland (figure 6). A more detailed discussion of the geographic range of this species is given below.

Margarites striatus (Leach, 1819)
(figures 8–13)

Trochus cincerarius Fabricius, 1780:391 (Greenland). [not *T. cinerarius* Linné, 1758].

Margarita striata Leach, 1819:464 (type locality, Baffin Bay); Gray, 1826:567

Turbo carneus Lowe, 1825:107–108, pl 5, figs. 12–13 (type locality, Argyllshire, Scotland); Gray, 1826:567.

Trochus margaritus Gray, 1826:567 [new name for *Turbo carneus* Lowe, 1825].

Margarita carnea, Sowerby, 1838a:25, Sowerby, 1838b:1, pl 133, fig. 9.

Margarita undulata Sowerby, 1838a:26 (type locality, Arctic Seas); Sowerby, 1838b:1, pl. 132, fig. 4, Gould, 1841:254, fig. 162 = 172; Reeve, 1842:169, pl 221, fig. 4; Möller, 1842:81; Binney, 1870:280, fig. 341; Sowerby II, 1878.pl. 1, fig. 2; Pilsbry, 1890:290, pl. 39, figs. 36–39, pl. 64, figs 42–44.

Turbo incarnatus Couthouy, 1838:98, pl. 3, fig. 13 (type locality, Phillips Beach, Massachusetts).

Margarita undulata trochiformis Möller, 1842:81 [new name for *Trochus cinerarius* Fabricius, 1780, not Linné 1758].

Trochus leachii Philippi, 1852:247, pl. 37, fig. 6 [new name for *Margarita striata* Leach, 1819, not *Trochus straitus* Linné 1767].

Trochus fabricii Philippi, 1852:284, pl. 42, fig. 2 [new name for *Trochus cincrarius* Fabricius, 1780, not Linné, 1758].

Trochus undulatus, Forbes and Hanley, 1853:528, pl. 68, figs. 1, 2, pl. 73, figs, 5, 6.

Margarita groenlandica var. *undulata*, Mörch, 1857:89

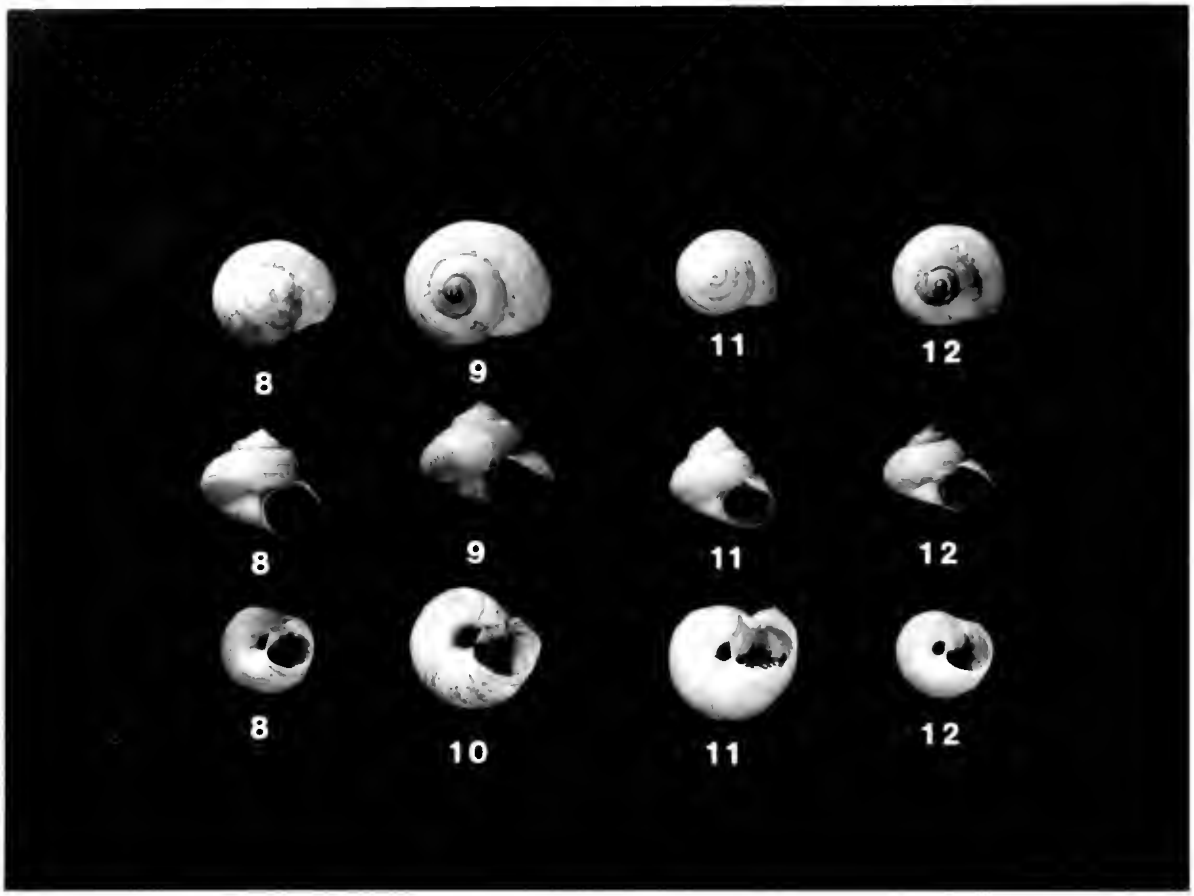
Margarita cinerea, Mörch, 1857:89 [not *Turbo cinerea* Couthouy 1838]

Trochus groenlandicus, Jeffreys, 1865:298–299, pl. 61, fig 5 [not *Trochus groenlandicus* Gmelin, 1791]

Margarita incarnata, Sowerby II, 1878, pl. 3, fig 18.

Margarita groenlandica, Sars, 1878:133–134, Posselt, 1895:80, Hagg, 1905:9–13, Odhner, 1912:56–62 [in part], pl. 4, figs. 4–14, 17, 20–27; Thorson 1941:13-14 [not *Trochus groenlandicus* Gmelin 1791].

Margarites groenlandicus, Johnson, 1915:88, Winkworth, 1932:



Figures 8–12. Shells of *Margarites striatus* (Leach), showing apertural, dorsal, and ventral views. 1.5 × **8.** Angmagssalik, Greenland (USNM 466647). **9.** Spitsbergen (USNM 181706). **10.** Spitsbergen (USNM 181736). **11.** Schooner Cover, Labrador (USNM 604949); **12.** Seal Harbor, Maine (USNM 438215).

220, Johnson, 1934:72; Abbott, 1954:108; Galkin, 1955:80–82, fig. 24; Abbott, 1974:36, Sneli, 1975:36, fig. 50; Fretter and Graham, 1977:42, fig. 28 [not *Trochus groenlandicus* Gmelin, 1791]

Margarites undulata (Sowerby) = *groenlandica*, Nordsiek, 1968:17, pl. 3, fig. 09.01

Margarites striatus, Rehder, 1981:370, fig. 300

Diagnosis: Shell reaching 15.5 mm in width, 14.75 mm in height, dull, moderately thick-shelled, broadly to elevated-conical; suture not impressed; color light grayish yellowish brown to light brown (Kelly & Judd, 1965); protoconch smooth, early post-nuclear whorls with spiral grooves or ridges rarely smoothish, later whorls strongly ridged, usually with short, low broad, wave-like axial ridges below the suture; body whorl slightly angled at the periphery; base somewhat flattened, with fine, low, spiral cords; umbilicus narrow, funnel-shaped, deep; aperture showing low, spiral ridges within the outer lip, corresponding to the external spiral sculpture.

Discussion: *Margarites striatus* is distinguished from *M. groenlandicus* by its generally heavier and more elevated shell, its smaller size, stronger spiral sculpture, a suture that is not impressed, and usually by the presence of broad, axial ridges below the suture, which are never found in *M. groenlandicus*. The base of *M. striatus* is flattened, with numerous fine spiral lirae, and the umbilicus is narrower and obscurely angled at the edge.

Meaurements of width, height, and the height/width ratio of 50 specimens of each species, randomly chosen from lots collected from throughout the range of each species, are given in condensed form in Table 1. These figures clearly show that *M. striatus* has a generally smaller, more elevated shell. The largest specimens of *M. groenlandicus* are less elevated than the smaller or average-sized specimens of the same species. The larger shells of *M. striatus* tend to be slightly less elevated than those of average size.

Misidentification of these two species seems to have started with Jeffreys (1865:298), who gave the spirally lirate specimens found in western Scotland and the Orkney and Shetland Islands the name *Trochus groenlandicus* Chemnitz.

Before Jeffreys (1865), *Margarites striatus* had generally been known as *Margarita* (or *Trochus*) *undulata* Sowerby, as the synonymy given above shows. Pilsbry (1890:290–291) continued to call this species, found from Massachusetts to northern Labrador, southern Green-

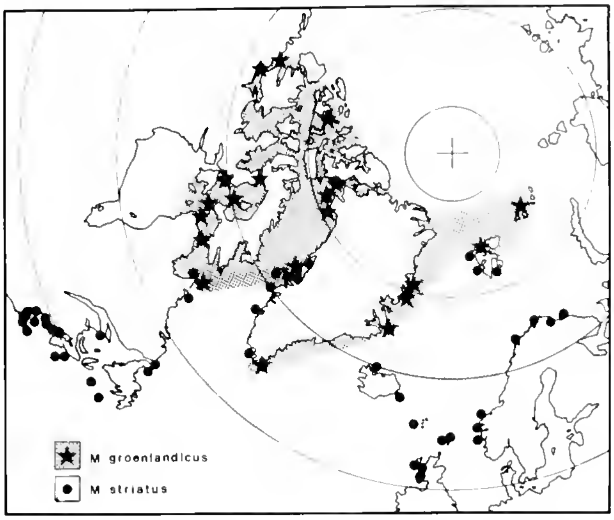


Figure 13. Map of the North Polar regions, northeastern North America, and northern Europe, showing distribution of *Margarites groenlandicus* and *Margarites striatus*.

Table 1. Summary of measurements of 50 specimens of each species. Measurements in mm.

	groenlandicus	*striatus*
Largest shell		
Diameter (d)	24.85	15.85
Height (h)	16.85	14.75
h/d	0.68	0.93
Smallest Shell		
Diameter (d)	7.90	6.90
Height (h)	6.65	6.00
h/d	0.84	0.97
Average		
Diameter (d)	14.54	9.43
Height (h)	10.92	8.48
h/d	0.75	0.90
Mean		
Diameter (d)	13.82	9.15
Height (h)	10.75	8.37
h/d	0.78	0.91
5 largest shells h/d	0.72	0.86

land, and northern Europe, *Margarita undulata*, and included in the synonymy of this species Chemnitz's *Trochus groenlandicus umbilicatus*, although he did not accept the name because it was nonbinomial. He overlooked Gmelin's validation of the Chemnitz name, and did not follow Jeffreys' use of *groenlandicus* because it was preoccupied by *Trochus gronlandicus* Philippi, 1852, which is the same, of course, as Chemnitz's species.

The species with larger, more depressed shells with a wider umbilicus, rounded whorls, and with the last whorl smooth or with fine, incised lines was called *Trochus umbilicalis* Broderip and Sowerby by Jeffreys (1877:237), who stated that, in his opinion, it was distinct from what he called *M. groenlandicus*. Pilsbry (1890:288) followed Jeffreys in this usage, and this name has since then been used for this Arctic species, either as a distinct species or as a subspecies, variety, or form. Galkin, for instance, in his otherwise excellent treatment of boreal and arctic Trochidae (Galkin, 1955:80–83) used *Margarites groenlandica groenlandica* for the typical boreal subspecies, and *M. groenlandica umbilicalis* for the arctic subspecies.

Although Galkin (1955:80–83) and Abbott (1974:36) have treated these two taxa as subspecies of one species, I prefer to consider them as separate species. The shell characters of each are quite distinctive, and in the few places where their distributional ranges overlap there is no evidence of hybridization or blurring of shell character differences. Future biochemical studies may suggest a closer relationship.

The species called *Margarites groenlandicus umbilicalis* (Broderip & Sowerby, 1829) by most recent authors must bear the name *Margarites groenlandicus* (Gmelin, 1791), and the species called *M. groenlandicus groenlandicus* (Gmelin, 1791), should bear the name *Margarites striatus* (Leach, 1819). Leach's diagnoses is very brief, but Gray (1826:567) stated that he compared Leach's type with the description and figure of *Turbo carneus* Lowe, 1825, and verified their identity. Lowe's species was based on specimens from northern Scotland.

The localities of almost 200 lots of both *M. groenlandicus* and *striatus* were plotted on a map of the North Atlantic (figure 13). The distributional pattern indicates that each species has a fairly discrete range. *Margarites groenlandicus* occurs only in the colder Arctic waters, from southwest of Victoria Island, Northwest Territories, Canada, eastward to northern Spitsbergen and Franz Joseph Land, and south to the northern tip of Labrador and the southern tip of Greenland. *Margarites striatus* is found from southern Massachusetts to northern Labrador along the west coast of Greenland only to slightly north of Disko and in Iceland, the Faeroes and Shetland Islands, northern Scotland, and the Norwegian coast from near Bergen to the Kola Peninsula, and in western and southern Spitsbergen.

It appears that in only two places do the ranges of the two species overlap: at the northern end of Labrador and in the central part of the west coast of Greenland. This distribution map (figure 13) agrees well with the map given by Galkin (1955:80–81), except that he included additional records from the Arctic north of Norway and the U.S.S.R., extending the range of *M. striatus* to the east coast of Novaya Zemlya Islands, and, to the north, the range of *M. groenlandicus* reaches to the Laptev Sea, just beyond the Taymyr Peninsula.

The presence of *M. striatus* on the shores of Iceland, Norway, Spitsbergen and Novaya Zemlya, so much farther north than in the western Atlantic, can be explained by the effects of the Gulf Stream and North Atlantic Current, and its extension, the Norwegian Coast Current. On the west coast of Greenland the warm West Greenland Current, and extension of the westward-turning gyre of the North Atlantic Current permitted the establishment of *M. striatus* as far north as Disko. The absence of *M. striatus* on the east coast of Greenland is due to the influence of the cold East Greenland Current coming from the Arctic.

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Two New Species of *Chicoreus* Subgenus *Siratus* (Gastropoda: Muricidae) From Northeastern Brazil

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ABSTRACT

Two new species of muricid gastropods are described herein from the vicinity of Salvador, Bahia, Brazil. Both forms have been known for some time but have been misidentified in the literature. *Chicoreus* (*Siratus*) *carolynae* has been identified as "*Murex chrysostoma* Sowerby," but differs in having a deflected siphonal canal. *Chicoreus* (*Siratus*) *coltrorum*, has been identified as "*Murex consuela* (Verrill)," but differs in having a paucispiral protoconch.

Key words: Muricidae; Gastropoda; *Chicoreus*; *Siratus*; Brazil

INTRODUCTION

Most authors (*e.g.*, Abbott, 1974; Rios, 1970, 1975, 1980) have identified mollusks from eastern Brazil by the names of well known Caribbean species. In some cases, these identifications are proving to be incorrect. In this paper two previously misidentified species of muricid gastropods are described.

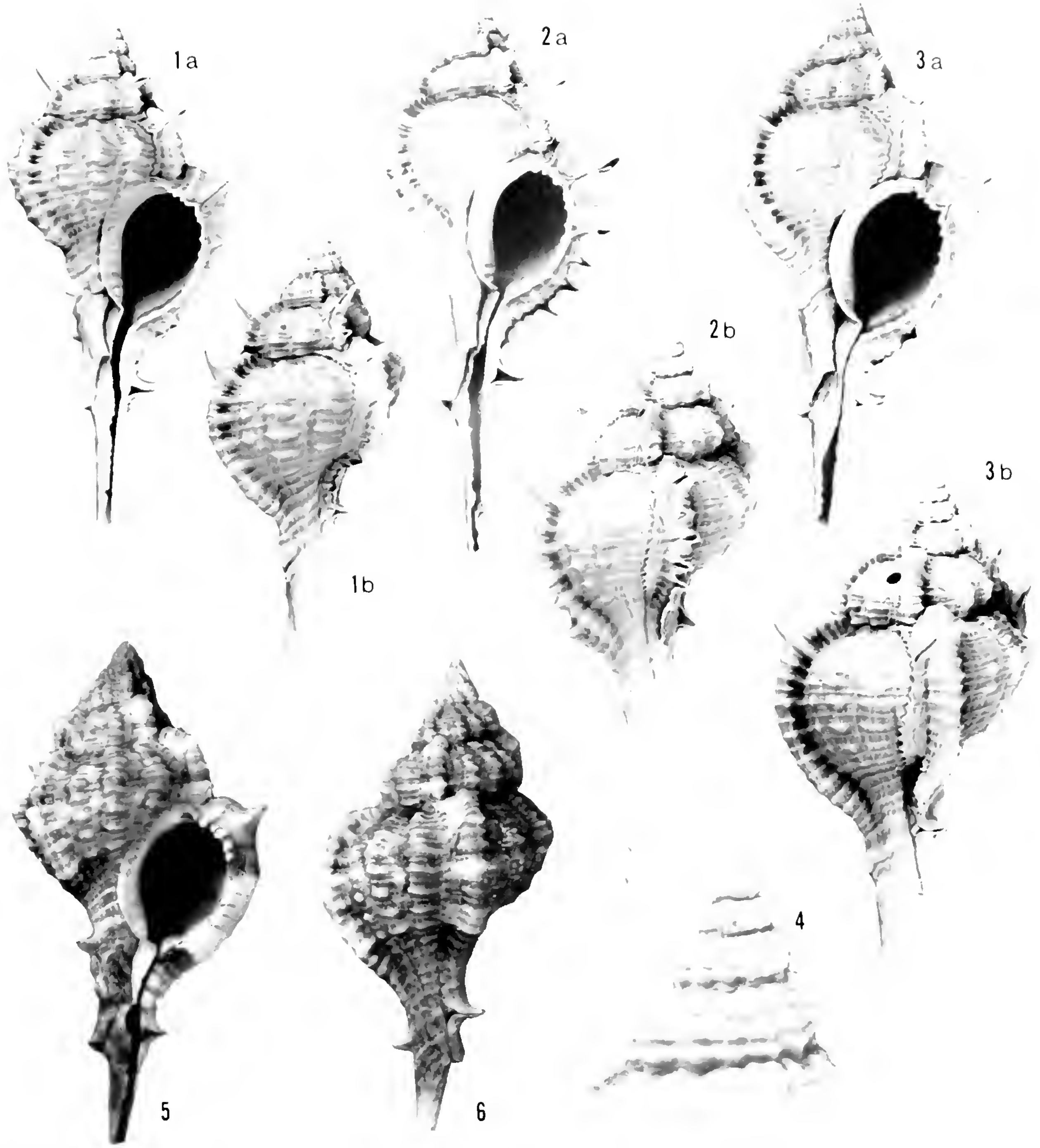
One of these, described herein as *Chicoreus* (*Siratus*) *carolynae*, is of particular interest as it demonstrates the close relationship, not well understood heretofore, between members of *Haustellum* Schumacher, 1817, and *Siratus* Jousseaume, 1880. When I first began studying the Muricidae of the western Atlantic (Vokes, 1963) I assigned all species with three spinose varices and a long siphonal canal to *Murex sensu stricto*. Within this group, I separated two subgroups: the "Indo-Pacific" form, with a straight siphonal canal; and the "Western Atlantic" form, in which the canal was deflected dorsally (see figure 1b). Further work on the family (Vokes, 1965) convinced me that the latter group should be taken out of *Murex* and transferred to the subgenus *Siratus*, which I felt was better placed within the genus *Chicoreus*, leaving only those species with a long *straight* canal in the genus *Murex*.

More recent work on the genus *Murex* in the Indo-west Pacific (Ponder and Vokes, 1988) disclosed that there are certain morphological differences between *Murex* and *Haustellum*, including the presence of a labral tooth in species of *Murex* but not in *Haustellum*, the presence of rugae on the parietal lip in species of *Haustellum* but not in *Murex*, as well as differences in early teleoconch ornamentation, color pattern, and other features. This convinced me that not only the three spinose varices present in both *Murex* and *Siratus* but also the long straight canal in *Murex* and *Haustellum* are a result of convergence. The ultimate conclusion brought about by work on the Indo-Pacific species of *Murex* and *Haustellum* was the somewhat disturbing realization that there are *no* species of *Murex* in the Western Hemisphere (with one possible exception—*Murex surinamensis* Okutani, 1982) and that all the western Atlantic "Indo-Pacific" forms of *Murex* (*sensu* Vokes, 1963) are actually to be placed in the genus *Haustellum*.

This shift in nomenclature was corroborated by work done on the fossil muricids of the Dominican Republic (Vokes, 1989), where one sees two species that are so similar as to be very difficult to distinguish—except that one (*Murex messorius* Sowerby, 1841) has a straight siphonal canal and is assigned to *Haustellum* and the other (*Murex domingensis* Sowerby, 1850) has a deflected canal and is assigned to *Siratus*. I believe that the similarities seen in these two species transcend convergence and reflect close phylogenetic affinity.

On the basis of the geologic history of the two groups, it seems probable that the New World species, which are taxonomically separated into two distinct genera—*Haustellum* and *Chicoreus*, are much more closely related to each other than either is to true *Murex*. Nowhere is this more obvious than in the species described below, which has heretofore been identified as *Haustellum chrysostoma*, or a variety thereof, but which is here placed in the subgenus *Siratus*. Perhaps the strongest similarity between *H. chrysostoma* and *C.* (*S.*) *carolynae*, n. sp., is the color pattern, in which the *Siratus* species repeats the typical brown and white striped pattern of many species of *Haustellum*.

This color pattern is just one of the many characters that is used to separate *Haustellum* from *Murex*. The true species of *Murex* are usually monochromatic cream or tan in color, have a distinct labral tooth and a smooth parietal lip. Species of *Haustellum*, and of *Siratus* usually have brown and white spiral bands, no labral tooth, and



Figures 1–6. *Chicoreus* (*Siratus*) *carolynae*, n. sp. (× 1½). **1.** USNM 860504 (holotype); height 52.8 mm, diameter 24.4 mm, Ilha de Itaparica, Bahia. **2.** USNM 860505 (paratype 1): height 56.0 mm, diameter 24.5 mm, Ilha de Itaparica, Bahia. **3, 4.** USNM 860505 (paratype 2): height 53.8 mm, diameter 27.0 mm (figure 4, × 10), Ilha de Itaparica, Bahia. **5.** MORG 20.748 (paratype 3); height 49.6 mm, diameter 25.3 mm, Itapuã, Bahia. **6.** MORG 22.129 (paratype 4); height 47.6 mm, diameter 23.2 mm, Yacht Club, Salvador, Bahia; 10 m. All specimens collected dead, all except that in figure 6 at low tide. Specimens in figures 1–4 whitened to show details of ornamentation.

a rugose parietal lip. In addition, in those species of *Haustellum* with relatively well-developed varical spines (*e.g.*, *Haustellum kiiensis* [Kira, 1959]) there is a tendency to develop webbing between the spines. This is carried to its fullest extreme in *Siratus*. The only difference between *Haustellum* and *Siratus* is the presence of a straight *vs.* a deflected siphonal canal. In other words, what I was attempting to distinguish in 1963 was not two groups of *Murex* but *Haustellum* and *Siratus*!

In the second species, described below as *C.* (*S.*) *col-*

trorum, we have a more straightforward case of two superficially similar forms, with the Brazilian species having previously been misidentified as *C.* (*S.*) *consuela*. These two species differ primarily by the nature of the protoconch. A similar case has also been discovered in the two similar appearing, and often synonymized, species *Chicoreus* (*Phyllonotus*) *pomum* (Gmelin, 1791) and *C.* (*P.*) *oculatus* (Reeve, 1845) that may be unequivocally distinguished by different types of protoconchs (Houart, 1987). Throughout the Muricidae the nature of the protoconch is extremely stable, and is the best means of distinguishing similar appearing species (Ponder and Vokes, 1988, p. 3).

SYSTEMATIC DESCRIPTIONS

Class **Gastropoda**
Family **Muricidae** Rafinesque, 1815
Subfamily **Muricinae** Rafinesque, 1815
Genus *Chicoreus* Montfort, 1810

Chicoreus Montfort, 1810, Conchyl. Syst., v. 2, p. 611.

Type species: *Murex ramosus* Linn., 1758, by original desig.

Subgenus *Siratus* Jousseaume, 1880

Siratus Jousseaume, 1880, Le Naturaliste, Année 2, no. 42, p. 335

Type species: "*Purpura sirat*" Adanson (= *Murex senegalensis* Gmelin, 1791), by original desig.

Chicoreus (*Siratus*) *carolynae*, n. sp.
Figures 1–6

Murex chrysostoma Sowerby, var.? Rios, 1970, Coastal Brazilian Seashells, p. 77, pl. 21; Rios, 1975, Brazilian Marine Mollusks Icon., p. 84, pl. 24, fig. 339

Murex chrysostoma Sowerby. Rios, 1985, Seashells of Brazil, p. 81, pl. 29, fig. 354 (*not* of Sowerby).

Description: Shell with seven teleoconch whorls. Protoconch of one and one-half rounded whorls with a small keel adjacent to the suture, ending at a sharp varix. Spiral ornamentation on early teleoconch whorls of three to five indistinct cords, best seen where crossed by axial ridges. Number of axial cords increasing gradually. Body whorl ornamented by six to eight cords, alternating with weaker secondary cords. In some cases, weaker tertiary threads present. Cord at shoulder somewhat stronger than others. Six to eight relatively weak cords on siphonal canal, some alternating with tertiary threads. Axial ornamentation on earliest teleoconch whorls of twelve rounded ridges per whorl. Beginning at fourth teleoconch whorl every fourth ridge strengthened into a small rounded varix. Remaining ridges persisting as intervarical nodes. Number of intervarical nodes between each pair of varices sometimes decreased to only two on latest teleoconch whorls but most commonly three present on all whorls. Three varices per whorl beginning on approximately sixth teleoconch whorl and persisting to adult stage. Raised ridges formed at intersection of spiral cords and varices. Small spines developed on varices only at shoulder and juncture of body whorl and siphonal canal. Rarely a small flange along the outer margin of the anterior portion of the varix. Aperture elongate-oval, parietal lip appressed at posterior end, free-standing at anterior end, with one strong anal tooth at posterior end and several rugae over entire length, but stronger on anterior half. Margin of outer lip scalloped by spiral cords, with a notch at intersection of each cord and edge of lip. Deeper notches corresponding to stronger cords. Anterior half of margin extended more adaperturally than posterior half. At meeting of spiral cords and axial ridges small elongate welts raised on top of ridges, giving entire surface of intervarical area a nodulose appearance. Siphonal canal long, narrow, almost sealed, open only by a narrow slit. Siphonal canal deflected dorsally, with terminations of former canals remaining as a series of spurs surrounding base of body whorl. Color ranging from white to tan with brown spiral bands. Brown band at shoulder and base of body whorl darker. On margin of outer lip a dark spot of brown staining each notch formed by spiral cords. Operculum reddish-brown, typically muricine with a terminal nucleus.

Holotype: USNM 860504; height 52.8 mm, diameter 24.4 mm (figure 1).

Paratype 1: USNM 860505; height 56.0 mm, diameter 24.5 mm; type locality (figure 2).

Paratype 2: USNM 860505; height 53.8 mm, diameter 27.0 mm; type locality (figures 3, 4).

Paratype 3: MORG No. 20.748; height 49.9 mm, diameter 25.3 mm; Itapuã, Bahia, low tide. Coll. L. C. Araújo, 1975 (figure 5).

Paratype 4: MORG No. 22.129; height 47.5 mm, diameter 23.2 mm; Yacht Club, Salvador, Bahia, 10 m depth. Coll. Bernardo Linhares, 1982 (figure 6).

Paratype 5: MORG No. 8016; height 45.3 mm, diameter 22.9 mm; Bahia, 13 m depth. Coll. B. Tursch, 1962 (Rios, 1970, pl. 21, *M. chrysostoma* var.?—apertural view only; 1975, pl. 25, fig. 339; 1985, pl. 29, fig. 354).

Other material studied: Five unfigured paratypes: MORG No. 8016; height 59.8 mm, diameter 28.7 mm; Bahia, 13 m. MORG No. 20.748; specimen *a*, height 47.0 mm, diameter 23.4 mm; specimen *b*, height 40.4 mm, diameter 22.3 mm; specimen *c*, height 36.9 mm, diameter 19.8 mm; Itapuã, Bahia, at low tide. MORG No. 22.129; height 53.3 mm, diameter 26.5 mm; Yacht Club, Salvador, Bahia 10 m. Also 14 additional specimens collected by Carolyn Voss, from type locality.

Type locality: Ilha de Itaparica, Bahia, at low tide.

Discussion: This species has been figured by Rios as *Murex chrysostoma* Sowerby, 1834, var.? (1970, 1975) and later as *Murex chrysostoma*. In the first two editions he correctly identified true *Haustellum chrysostoma*

(1970, pl. 20; 1975, pl. 24, fig. 338) but in the third edition (1985) he changed this identification to *Murex messorius* Sowerby, 1841 (1985, p. 81, pl. 29, fig. 355) and changed the former "*Murex chrysostoma* var.?" to *Murex chrysostoma* (1985, p. 81, pl. 29, fig. 354), indicating the reason for the change was that *M. chrysostoma* may be "distinguished from *messorius* by the radular teeth." This statement is based upon a mix-up of illustrations in an otherwise excellent study of the muricid species found on the coast of Venezuela by Gonzalez and Flores (1972). In this work they illustrate (figure 9-c) a thaidine radula (probably *Thais haemastoma*) as "*Murex chrysostomus*." It appears very different from the radula of *Murex messorius*. There is no difference between the radulae of *M. messorius* and *M. chrysostoma*, both are typically muricine. Gonzalez and Flores have also illustrated as the radula of *Murex donmoorei* Bullis, 1964 (their figure 9-b), another thaidine radula. It would appear that two illustrations have been switched, their figures 9 and 2, for the latter shows as rachidian teeth of *Thais deltoidea*, *T. rustica*, and *T. haemastoma floridana*, three illustrations of muricine radulae (presumably *Murex* cf. *messorius*, *M. donmoorei*, and *M. chrysostoma*, as indicated for figure 9).

Although confounded with *Haustellum chrysostoma* by Rios, the two forms bear only a general resemblance to each other, in that both have three essentially nonspinose varices, a long siphonal canal, and brown color bands. The closest relationship is actually with the members of the group of *C.* (*S.*) *motacilla* (Gmelin, 1791), *C.* (*S.*) *cailleti* (Petit de la Saussaye, 1856), and *C.* (*S.*) *cailleti kugleri* (Clench and Pérez Farfante, 1945). These three closely related forms have been well figured by Clench and Pérez Farfante (1945: pl. 9, figs. 1, 2, *C. cailleti* form *kugleri*; figs. 3, 4, typical *C. cailleti*; and figs. 5, 6, *C. perelegans* Vokes, 1965 [new name for *Murex elegans* Sowerby *non* Donovan], not *C. cailleti*, as indicated; and pl. 11, *C. motacilla*). This new species differs from *C. motacilla* in being more slender, with a narrower siphonal canal and with usually three weaker intervarical nodes between each pair of varices, in contrast to the invariably two, strong nodes seen in *C. motacilla*. In this respect, *C. carolynae* more nearly resembles *C.* (*S.*) *cailleti* form *kugleri*, which in the early whorls usually has four intervarical nodes between each pair of varices. This number decreases to only two in the adult stage, as in typical *C. cailleti* and *C. motacilla*. Again, the differences between *C. carolynae* and *C. kugleri* are the more slender body and less deflected siphonal canal in *C. carolynae*.

This new species is known to occur only in the State of Bahia, Brazil, in shallow water. In addition to the type material, Rios has reported it from Ponta Jaburu, in 7 fms (10 m), and Pôrto da Barra, noting that it lives on sandy bottoms. He suggests that it is "perhaps a shallow water form" of *H. chrysostoma* (1970, p. 77). In the latest edition (1985, p. 81) he states that the species is dredged from 18 to 90 m on sandy bottoms, but this may reflect confusion with true *H. chrysostoma*. All type material was collected in water shallower than 10 m, but most of it was beach material inhabited by hermit-crabs, and consequently the living depth is unknown.

Chicoreus (*Siratus*) *coltrorum*, n. sp.

Figures 7–13

Murex (*Murex*) *pulcher* Adams. Clench, 1959, Johnsonia, v. 3, no. 39, p. 333

[?] *Murex* (*Murex*) *consuelae* Verrill. Bullis, 1964, Tulane Stud. Zoology, v. 11, no. 4, p. 103

Murex (*Murex*) *pulcher* Adams. Rios, 1970, Coastal Brazilian Seashells, p. 77, pl. 20

Siratus consuela (Verrill). Rios, 1975, Brazilian Marine Mollusks Icon., p. 84, pl. 24, fig. 342

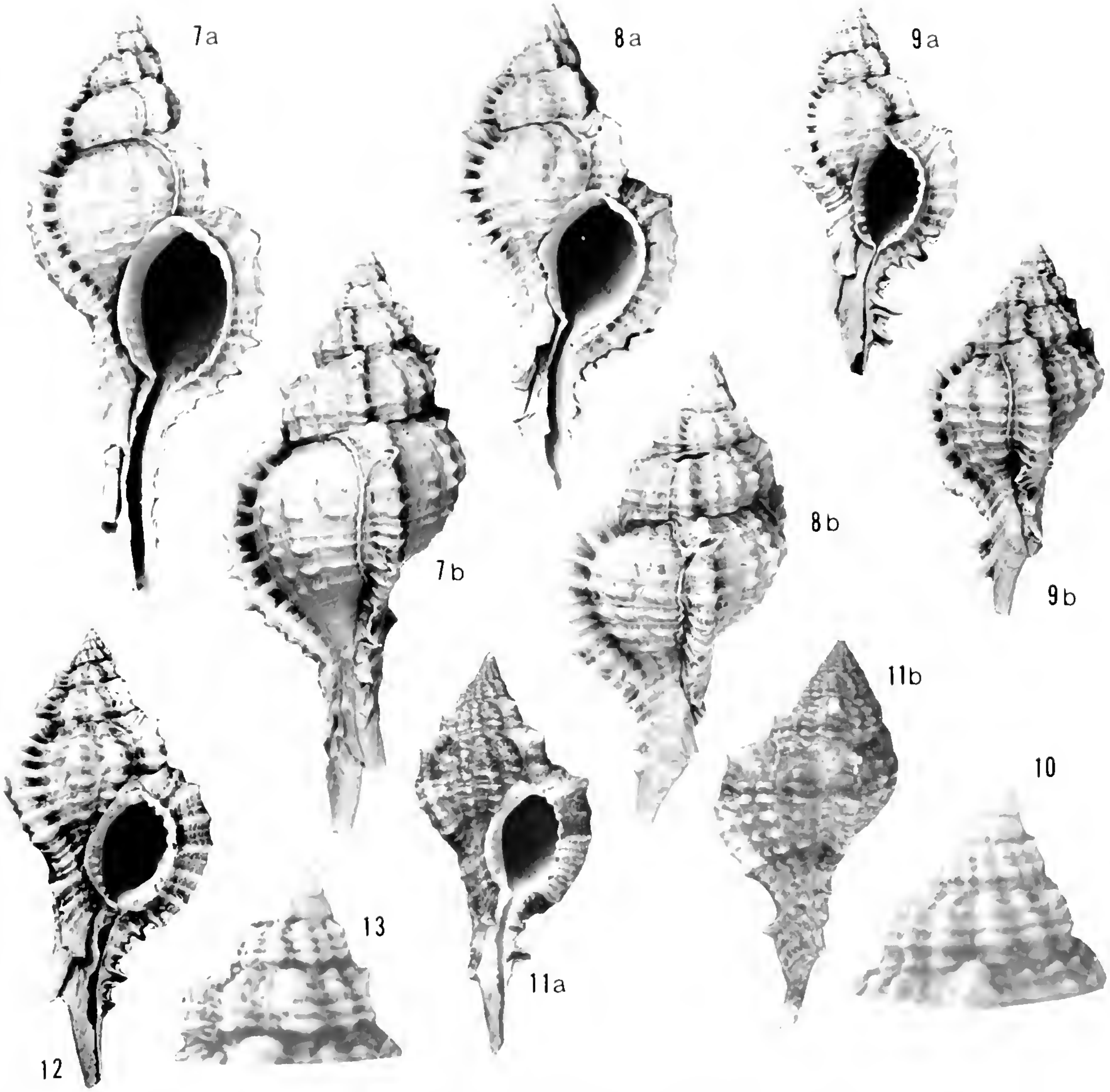
Murex (*Murex*) *consuelae* (Vokes) [*sic*]. Rios, 1985, Seashells of Brazil, p. 82, pl. 29, fig. 357.

Description: Shell with seven teleoconch whorls. Protoconch of one and one-half bulbous whorls, ending at a small, sharp varix. Suture deeply impressed. Spiral ornamentation on earliest teleoconch whorls of three small cords. A fourth cord and intermediate secondary cords gradually appearing on shoulder ramp. On body whorl eight major cords present, plus an additional four or five on siphonal canal, each pair separated by a secondary thread. Axial ornamentation on earliest teleoconch whorls of about 12 small ridges, forming nodes at intersection with spiral cords. On approximately fourth teleoconch whorl every fourth ridge enlarging into a small, rounded varix. Other three remaining as intervarical ridges between each pair. These persisting up to body whorl, most adapertural ridge sometimes weaker than other two. On about fifth teleoconch whorl small open spines developed on shoulder, at juncture of spiral cord and varices. In intervarical area, at intersection of spiral cords and axial ridges, small elongated nodes produced, two nearest to spiral cord at shoulder often fused into one larger node. Raised welts at crossing of spiral cords over varices, corresponding in size to strength of cord. A small flange sometimes produced on anterior portion of varices but not extending onto siphonal canal. The latter, instead, with usually two small open spines. Aperture elongate-oval. Parietal lip free-standing at anterior end, appressed at posterior end with a large anal tooth. Several rugae along entire length of parietal lip but stronger on its anterior half. Margin of outer lip crenulated by termination of spiral cords, inner side of outer lip with a series of elongate, often paired lirae. Siphonal canal long, almost straight, distal end deflected dorsally. Siphonal canal almost sealed, open only by a narrow slit. Color white to orange to tan with two darker brown spiral bands, one at periphery and one at base of body whorl. Operculum unknown.

Holotype: MORG No. 20.749; height 54.0 mm, diameter 22.4 mm (figure 7).

Paratype 1: MORG No. 20.749A; height 45.2 mm, diameter 21.1 mm; type locality (figure 8).

Paratype 2: MORG No. 15.203; height 28.7 mm, diameter 14.1 mm; off Recife, Pernambuco, 100 m. R. V



Figures 7–11. *Chicoreus* (*Siratus*) *coltrorum*, n. sp. **7.** MORG 20 749 (holotype); height 54 0 mm, diameter 22.4 mm (× 1½), Ilha de Itaparica, Bahia **8.** MORG 20 749A (paratype 1); height 45 2 mm, diameter 21.1 mm (× 1½), Ilha de Itaparica, Bahia **9, 10.** MORG 15 203 (paratype 2); height 28 7 mm, diameter 14 1 mm (figures 9a, 9b, × 2, figure 10, × 10), Recife, Pernambuco, 100 m. **11.** USNM 860506 (paratype 3); height 30.6 mm, diameter 14 2 mm (× 2), Ilha de Itaparica. Bahia. Except for specimen in figures 9, 10, all specimens taken dead at low tide **Figures 12, 13.** *Chicoreus* (*Siratus*) *consuela* (Verrill) Vokes Coll.; height 46.3 mm, diameter 20 0 mm (figure 12, × 1½; figure 13, × 10), Soufrière, Dominica, West Indies; 30–40 fms (54–73 m) in fish-trap). All specimens except specimen in figure 11 whitened to show details of ornamentation

Almirante Saldanha, 1968; specimen figured by Rios, 1970, pl. 20 (back view) (figures 9, 10).

Paratype 3: USNM 860506; height 30.6 mm, diameter 14.2 mm; type locality (figure 11).

Paratype 4: MORG No. 15.082; height 29 mm, diameter 15 mm; off Recife, Pernambuco; specimen figure by Rios: 1970, pl. 20 (apertural view); 1975, pl. 24, fig. 342; 1985, pl 29, fig 357.

Other material studied: Six unfigured paratypes. MORG No. 20.749; specimen *a*, height 53.0 mm, diameter 24.9 mm; specimen *b*, height 43.0 mm, diameter 20.7 mm; type locality. MORG No. 11.234; specimen *a*, height 38.2 mm, diameter 18.0 mm; specimen *b*, height 34.4 mm, diameter 15.2 mm; Pôrto da Barra, Salvador, Bahia. MORG No. 19.315; specimen *a*, height 40.9 mm, diameter 18.6 mm; specimen *b*, height 36.5 mm, diameter 16.4 mm; type locality. Plus eight additional specimens collected by José and Marcos Coltro, from type locality, and one collected by them from Guarapari, Espírito Santo.

Type locality: Ilha de Itaparica, Bahia, at low tide.

Discussion: As is obvious from the synonymy given above, this species has been considered to be the form originally described as *Murex pulcher* A. Adams, 1853. This taxon is preoccupied by *Murex pulcher* Sowerby, 1813, and DeFrance, 1827, and the next available name is *Murex consuela* Verrill, 1950. The Brazilian species is a similar-appearing form that differs, however, in one critical feature—the protoconch is markedly different.

Both *C. consuela* and *C. coltrorum*, n. sp., are presumed to be descendants of *C.* (*S.*) *eumekes* Vokes, 1989, described from the Mio-Pliocene Gurabo Formation of the Dominican Republic. This fossil species has a protoconch consisting of three and one-half whorls; *C. consuela* has a protoconch of two and one-quarter whorls (see figure 12) and the Brazilian species has a protoconch of one and one-half whorls (see figure 10). Inasmuch as the usual trend in the Muricidae is to decrease the number of whorls through time, implying a change in reproductive strategy from planktotrophic to lecitrophic to direct development, this decrease would suggest that the Brazilian species is the most recent offshoot from the ancestral line.

With the exception of the protoconch, the differences between *C. consuela* and *C. coltrorum* are minimal. One other noticeable difference is the suture, which is more impressed in *C. coltrorum*, causing the individual whorls to appear more rounded and distinct than in *C. consuela*. In *C. coltrorum* the siphonal canal is narrower, less deflected dorsally, and does not develop the flange that is seen in *C. consuela*. The development of the varices on the early whorls in *C. coltrorum* differs in that no varices appear until the fourth teleoconch whorl and no spines are produced on these varices until the fifth whorl. In contrast, in *C. consuela* the pattern develops one whorl earlier, *i.e.*, varices on third teleoconch whorl and spines on fourth whorl.

In the Pleistocene and Recent faunas of the Caribbean *C. consuela* is widespread, occurring in the Pleistocene Moín Formation of Costa Rica, and in the Recent fauna from off the coast of Texas (Houston Mus. Nat. Sci., from Flower Garden Banks) to Curaçao (de Jong and Coomans, 1988, p. 71), but most commonly in the Lesser Antilles, usually in depths of 70 to 100 m.

The new species seems to be restricted to the coast of northeastern Brazil from the islands off Rio Grande do Norte as far south as Espírito Santo. Rios (1975, p. 84) has reported it from Atol das Rocas, Fernando de Noronha, off Recife, Pernambuco, and off Vitoria, Espírito Santo, in depths from 35 to 100 m. Except for Rios' figured specimen (paratype 2) from 100 m, most of the type lot was collected at low tide, and consists of shells occupied by hermit-crabs.

Clench (1959, p. 333) reported "*Murex* (*Murex*) *pulcher*" from about 30 km off northernmost Bahia, in 40 fms (= 73 m). His specimen (MCZ 164967) unfortunately lacks the critical protoconch, but otherwise is identical to Rios' figured specimen (paratype 2, herein), and, given the locality there seems little doubt about the reference to the new species.

Bullis (1964, p. 103) has also reported "*Murex* (*Murex*) *consuelae*" from about 300 km east of Ilha de Maracá, Amapá, just north of the mouth of the Amazon, in 53 fms (= 97 m). This specimen cannot be located in the U.S. National Museum and given its locality, north of the Amazon, is only questionably included.

ACKNOWLEDGEMENTS

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ABBREVIATIONS OF REPOSITORY COLLECTIONS

MCZ—Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA.
MORG—Museu Oceanográfico, Fundação Universidade do Rio Grande, Rio Grande do Sul, Brazil.
USNM—U.S. National Museum of Natural History, Washington, D.C., USA.

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Distorsio ridens (Reeve, 1844): A Synonym of *Distorsio clathrata* (Lamarck, 1816) (Gastropoda: Personidae)

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ABSTRACT

A reevaluation of the identity of *Distorsio ridens* (Reeve, 1844), suggests that this taxon was based on specimens of two New World species having erroneous locality data, and we conclude that this taxon is a junior subjective synonym of *Distorsio clathrata* (Lamarck, 1816). We correct the erroneous type locality of *D. ridens* and select Key West, Florida as the type locality.

INTRODUCTION

We were recently asked to identify specimens of two species of *Distorsio* obtained by commercial fishermen trawling off Somalia in deep water. As a result of this study, we found that a reexamination of the status of *Distorsio ridens* (Reeve, 1844) was in order before we could proceed with our review of the Somalian specimens. This paper is a result of our investigation.

It should be noted in passing, that the genus *Distorsio* and related genera were recently removed from Ranellidae Gray, 1854 (= Cymatiidae Iredale, 1913) and awarded familial recognition, Personidae Gray, 1854, as a sixth family of Tonnoidea by Beu (1988).

HISTORICAL REVIEW OF *DISTORSIO RIDENS*

Triton ridens Reeve (1844a, pl. 12, *Triton* sp. 46) was briefly described in both Latin and English texts and was illustrated by a colored lithograph executed by G. B. Sowerby, 2nd. Only an apertural view was presented of the figured specimen, which was said to be from the Philippine Islands and collected by Hugh Cuming. Reeve compared *T. ridens* with "*Murex cancellinus* de Roissy", (1805:56, 57; see Emerson & Puffer, 1953:97), which is now recognized as a junior synonym of the Indo-Pacific *Distorsio reticularis* (Linné, 1758); see Beu (1987:314). Some seven months later, the same description, together with the remarks in a slightly altered form, appeared without an illustration in the Proceedings of the Zoological Society of London (Reeve, 1844b:115). This taxon, therefore, dates from the original description in Conchologia Iconica (Reeve, 1844a).

Unfortunately, subsequent workers have confused Reeve's taxon with other earlier or later described congeners from several biogeographical faunal provinces. The resulting taxonomic vicissitudes have caused a general disagreement on the identity of *D. ridens*. For example, Reeve's figured specimen was reproduced by Tryon (1880:35, pl. 17, fig. 177) as "*Distorsio cancellinus* Roissy" and by Wagner and Abbott (1978:12–802, fig. 13–116) as "*Distorsio reticulata* Röding". The questionable identity of *Distorsio ridens* has resulted in this name being misapplied to *D. smithi* von Maltzan, 1844, from West Africa, by Nicklés (1950:86, fig. 133), to *D. perdistorta* Fulton, 1938, from Japan, by Oyama (1958: pl. 1, figs. 7, 8), to *D. reticulata* (Röding, 1798) [= *D. reticularis* Linné, 1758] from the Philippines, by Emerson and Puffer (1953:103); Puffer (1953:114); Springsteen (1984:5; 1985:3); Springsteen and Leobrera (1986:117), and to *D. decussata* Valenciennes, 1832, from the eastern Pacific, by Beu (1985:62) and Parth (1989:54).

Lewis (1972:47, 48, figs. 45–48) discussed at length the status of *Distorsio ridens* and accorded this taxon full specific recognition on the basis of the data then available to him. For *D. ridens*, he selected and illustrated a lectotype, provided photographs of a paralectotype, and found this taxon to be separable from *D. reticularis*, *D. perdistorta* and *D. decussata*. He did not compare *D. ridens* with *D. clathrata* (Lamarck) from the western Atlantic. Wolfe (1976:12) and Springsteen (1981:8) also considered *D. ridens* a distinct species.

REEVALUATION OF THE IDENTITY OF *DISTORSIO RIDENS*

In our view, two factors have been largely responsible for the misinterpretation of *D. ridens*. First, was the lack of a dorsal view of the specimen figured by Reeve (1844a). As a result, the nature of the sculpture on the dorsum could not be determined with certainty from the illus-


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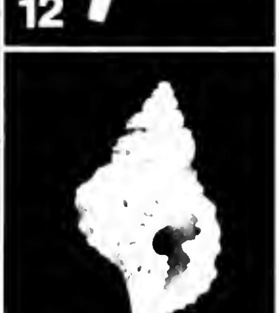
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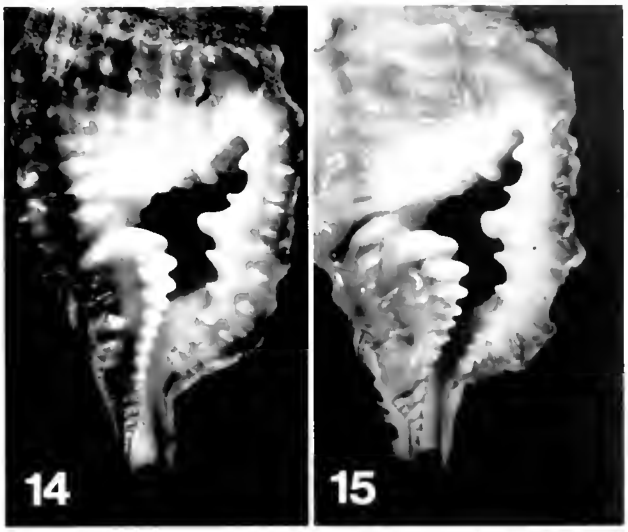

Figures 14, 15. *Distorsio clathrata* (Lamarck, 1816), aperture enlarged to show bifid tooth of the primary columellar pica. **Figure 14.** Specimen illustrated in figure 4. **Figure 15.** Lectotype illustrated in figure 2.

tration or from the brief description. Second, is the general acceptance of the validity of the type locality, the Philippine Islands. This has led most reviewers to limit comparisons with Indo-Pacific species. We shall expand on these subjects.

Lewis (1972:48) searched the collection of the British Museum (Natural History) for potential syntypes of *D. ridens*. He could not locate the specimen figured by Reeve (1844a: pl. 12, sp. 46). Therefore, he selected a specimen in the collection of the American Museum of Natural History (AMNH) which he stated "... so very closely matches Reeve's figure that I feel it is reasonable to designate it as the lectotype" (Lewis, 1972:48, fig. 48). The specimen (AMNH 6369), labeled "Philippines", was from the William A. Haines Collection, received by the Museum in 1879. Haines (1822–80), who was a member of the AMNH Board of Trustees in the decade before his death, was a colleague of the New York conchologist, John C. Jay (1808–91). He could have obtained the specimen from Jay or perhaps from England directly from Lovell A. Reeve (1814–65) or Hugh Cuming (1791–1865), who is known to have been a dealer in shells (*cf*. Lewis, 1972:48). The source of Haines' specimen, however, is not known, for the AMNH catalog entry lacks such data.

We agree with Lewis' conclusion (1972:48) that the specimen designated by him as the lectotype of *D. ridens* closely resembles the morphological features of the specimen figured by Reeve (1844a); see figures 1–3. Lewis noted some differences in the artist's depiction of the apertural morphology. He attributed to artistic exaggerations the distorted representation of the second row of plicae on the lower left parietal shield and the extravagant manner shown for the character of the groove on the lower shield at the point of entry into the aperture. These apparent morphological discrepancies may reflect a composite drawing based on more than one specimen, most likely representing different species in the type lot. Reeve's drawing, however, illustrates well the major columellar plica as a bifid tooth, a character not uncommonly found in specimens of *D. clathrata* (*cf*. figures 1, 14, 15). The wide groove shown entering the aperture below the parietal shield is, however, more reminiscent of *D. decussata* (*cf*. figures 1–3 with figures 10, 12). It is our conclusion that the specimen of *D. ridens* illustrated by Reeve (1844a; figure 1, herein), together with the specimen designated the lectotype (AMNH 6369) by Lewis (figures 2, 3, herein), and the paralectotype figured by Lewis (1972: figs. 45, 46), are all referable to *D. clathrata* (Lamarck, 1816: pl. 413, figs. 4a, 4b, Liste p. 4).

At this point, it should be mentioned that a more inflated, lower spired, and shorter canalled morph of *D. clathrata* was named *D. robinsoni* by Petuch (1987:64, 65, pl. 11, figs. 3, 4), on the basis of a few specimens from Honduras and Brazil. An examination of a large series of specimens in the AMNH collection from North Carolina to the Gulf of Mexico and in the Caribbean region, including Honduras, indicates that *D. robinsoni* is an infrasubspecific form that appears in the samples of the typical form of *D. clathrata* (*cf*. figures 4, 5 with figures 8, 9). Also, see comments on *D. robinsoni* Petuch by Parth (1989:52, fig. 1, right) and Manoja (1989:29).

We subsequently were able to examine personally the three paralectotypes of *D. ridens* remaining in the British Museum (Natural History; Registry number 1967630, Acquisition number 1829, "H. Cuming Collection, Philippines"). Two of these specimens are referable to *D. clathrata*; the smaller one measures 70.8 mm in height (figures 6, 7), and the larger specimen (Lewis, 1972: figs. 45, 46) measures 78.6 mm in height (apical whorls are lost). The third paralectotype is referable to *D. decussata* (figures 10, 11). It measures 62.2 mm in height, essentially the same as the height of Reeve's (1844a) figured specimen, which measures 63.1 mm in height. The specimen designated the lectotype by Lewis (1972:48; fig. 48) is also close to the height of Reeve's figured specimen,

←

Figures 1–9. *Distorsio clathrata* (Lamarck, 1816). **Figure 1.** Copy of original illustration of *Triton ridens* Reeve (1844a, *Triton* sp. 46). **Figures 2, 3.** Lectotype of *Distorsio ridens* (AMNH 6369), W. A. Haines Collection. **Figures 4, 5.** A specimen with orange-pigmented shield and outer lip as in the lectotype, trawled off Punta Patuca, Atlantic Honduras, in 18 to 27 meters (AMNH 238556), ex E. García Collection. **Figures 6, 7.** Paralectotype of *D. ridens* [BM(NH) 1967630]. **Figures 8, 9.** Specimen of morph *robinsoni* Petuch, 1987, from same lot as the specimen illustrated by figures 4, 5. **Figures 10–13.** *Distorsio decussata* (Valenciennes, 1832). **Figures 10, 11.** Paralectotype of *D. ridens* [BM(NH) 1967630]. **Figures 12, 13.** Paralectotype of *D. ridens* (MCZH 186600). All ×1.

measuring 64.3 mm (tip of the siphonal canal is broken) *vs.* 63.1 mm. We suspect that Reeve's figured specimen may be a composite drawing based on specimens of *D. clathrata* and *D. decussata* in the type lot. However, we cannot be certain that the three paralectotypes in the British Museum (Natural History) actually were the specimens available to Reeve at the time he described *D. ridens*. One of the label scraps accompanying the type specimens reads: "St. Johns [?= Saint Johns, Antigua, 17°06"N, 61°51"W], Mr. Hartvig". Thus, at least one of the three specimens forming the paralectotype lot in the British Museum (Natural History) may have been added after the taxon was described. Furthermore, there is a paralectotype in the Museum of Comparative Zoology, Harvard University (186600) labeled "*Triton ridens* Reeve, Philippine Islands, H. Cuming, C. B. Adams Coll., exch. Amherst College, 1942, Acc. 1173". This specimen, which measures 37.1 mm in height, is referable to *D. decussata* (see figures 12, 13), as Lewis (1972:48) has pointed out.

It should be noted that the taxa, *D. decussata* (Valenciennes, 1832) and *D. clathrata* (Lamarck, 1816), were not recognized by Reeve (1844a,b). He does not mention Valenciennes' taxon and he refers "*Triton clathratus*, Lamarck" to the synonymy of "*Murex cancellinus* De Roissy", which is a junior synonym of *Distorsio reticularis* (Linné, 1758; see Beu, 1987:314). Reeve apparently confused Lamarck's *D. clathrata* with *D. reticularis* from the Indo-Pacific and did not recognize the presence of *D. clathrata* in the Western Atlantic.

Therefore, it is clear that the type locality of *D. ridens*, "Philippine Islands, Cuming", is in error. Although Hugh Cuming is known to have collected extensively in the Philippine Islands (1836–40) and on the west coast of South America (1828–30), he apparently did not collect in the Caribbean region (Dance, 1986:111–131). He most certainly, early in his career, however, had access to common marine shells of the western Atlantic by exchanges. (He is pictured with a Caribbean shell in a photograph taken *ca.* 1861, Dance, 1986: pl. 25). As others have pointed out (Clench, 1945; Dance, 1986), much of the material in the Cuming collections was accompanied by mislocalized data. This would seem to be the case for *D. ridens*, as all of the type specimens represent New World species. We here correct the type locality of *D. ridens* and select Key West, Florida as the type locality.

In summary, we must address the question: should *D. ridens* be placed in the synonymy of *D. clathrata* from the western Atlantic or *D. decussata* from the eastern Pacific? As we have noted, Reeve's (1844a) figured specimen more closely resembles the apertural characters of *D. clathrata* than those of *D. decussata*, although the drawing may represent a composite based on specimens of both species. Furthermore the description (Reeve, 1844a,b) states that the ". . . transverse ridges [are] duplicate . . .", suggesting the presence of a double row of spiral cords at the periphery of the whorls, a morphological feature common to *D. decussata*. On the other hand, Reeve described the cancellated sculpture of *D. ridens* as being wider and more prominent than that found in *D. reticularis*. These are sculptural features characteristic of *D. clathrata*. This statement serves to contradict his description of duplicate transverse ridges. Again, these descriptive conflicts reinforce our conclusion that two different species formed the basis for the description of *D. ridens*. Moreover, Reeve remarked, ". . . the orange-stained colouring of the enamelled disc is particularly characteristic" of *D. ridens* (see figure 4). This pigmentation is not infrequently found in *D. clathrata*, but is not known in *D. decussata*. Furthermore the dorsal sculpture of the lectotype of *D. ridens* is consistent with that of *D. clathrata* and not "duplicate" as in *D. decussata*.

Inasmuch as none of the existing types of *D. ridens* can be attributed without doubt as being the specimens used by Reeve to describe this taxon, we believe Reeve's figured specimen (figure 1, herein) should be the primary source for the identity of this species. Additionally, we consider the lectotype virtually identical to Reeve's figured specimen. Therefore, we must conclude that *Distorsio ridens* (Reeve, 1844) is best placed in the synonymy of *D. clathrata* (Lamarck, 1816).

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Freshwater Mussel Fauna (Bivalvia: Unionidae) of the New River Gorge National River, West Virginia

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ABSTRACT

An extensive freshwater mussel survey of the New River Gorge National River, a national park in West Virginia, during the summers of 1984 and 1985 yielded seven species of living mussels and empty valves of an eighth species. *Actinonaias ligamentina* dominated the mussel fauna in all beds, constituting 94% of the mussels counted. Mussels were abundant throughout most of the study area; the estimated total exceeded 1.5 million individuals. Most mussel beds occurred in the upstream third of the park. Lack of suitable habitat appears to preclude the establishment of mussel beds in the extreme lower portions of this river reach. The mussel fauna within the park differed significantly in species composition and richness from that reported in upstream reaches of the New River and the upper Kanawha River, about 19 km downstream from the park boundary. Of particular note was the dominance of *A. ligamentina* in the park and its scarcity or absence elsewhere in the drainage.

INTRODUCTION

The freshwater mussel fauna (Unionidae) of the New River has been sampled periodically throughout this century, beginning with a brief survey by Ortmann (1913). Since then, several other mussel surveys have been conducted in various areas in the New River drainage (Jirka & Neves, 1985), but none have focused on the stretch of river designated as the New River Gorge National River (NRGNR) in West Virginia (figure 1). This national park includes the 84-km section of river from Hinton, West Virginia, at New River Mile (RM) 63 to a point just downstream from Fayetteville, West Virginia (RM 11). The lack of faunal surveys in this river reach is mainly due to its extensive white-water rapids and limited accessibility. Surveys that have included sites in the park were cursory, and most of the New River Gorge has remained virtually unexplored biologically.

We present the results of an extensive mussel survey conducted from June 1984 to September 1985 throughout the stretch of New River within NRGNR. Objectives of the survey were to identify locations supporting concentrations of mussels and to determine species composition and mussel abundance within NRGNR. Of particular interest to personnel at the park was the possible presence of the federally endangered pink mucket, *Lampsilis abrupta* (Say, 1831), since live specimens of this species were collected below Kanawha Falls, 2 km downstream of the mouth of the New River and about 19 km downstream from NRGNR (Stansbery, 1980; Clarke, 1982; Taylor, 1983).

METHODS

In June 1984, we conducted a preliminary reconnaissance of the river by inflatable raft to locate important mussel beds in NRGNR. River reaches having high concentrations of mussels or potentially suitable mussel habitat were identified for later qualitative sampling. Qualitative sampling consisted of searching a total of 44 sites for mussels by snorkeling, handpicking, using waterscopes, and sorting middens of muskrats (*Ondatra zibethicus*) to determine species present. Most areas were examined for 0.5–1.0 hour by three or four individuals using snorkels; mussels were identified, counted, and returned to the substratum.

On the basis of the qualitative sampling, we chose eleven mussel beds for quantitative sampling to estimate mussel abundance. Criteria used in selecting these sites were species diversity, overall mussel abundance, uniqueness of habitat type, and location within NRGNR. We attempted to locate study sites throughout the length of the park to record changes in species composition and abundance in different reaches of the river (figure 1).

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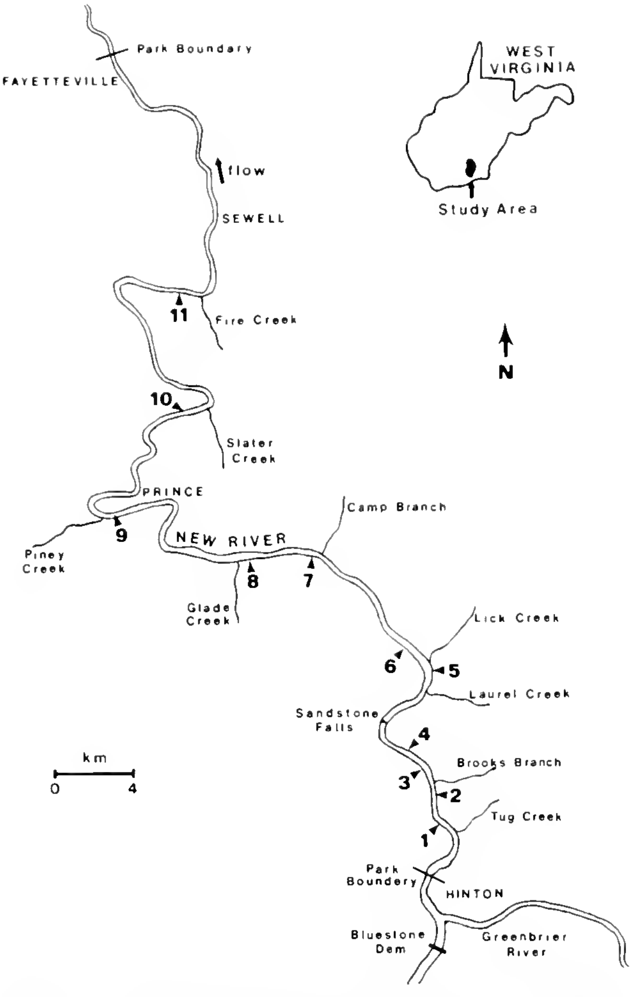

Figure 1. Location of major mussel beds (1–11) in the New River Gorge National River, West Virginia.

We sampled mussels quantitatively by snorkeling along transects at each site. Transects were established using a stratified random sampling design to ensure that the different habitats within a bed were sampled in proportion to their areas. Some areas of certain beds could not be effectively sampled because depths were unsuitable (<0.25 or >2.0 m) or time constraints prevented sampling of exceptionally large beds. However, areas chosen for sampling were representative of most of the bed.

Sampling consisted initially of laying a plastic tape of known length (usually 50 m) along the river bottom parallel to the current. Densities of mussels (no./m^2) along the transect were determined by identifying and counting all mussels within 0.5 m of each side of the tape and dividing the total by the length of the tape. Two snorkelers were used on all transects, each counting the mussels on one side of the tape. The presence of empty valves of each species was also noted. The length and number of transects on each bed varied with the dimensions of the bed; at least six transects, each 50 m long, were used on most beds. Densities from transects in the same bed were averaged to estimate mean mussel density for the bed. This mean density was multiplied by the area of the bed to obtain a minimal estimate of adult mussel abundance at each site. Nomenclature of mussels is according to Turgeon *et al.* (1988).

RESULTS

Faunal Description

Dense mussel assemblages were found throughout most of the park (figure 1). In addition to these major mussel beds, numerous smaller beds and scattered individuals were found in areas between these larger concentrations. Live mussels were found in all reaches of the river from Hinton (RM 63) downstream to Sewell (RM 19). Most mussel beds were in the upstream third of the river reach in NRGNR, and their abundance decreased markedly downstream from Glade Creek (RM 45). No live mussels or valves were found downstream from a large pool at Sewell.

Seven species of mussels were collected alive during the survey (table 1), together with two empty valves of an eighth species, *Lasmigona subviridis* (Conrad, 1835). *Actinonaias ligamentina* (Lamarck, 1819) was by far the dominant species, composing about 94% of the total mussels collected and present at all locations having mussels. *Cyclonaias tuberculata* (Rafinesque, 1820) accounted for 4% and *Elliptio dilatata* (Rafinesque, 1820) for 1% of the fauna; these species were in all of the major beds in the park. *Tritogonia verrucosa* (Rafinesque, 1820) was relatively common upstream from Sandstone Falls (RM 55), composing over 2% of the mussels found in this reach. Since no live specimens of this species were collected below RM 52.5, it made up less than 1% of the total mussels in the park. *Lampsilis ovata* (Say, 1817), *L. fasciola* (Rafinesque, 1820), and *Alasmidonta marginata* (Say, 1817) were collected infrequently and are considered uncommon throughout the river below Bluestone Dam. No specimens or valves of *Lampsilis abrupta* were collected in NRGNR.

Mussel Densities

Naiad densities in the beds ranged from 2.5 to 13.7/m^2 (table 2). The density was highest in bed 9 and the lowest in bed 11. No discernible pattern of overall mussel density was detected within the park, though some species showed evidence of shifting abundance in certain reaches of the river. Densities of *Actinonaias ligamentina* were relatively high in all beds, and freshly dead animals or relic shells (shells with a dull, chalky nacre from specimens presumed dead for at least a year) of this species were present at every site. The abundance of *Cyclonaias tuberculata* was generally low in beds upstream from Sandstone Falls and was highest in beds 6 to 8. Densities of *Elliptio dilatata* were highest in the river upstream from Sandstone Falls and showed a general trend of decreasing numbers downstream. Relic valves of this species were seen in all beds. *Tritogonia verrucosa* was fairly common in most beds above Sandstone Falls but

Table 1. Species composition and relative abundance of freshwater mussels in the New River Gorge National River, West Virginia

Species	Common name	Relative abundance (%)
Actinonaias ligamentina (Lamarck, 1819)	Mucket	94
Cyclonaias tuberculata (Rafinesque, 1820)	Purple wartyback	4
Elliptio dilatata (Rafinesque, 1820)	Spike	1
Tritogonia verrucosa (Rafinesque, 1820)	Pistolgrip	<1
Lampsilis fasciola (Rafinesque, 1820)	Wavy-rayed lampmussel	<1
Lampsilis ovata (Say, 1817)	Pocketbook	<1
Alasmidonta marginata (Say, 1818)	Elktoe	<1

was collected alive only in bed 6, among the beds below the falls. However, a few relic shells of this species occurred in every bed *Lampsilis fasciola*, *L. ovata*, and *Alasmidonta marginata* were patchily distributed and were uncommon throughout NRGNR. Valves of *Lampsilis fasciola* and *L. ovata* were often found in beds where no live individuals of these species were collected.

MUSSEL ABUNDANCE

Estimates of total numbers of mussels in the major beds sampled ranged from 5,475 in bed 2 to 392,175 in bed 8 (table 2). The estimated total number of mussels in all 11 beds combined was about 1.2 million, of which 94% were *Actinonaias ligamentina*. These estimates do not include juveniles, the smaller mussel beds, or numerous pockets of mussels that were not counted during the quantitative portion of the survey. Records from the qualitative survey indicated the existence of at least 16 minor mussel beds and two additional major beds within the park. A conservative estimate of 3,000 mussels per minor bed and 150,000 mussels per major bed would put the estimated minimal number of adult mussels within beds of NRGNR at more than 1.5 million animals. Mussels were most abundant between Sandstone Falls (RM 55) and Piney Creek (RM 38).

DISCUSSION

The NRGNR supports an abundant mussel fauna that is relatively low in diversity. Large beds of naiades are found from its upstream boundary, downstream to Sewell in the lower gorge. Mussel colonization of the river downstream from Sewell appears to be precluded by a scarcity of suitable habitat and possibly by a lack of suitable fish hosts for certain mussel species.

The mussel fauna of the park varies considerably from the fauna found elsewhere in the New River—most notably, in the dominance of *Actinonaias ligamentina* within NRGNR. The dominant species in the river immediately above Bluestone Lake, only 35 km upstream from NRGNR, are *Cyclonaias tuberculata* and *Lampsilis ovata* (Tolin, 1985). Further upstream in Virginia, *Tritogonia verrucosa* and *Elliptio dilatata* are also common (Dillon, 1977). Species reported from the New River drainage by Jirka and Neves (1985) that were not recorded in the present survey were *Anodonta grandis* (Say, 1829); *Toxolasma parvus* (Barnes, 1823); *Villosa iris* (Lea, 1829); and *Quadrula quadrula* (Rafinesque, 1820). In 1984, an empty valve of *Anodonta grandis* was found immediately below Bluestone Dam by one of us (R.J.N.), and another valve was collected near the lower end of Brooks Island, in NRGNR by W. A. Tolin (USFWS, pers. comm.). *Toxolasma parvus* has been found only near the mouth of the New River at Gauley Bridge, West Virginia (D. H. Stansbery, Ohio State Museum, unpublished records). The record of *Quadrula quadrula* in the river near Sandstone Falls (Bates, 1979) is questionable since this species is unreported for the New River drainage. *Villosa iris* has not been found in the main stem of the New River, but one specimen was recently reported from the Bluestone River, a major tributary of the New River, by Tolin (1985).

Most of the mussel species collected appeared to have healthy populations in at least a portion of the park, and those in the river that are considered rare were generally widespread. Possibly *Lasmigona subviridis*, of which only two empty valves were collected (at RM 57 and RM 19), also has a small population within NRGNR, and the same may be true of *Anodonta grandis*. The distributions of two species, *Tritogonia verrucosa* and *Lampsilis ovata*, were unexpected, particularly in the numbers and lo-

Table 2. Mussel density and abundance in eleven major mussel beds within the New River Gorge National River, West Virginia.

Bed[1]				
No	Area (m²)	Transect area (m²)	Mussel density (no/m²)	Population estimate
1	4,200	335	3.6	15,120
2	1,165	217	4.7	5,475
3	9,350	300	5.4	50,490
4	18,750	350	3.7	69,375
5	14,700	350	6.8	99,960
6	39,600	300	7.6	300,960
7	1,600	241	3.7	5,920
8	37,350	300	10.5	392,175
9	14,850	300	13.7	203,445
10	9,100	300	7.0	63,700
11	5,500	300	2.5	13,750
Total				1,220,370

[1] See Figure 1 for locations

cations of empty valves collected. Although a healthy population of *Tritogonia verrucosa* lives above Sandstone Falls, no live specimens of this species were seen below bed 6, about 4 km below the falls. However, numerous relic shells were found in all major beds downstream from Brooks Island, suggesting that *T. verrucosa* may have once been relatively common throughout the river below Sandstone Falls but have since declined in abundance. Similarly, although live *Lampsilis ovata* were collected from several sites throughout the park, many areas contained numerous relic valves but no living specimens, indicating that this species may have been more common in the river in the recent past than during our survey.

The relatively low diversity of the mussel fauna in NRGNR, and in the New River as a whole, is notable when compared with the 34 species of naiades reported in the Kanawha River (Stansbery, 1980; Clarke, 1982; Taylor, 1983), which is joined by the New River about 19 km downstream from NRGNR. Many factors have been suggested as potential causes of the scarcity of mussel species in the New, but none have been substantiated. Most of these factors relate to the river's geologic and climatic past, the presence of physical barriers to dispersal, lack of a diverse fish fauna in the river, or stream captures by other drainages (Ross & Perkins, 1959; Neves, 1983; Jirka & Neves, 1985). Physical barriers to upstream dispersal of fish and mussels, particularly Kanawha Falls, have probably had the greatest influence on mussel diversity in the New River since 34 species occur immediately below the falls (Taylor, 1983).

The overall abundance of naiades in NRGNR is among the highest in West Virginia. The NRGNR supports a mussel assemblage of at least 1.5 million individuals—an abundance at least comparable to that in the upper Kanawha River and considerably greater than that in any reach of the upper New River in Virginia. The abundance of mussels in NRGNR is strong evidence that it is not a lack of suitable habitat or poor environmental quality that has limited the number of species in this river, but rather, impediments to mussel colonization of suitable habitats throughout much of NRGNR.

The most striking aspect of the mussel fauna of the NRGNR is the extreme dominance of *Actinonaias ligamentina* which constituted 94% of the mussel fauna and exceeded 1.4 million individuals. In contrast, Taylor (1983) reported that this species represented an average of only 5% of the mussels at 14 stations sampled in the upper Kanawha River. Also notable is the scarcity of *A. ligamentina* in the New River immediately above Bluestone Dam, only 3 km upstream from NRGNR, and the absence of this species in the New River above Roundbottom Creek, about 40 km upstream from NRGNR. Why *A. ligamentina* has flourished within NRGNR while being only a minor or missing component of the mussel fauna elsewhere in the New Kanawha drainage is not known. An explanation for this distribution pattern would probably add insight into the factors influencing faunal diversity and composition within NRGNR and the entire New River.

ACKNOWLEDGEMENTS

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Copper, Lead and Cadmium Concentrations in a Sample of Lake Winnipeg *Anodonta grandis*

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ABSTRACT

A sample of *Anodonta grandis* from southern Lake Winnipeg was analyzed for tissue content of cadmium, copper and lead. Copper and lead concentrations in tissues were each significantly inversely correlated with shell weight and shell length, copper was also significantly inversely correlated with tissue dry weight. However total body content of cadmium, copper and lead was each positively correlated with shell weight, shell length and tissue weight. Thus, while older individuals carried greater total body burdens for all 3 metals, younger individuals showed higher levels of copper and lead per unit body weight.

Key words: Copper, Lead, Cadmium, *Anodonta*

INTRODUCTION

Unionid clams form an important component of the benthic communities of many freshwater lakes. These mollusks have much longer lifespans than most other freshwater invertebrates. Thus they are exposed to their environment, and particularly to toxicants such as heavy metals, for a longer period, presenting a greater potential for tissue accumulation. Although concentrations of heavy metals have been studied in freshwater insects (*e.g.*, Brown, 1977; Burrows & Whitton, 1983), zooplankton (*e.g.*, Mathis & Kevern, 1975) and gastropods as well as other macroinvertebrates (*e.g.*, Gale *et al.*, 1973; Leland & McNurney, 1974; Namminga *et al.*, 1974; Enk & Mathis, 1977; Mathis *et al.*, 1979; Newman & McIntosh, 1982), corresponding data concerning unionids are difficult to find in the literature. Some experimental studies have been conducted on the toxicity of metals such as cadmium (Lukacsovics & Salanki, 1964; Radhakrishnaiah, 1988) and copper (Imlay, 1971) to freshwater clams, but field studies are rare. Mathis and Cummings (1971, 1973) reported on metal levels in Illinois River clams and found that whole-animal tissue concentrations exceeded the concentrations found in the water. Anderson (1977) included a few unionid individuals in a survey of macroinvertebrates from the Fox River.

In the present study cadmium, copper and lead tissue contents of a sample of *Anodonta grandis* Say, 1829 from Lake Winnipeg were compared with shell length, shell weight and animal weight.

MATERIALS AND METHODS

A random sample of 33 *A. grandis* was collected on September 28, 1986 at Sandy Hook, on the western shore of Lake Winnipeg's south basin (50°32′N, 96°59′W). The clams were taken to the laboratory, where they were kept in an aquarium for 3 days in order to evacuate the gut. The clams were then frozen, freeze-dried and the tissues of each individual ground to a powder.

Each tissue sample was divided for assay into 3 equal aliquots, each consisting of up to 0.5 g of dry powder. Each aliquot was digested by adding 7.5 ml of concentrated nitric acid (HNO_3) and 1.5 ml 70% perchloric acid ($HClO_4$). The mixture was heated but not allowed to boil for 1 hr. Ten ml of 1% nitric acid were then added. The solution was filtered through Whatman No. 541 hardened ashless lead-free filter paper to remove insoluble material. The filtrate was diluted to a volume of 50 ml with 1% nitric acid and aspirated into a IL151 atomic absorption spectrophotometer (Instrumentation Laboratory Inc., Wilmington, MA, USA). The method of standard additions was used to compensate for matrix absorption effects (*e.g.*, Newman & McIntosh, 1982). Procedural controls, consisting of all reagents and steps in the procedure less the sample, were run with each series. All glassware was acid-washed prior to use.

Sediment samples consisting of the top 3 cm layer of sediment were freeze-dried. One gram samples were analyzed in triplicate, each extracted with the same acid mixture as above (Bolter *et al.*, 1975). Unfiltered water samples 1 L in volume were frozen and freeze-dried. The residue was resuspended in a measured volume of 10% nitric acid, heated for 1 hr and aspirated for analysis.

The critical significance level for all statistical tests was $p < 0.05$.

RESULTS

Shell weight and shell length were significantly correlated ($r = 0.97$, $p < 0.001$) (both variables log trans-

Table 1. Summary of parameters for the *Anodonta grandis* sample (n = 33). Values in parentheses are standard errors

	$\bar{x}$	Minimum	Maximum
Shell weight (g)	4.1 (0.5)	1.2	15.6
Shell length (mm)	49.5 (1.3)	36.4	71.9
Animal tissue dry weight (g)	0.79 (0.07)	0.22	1.55
Cadmium (μg/g dry tissue weight)	3.0 (<0.5)	<1.0	10
Copper (μg/g dry tissue weight)	45.3 (3.1)	5.0	80
Lead (μg/g dry tissue weight)	97.8 (7.1)	<4	>150

formed). Dry weight of tissue was significantly correlated with shell weight ($r = 0.81$, $p < 0.001$) and shell length ($r = 0.85$, $p < 0.001$) (all variables log transformed).

Concentrations of cadmium, copper and lead in the tissues are summarized in Table 1. Copper content was highly significantly negatively correlated with shell weight ($r = -0.60$, $p < 0.001$) and shell length ($r = -0.58$, $p < 0.001$) (untransformed variables). Logarithmic transformations of all variables improved both correlation coefficients to -0.63 ($p < 0.001$). Lead concentration was also negatively correlated with shell weight and shell length ($r = -0.39$, $p = 0.017$ and $r = -0.40$, $p = 0.015$, respectively) (transformed variables). Correlations with cadmium concentrations were not significant.

Correlations between metal concentrations and the dry weight of the animal (excluding shell) were significant and inverse for copper ($r = -0.44$, $p = 0.006$), but not significant for cadmium or lead. Concentrations among the three metals were correlated only between copper and lead ($r = 0.71$, $p < 0.001$) (transformed variables).

The total body burden (excluding shell) of each metal was significantly positively correlated with dry weight of animal for all three metals [cadmium $r = 0.47$, $p = 0.003$; copper $r = 0.64$, $p < 0.001$; lead $r = 0.77$, $p < 0.001$ (untransformed variables)]. For cadmium, r improved to 0.75 ($p < 0.001$) when cadmium content was log transformed.

Total body content of copper ($r = 0.38$, $p = 0.015$) and lead ($r = 0.40$, $p = 0.013$) were correlated with log shell length; for log shell weight these correlations were also significant ($r = 0.33$, $p = 0.031$ for copper, and $r = 0.37$, $p = 0.022$ for lead). For cadmium, correlations increased for shell weight ($r = 0.58$, $p = 0.001$) and shell length ($r = 0.65$, $p < 0.001$) when metal content was log transformed also.

Total cadmium content was significantly correlated with copper ($r = 0.74$, $p < 0.001$) and with lead ($r = 0.54$, $p = 0.003$). Copper and lead levels were correlated as well ($r = 0.82$, $p < 0.001$) (all transformed).

Stepwise multiple regression with shell length, shell weight and dry animal weight in the regression block (all log transformed) and total body burden of each metal as the independent variable (not transformed) indicated that approximately half of the variance in the metal content in *A. grandis* could be accounted for by dry weight of the animal: 41% for copper ($R^2 = 0.41$, $p < 0.001$) and 52% for lead ($R^2 = 0.52$, $p < 0.001$). Shell weight also entered the equations, but with a negative beta value in both cases, increasing the R^2 values to 0.51 and 0.65, respectively ($p < 0.001$). For cadmium, dry tissue weight was the only variable entered into the equation ($R^2 = 0.55$, $p < 0.001$) (both independent and dependent variables log transformed).

Metal concentrations in the water and the coarse sand sediments were below the detection limits for the procedure used (*i.e.*, <1 μg for cadmium, <2 μg for copper and <4 μg for lead per gram dry sample, or per liter of water).

DISCUSSION

The values obtained for *A. grandis* in the present study were comparable to those reported by Anderson (1977) for mussels from the Fox River, Illinois. The results showed that as clams increase in size and weight, their total body burdens of metals increase. However when metal concentrations were examined in tissues, concentrations of copper and lead decreased as clam size increased, suggesting that smaller individuals take up this metal at a greater rate (or dispose of it more slowly) than do larger clams of the same species. While size also probably reflected age of the mussels, *A. grandis* is known to exhibit considerable variation in size at a given age within the same body of water (Hanson *et al.*, 1988).

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A New Fossil Land Snail (Gastropoda: Pulmonata: Polygyridae) from the Middle Miocene of Northern Florida

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ABSTRACT

A new fossil land snail, *Praticolella prisca* n. sp., is described from the Charlton Member of the Coosawhatchie Formation (middle Miocene) at Brooks Sink, Bradford County, Florida. This new species is assigned to *Praticolella* s.s. Martens, 1892 based on sculpture, palatal lip expansion and a narrow constriction behind the lip. This subgenus is presently confined to central and southern Texas and Mexico under environmental conditions known to have occurred in northern Florida during the Miocene. *Praticolella prisca* n. sp. appears to be the earliest known member of the genus.

Key words: Gastropoda; Polygyridae; *Praticolella*; Miocene; Florida.

INTRODUCTION

Collections of invertebrate fossils containing a new species of terrestrial gastropod, *Praticolella prisca* n. sp., were made by the authors in the mid 1980's from Brooks Sink, a large, nearly circular, vertical-walled sink hole located 16.89 kilometers west of Starke, Bradford County, Florida (figure 1). Brooks Sink provides one of the best natural exposures of Hawthorne Group sediments in Florida. Exposed in approximately 23.0 meters of section are, in ascending order, the Marks Head Formation, the undifferentiated Coosawhatchie Formation, and the Charlton Member of the Coosawhatchie Formation (figure 2).

The age of the Charlton Member (formerly Charlton Formation) was considered to be Pliocene by Veatch and Stephenson (1911) and Cooke (1943, 1945). Based upon ostracods from this unit, identified by Harbans Puri as middle Miocene and/or upper Miocene, Pirkle (1956) reported the age to be older. More recently, Jones and Portell (1988) recognized the middle Miocene clypeasteroid echinoid, *Abertella aberti* (Conrad, 1842) from this unit. Huddleston (1988) assigned an age of middle Miocene to the Charlton Member in Georgia based on molluscan faunas, stratigraphic relationships, and the occurrence of several age-diagnostic planktonic foraminifera. Jones and Portell (1988) reported over 30 fossil invertebrate taxa within the Charlton Member of the Coosawhatchie Formation at Brooks Sink including *Praticolella* sp., the taxon described below.

MATERIALS AND METHODS

No fossilized shell material was recovered. The specimens representing this taxon are preserved only as internal and external molds comprised of fine-grained dolostone. We use the term external mold to indicate the impression in the matrix of the outer surface of the shell. The matrix containing the external mold UF 14397 was reduced and the specimen sonicated for observation of the shell ultrastructure under a scanning electron microscope. Some of the specimens are incomplete in certain aspects. Nevertheless, standard shell parameters were measured with vernier calipers whenever possible. All specimens are reposited in the Florida Museum of Natural History, Invertebrate Paleontology Division, University of Florida, Gainesville, Florida 32611.

DESCRIPTION

Family **Polygyridae** Pilsbry, 1930
Subfamily **Polygyrinae** Pilsbry, 1895
Genus *Praticolella* Martens, 1892
Praticolella prisca new species
(figures 3–10, table 1)

Adult shell large (width 10.0–13.9 mm, height 6.7–10.0 mm); helicoid, depressed-globose, 0.64–0.72 times as high as wide; spire moderately elevated, convex in outline (figures 3, 6, 7); base round and inflated; the 4.6–5.0 convex whorls slowly increasing in size (figure 4); sutures impressed; body whorl large, slightly flattened at suture, round at periphery and below; deflection variable, slightly upward or downward in the final 0.25 whorl, but always descending very slightly before constricting and inflecting; narrowly constricted posterior to palatal lip, more deeply constricted along base (figures 4, 6); umbilicus narrow, tubular, about 0.10 the diameter of shell and partially covered by reflected columellar lip (figures 5, 8); the 1.7 protoconch whorls are smooth except for a

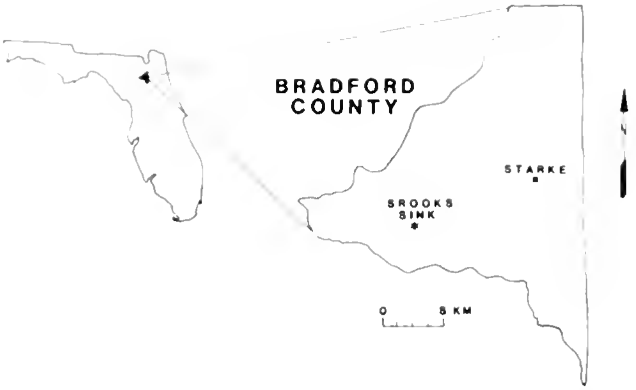


Figure 1. Location of Brooks Sink in Bradford County, Florida (SW¼, SW¼, sec. 12, T7S, R20E, Brooker 7.5 Minute Quadrangle).

Table 1. *Praticolella prisca* new species. Linear shell measurements (mm) and whorl counts of holotype and 9 paratypes. Most of the specimens are incomplete in some aspects, hence the different N for the measured parameters

Character	N	Range	$\bar{x}$	SD
Shell width	10	10.0–13.9	12.0	1.2
Shell height	5	6.7–10.0	8.5	1.1
Height/width	5	0.64–0.72	0.68	0.03
Aperture height	2	5.5–6.2	5.9	0.4
Aperture width	2	6.4–7.2	6.8	0.4
Ap. height/Ap. width	2	0.85	0.85	0.0
Umbilicus width	7	0.8–1.5	1.1	0.2
Umb. width/shell width	7	0.07–0.11	0.09	0.02
Whorls	4	4.75–5.5	5.2	0.3

few axial striations on the last 0.20 turn (figure 10); subsequent whorls are smooth except for a few axial striations on the last 0.20 turn (figure 10); subsequent whorls and base with fine, irregular, oblique axial striations, strongest at the suture (figure 9); spiral sculpture absent; aperture lunate and relatively large, 0.85 times as high as wide; parietal and palatal barriers absent; palatal lip broadly expanded, thickened within (figure 7); in lateral view lip moderately reflected along periphery and base, expanded forward above, unreflected (figure 6).

Etymology: The species name *prisca* is derived from the Latin *priscus*, meaning ancient.

Type locality: Brooks Sink, 16.89 kilometers west of Starke, Bradford County, Florida (SW¼, SW¼, sec. 12, T7S, R20E, Brooker 7.5 Minute Quadrangle), Coosawhatchie Formation, Charlton Member, approximately 8.0 meters below surface.

Holotype: UF 14446, 12.5 mm width, 8.9 mm height, internal mold, protoconch missing.

Paratypes: Width 10.0–13.9 mm, height 6.7–10.0 mm; UF 14395, 5 adults, internal molds; UF 14397, 1 adult, external mold and rubber peel; UF 14406, 1 adult, external mold; UF 14407, 1 adult, external mold and rubber peel; UF 14408, 1 adult, internal mold; UF 14450, 1 partial adult body whorl, internal mold.

Other material examined: UF 28983, 9 fragments, internal molds; UF 14405, 1 subadult, external mold and rubber peel; UF 14433, 1 adult, external mold and rubber peel; UF 14443, 1 adult, internal mold; UF 22347, 4 adults and 3 fragments, internal molds; UF 22348, 6 juveniles, internal molds, obtusely angulate at periphery and have indications of growth stoppage at 3.5–4.0 whorls.

COMPARATIVE REMARKS

The external mold UF 14405 (figures 7, 8) is tentatively assigned to this new species. It is slightly smaller and more depressed (10.5 mm wide, 6.7 mm height) than most of the other specimens. The palatal lip is simple, except basally where it is barely reflected. The body whorl is slightly constricted on the basal portion. However, this specimen is identical to the larger, more globose specimens in other character-states such as sculpture, spire whorlation and umbilicus. It is our opinion that this is a small subadult of *Praticolella prisca* n. sp. and does not represent a second undescribed taxon.

The classification of pulmonate land snails is based primarily on features of the soft anatomy making assignment of fossil forms difficult. Within the Stylommatophora several families have evolved strikingly similar shell forms. Convergences in helicoid families such as the Camaenidae, Polygyridae and Helminthoglyptidae are frustratingly commonplace. However, careful analysis of various morphological shell character-states can elucidate differences and general trends within and between families. The combination of sculpture, palatal lip expansion and the narrow constriction of the body whorl suggest that this species is best assigned to the polygyrid genus *Praticolella* Martens, 1892.

Praticolella Martens, 1892 is characterized in shell form by its relatively small size, depressed-globose shape, rounded periphery, narrow umbilicus and rounded base. The aperture is lunate and the lip is slightly expanded or reflected and thickened within. The sculpture is of fine, irregularly spaced axial striations (Pilsbry, 1940). *Praticolella* is divided into three subgenera based on genitalic anatomy and sculpture of the protoconch (Pilsbry, 1940). The subgenus *Filapex* Pilsbry, 1940 has distinct spiral sculpture on the protoconch. *Farragutia* Vanatta, 1915 and *Praticolella* s.s. Martens, 1892 have smooth protoconchs. *Farragutia* is relatively smaller than *Praticolella* s.s., is slightly more depressed and has a less rounded base. *Praticolella prisca* n. sp. is clearly referred to *Praticolella* s.s. A close relationship to any extant species cannot be made.

The polygyrid genera *Mesodon* s.s. Rafinesque, 1821, *Neohelix* s.s. Ihering, 1892 and *Praticolella* Martens, 1892 are quite similar in general shell shape. *Mesodon* s.s. and *Neohelix* s.s. generally have distinct, regular axial striae and engraved spiral lines, while *Praticolella* has a smoothish shell sculptured only by weak, irregular axial

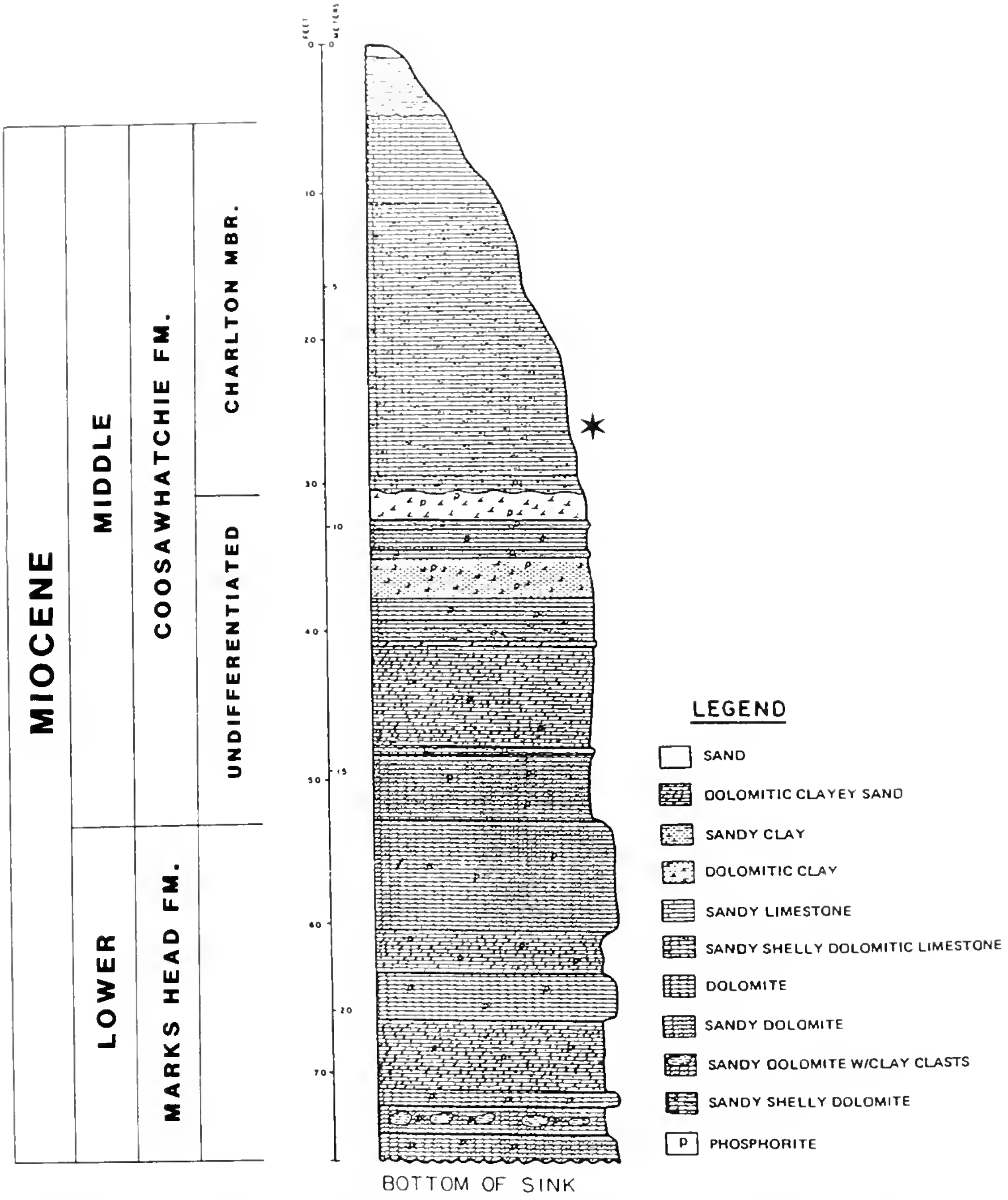


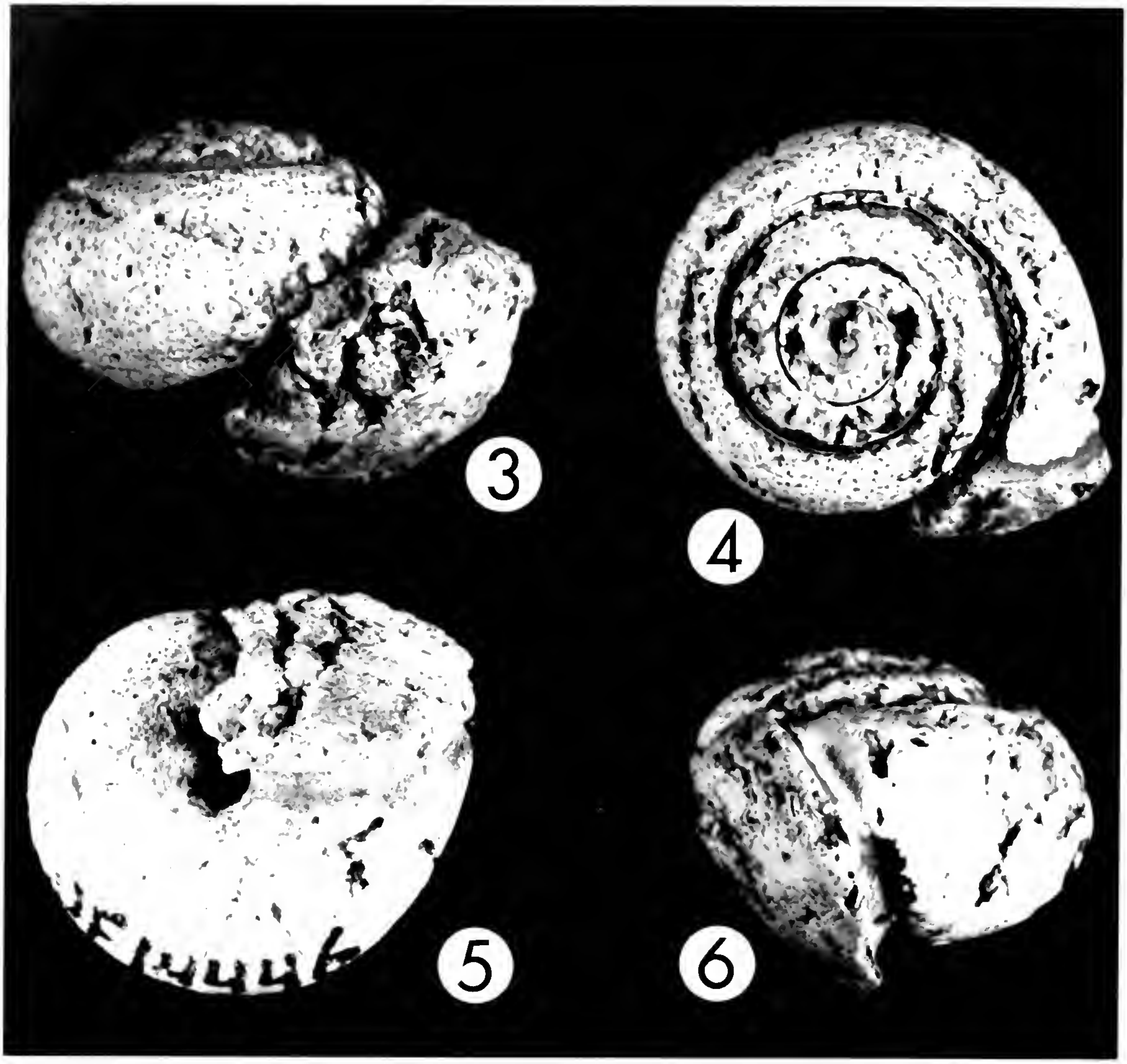
Figure 2. Geologic section at Brooks Sink modified from Scott (1982). Asterisk indicates zone where *Praticolella prisca* new species occurs

growth striae. The maximum shell size of *Praticolella* and the minimum size of *Mesodon* s.s. overlap, while *Neohelix* s.s. is much larger. The relative palatal lip width and degree of reflection of *Praticolella* rarely attains that of *Mesodon* s.s. The possibility that this new species is a small unsculptured *Mesodon* s.s. cannot be dismissed.

Praticolella prisca n. sp. superficially resembles the Miocene camaenids *Pleurodonte crusta* (Dall, 1890) and *Pleurodontites diespiter* (Dall, 1890). These species, however, have papillose sculpture, shells which are larger and more depressed than *Praticolella prisca* n. sp. and body whorls which descend greatly over the last ¼ turn.

DISCUSSION

The method of preservation of fossil mollusks has an important bearing on the interpretation of certain morphological characters. Internal molds are particularly dif-

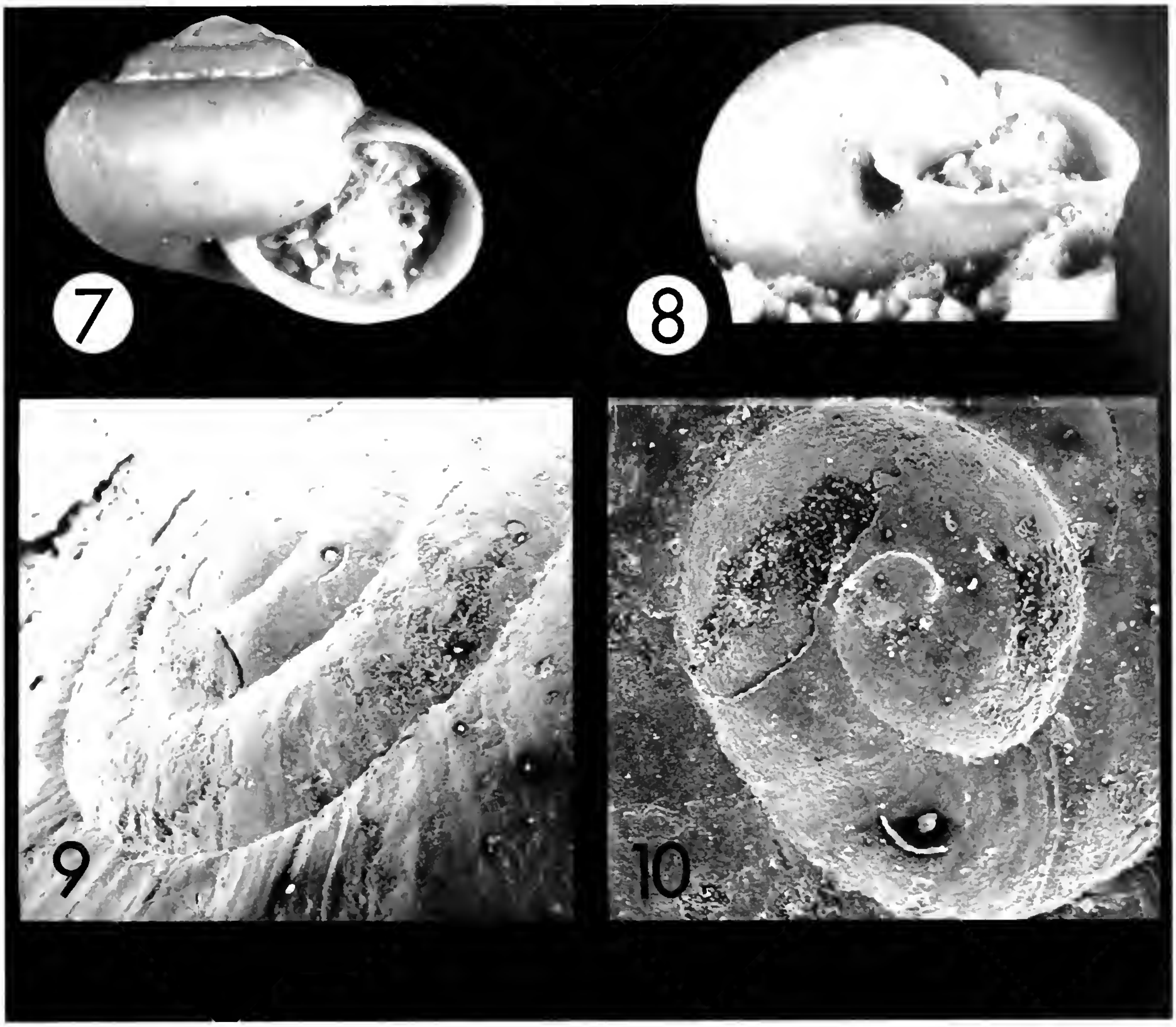


Figures 3–6. *Praticolella prisca* new species. Holotype, UF 14446, apertural, dorsal, basal, and lateral views, ×6.4

ficult to interpret. For example, if a shell with an internally thickened palatal lip is filled with and encased in sediment and the shell dissolves, the thickened portion of the lip may appear as a constriction on the outside of the body whorl. A true constriction may be greatly enhanced by this process. *Praticolella prisca* may in fact be only slightly constricted behind the lip or not constricted at all, only thickened internally. With more adequate material the true nature of this character-state will be better known.

To our knowledge *Praticolella prisca* n. sp. represents the oldest known member of this genus. Fossil forms of *Praticolella* s.s. Martens, 1892 from probably the late Pleistocene epoch of Texas are attributed to extant species (Hubricht, 1983, 1985). This subgenus is presently confined in its native distribution to savannah and xeric habitats in southern and central Texas and Mexico. A similar savannah-like environment is known to have occurred in northern and central Florida during the Miocene (Webb, in press). This ecological association is compatible with the taxonomic assignment of *Praticolella prisca* n. sp.

Thirteen genera (23 species, 1 subspecies) of land snails have been recorded from the Miocene sediments of Florida (Dall, 1890, 1915; Mansfield, 1937). Eleven of these genera are extant. If current taxonomic assignments are correct, eight genera (61%) have Caribbean affinities, four genera (31%) probably emigrated from areas west



Figures 7–10. *Praticolella prisca* new species. **7, 8.** UF 14405, apertural and basal views of rubber peel of external mold of probable subadult (see Comparative Remarks), ×6.6. **9, 10.** Paratype, UF 14397, scanning electron micrograph of protoconch of external mold. **9.** ×28. **10.** ×47.

of Florida, and one genus (8%) came from the north. The bulimulid genus *Hyperaulax* Pilsbry, 1897, which has an enigmatic distribution of several species from the Miocene of Florida and a single extant species on Fernando de Noronha Island off Brazil, is considered here to be part of the Caribbean component of the Miocene fauna. Many of the Miocene terrestrial vertebrates of Florida are believed to have been associated with both mesic and xeric tropical habitats (Auffenberg, 1963; Webb 1978, in press) and some appear to be closely related to groups now found in dry regions of Central America and Mexico. It is possible that some of these Florida Miocene land snails attributed to genera presently found only in the Caribbean region may be more appropriately assigned to genera occurring in mesic or xeric areas of Central America and Mexico and thus entered Florida via a dry tropical corridor along the Gulf of Mexico.

The fifty genera of native land snails presently found in Florida reveal a different zoogeographic pattern than is suggested by the fossil record. Of this current land snail fauna, sixteen genera (32%) are well-represented in the Caribbean region, six genera (12%) probably entered Florida from the West, while twenty-eight (56%) came from the North. This present zoogeographic pattern reflects the strong post-Miocene trend toward cooler, wetter climates, allowing immigration of the northern taxa into Florida. However, the timing of this immigration can not be determined from the fossil record.

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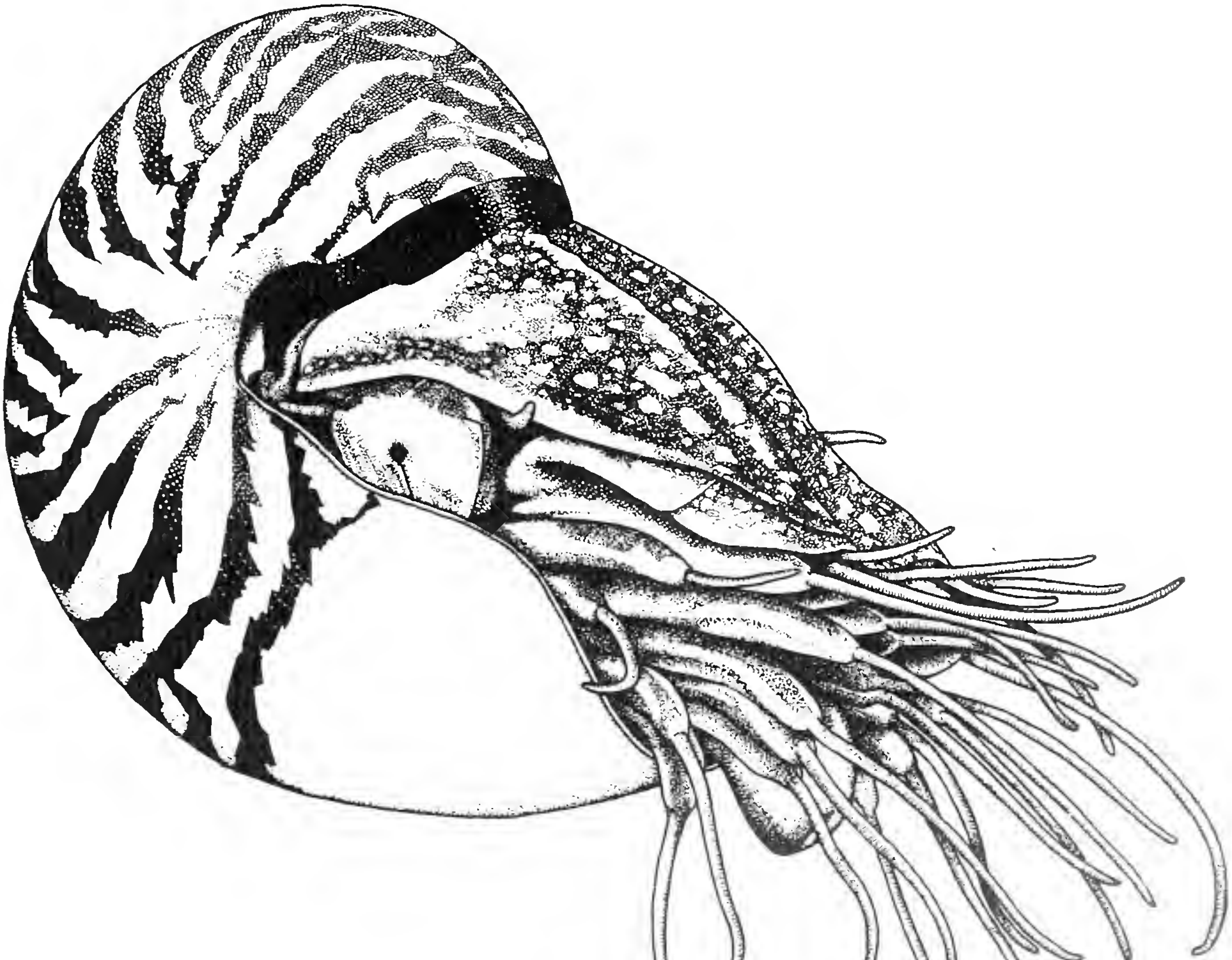

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Catalogue of the Superfamily Cancellarioidea Forbes and Hanley, 1851 (Gastropoda: Prosobranchia)

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ABSTRACT

This catalogue of cancellarioidean taxa is composed of three sections. The first lists alphabetically 124 genus-group taxa originally proposed or later included in the superfamily. The second section lists alphabetically over 1,800 species-group taxa erected in or subsequently referred to genera now considered to belong in Cancellarioidea. The third section consists of a bibliography of works on the systematics of cancellarioideans referred to in this paper.

key words: Cancellarioidea, genus-list, species-list, bibliography.

INTRODUCTION

The Cancellarioidea comprise a highly-specialized, poorly known, and taxonomically enigmatic group of marine neogastropods that inhabit subtidal to bathyal sand and mud bottoms of tropical and temperate latitudes. Although most taxa at all levels within the superfamily were described on the basis of shell characters, it was a series of adaptations to suctorial feeding that resulted in a succession of adaptive radiations beginning during the late Mesozoic that gave rise to the Cancellarioidea. Diagnostic synapomorphies of the superfamily include: an anteriorly tubular, posteriorly saddle-shaped jaw that spans the dorsal surface of the buccal mass; a uniserial radula composed of extremely elongated (L/W>15), ribbon-like, tricuspid teeth with secondary dentition on one or more cusps [there are several aradulate taxa]; an extremely short anterior esophagus, with the valve of Leiblein and buccal ganglia situated at the posterior margin of the buccal mass; and the lack of a gland of Leiblein. Although the superfamily forms a monophyletic and morphologically compact natural assemblage, its relationships to other prosobranchs is less than certain. The group had, at various times, been included in the Toxoglossa (Troschel, 1865; Tryon, 1882; Fischer, 1883), the Volutoidea (Thiele, 1929; Wenz, 1943; Taylor and Sohl, 1962) and its own order, Nematoglossa (Olsson, 1970). Most subsequent authors follow Ponder (1973) in considering the Cancellarioidea a superfamily within Neogastropoda. Taylor *et al.* (1980) speculated that the Cancellarioidea are an early offshoot from the Mesozoic Purpurinidae.

In the Tenth Edition of *Systema Naturae* Linné (1758) described a single species of cancellariid, including it in the genus *Murex*. In 1767, he transferred that species to *Voluta*, and described a second species, also as *Voluta*. By the end of the 18th century, twelve nomina had been proposed for cancellarioideans, allocated to the genera *Murex*, *Voluta*, *Tritonium*, *Buccinum* and *Cantharus*. To date, there have been about 1,800 species-group taxa proposed in the Cancellarioidea, many as 'varieties' of Tertiary species.

Lamarck (1799) was the first to recognize that the then known cancellariids comprised a distinct group and erected the genus *Cancellaria*. The second genus group name to be proposed for a cancellariid was *Trigona* Perry, 1811 (preoccupied and replaced by the equivalent *Trigonostoma* Blainville, 1827). The third genus-level name to be introduced was *Admete* (Kröyer in Möller, 1842). A decade or so later, the flood-gates opened and many new genera and subgenera were introduced. Marks (1949) published a list of supra-specific taxa in Cancellariidae, citing 58 nominal taxa. We now list 124 genus-group taxa of which seven are emmendations, errors, or *nomina nuda;* seven were originally proposed in Cancellariidae, but belong elsewhere; seven are homonyms; and three are objective synonyms. One hundred validly proposed taxa remain. Genus-group taxa proposed for cancellariids have not been treated uniformly in the literature, as authors have differed widely in their use of available taxa.

As noted by some authors, many of the nominal genera and subgenera of cancellariids seem to be unnecessary. At the same time, there are numerous species that do not readily fit any of the named taxa. Dall (1909a:30) wrote: "I may add that what, on a cursory survey, appears to be a totally unnecessary number of names has been applied to subdivisions of the genus *Cancellaria*; but time fails me at present to review them in detail. Most of them are based on slight modification of form which gradually merge into one another when a full series of specimens is considered". This did not, however, preclude Dall from subsequently proposing several new genus-group taxa in the family.

As a prodrome to a series of systematic revisions of this poorly-understood superfamily, it has been our objective to compile a list of all names proposed or currently used for cancellarioideans. We have attempted to make this work as complete as possible, but recognize that some taxa have undoubtedly been omitted. We request that colleagues bring to our attention any errors and omissions, which will be published in a future addendum.

This catalogue of superfamily Cancellarioidea is composed of three sections: an alphabetical listing of genus-group taxa, an alphabetical listing of species-group taxa, and a bibliography of systematic works on cancellarioideans. The genus-group list contains all taxa at the genus-group level, as defined by Article 42 of the International Code of Zoological Nomenclature (Third Edition), that have been referred to the Cancellarioidea or any of its families or subfamilies, either originally or subsequently. Genus-group taxa originally proposed in Cancellarioidea but later referred to other superfamilies are included in our list.

The species-group list contains all taxa proposed at the species-group level, as defined by Article 45 of the International Code of Zoological Nomenclature (Third Edition). Names originally proposed as subspecies, varieties, forma or other infrasubspecific categories are included, with the category used by the author identified. We have listed all names originally proposed in, or now considered as being referable to, genera presently included in Cancellarioidea. In addition, we have included several taxa that were transferred to cancellarioidean genera at one time, but which we now know to have been so placed incorrectly. Only such of these cases as might be a source of confusion are listed. *Nomina nuda*, excluded from some lists of taxa, are included here, as they have appeared in print and may cause confusion if their status is unclear.

We have also endeavored to attribute authorship correctly, but this task was not always easy or precise. Many names were first published by authors having access to other workers' manuscripts or labeled specimens. There are numerous instances where an author attempted to credit a taxon to a colleague, but did so in a manner requiring that authorship be attributed to the author of the work and not the colleague. A series of examples illustrate these points. In 1817 Faujas de Saint Fond described and illustrated several species, citing them as though they had already been published by Lamarck. However, there is nothing in the work to indicate that Lamarck had provided Faujas de Saint Fond with the names, descriptions or illustrations, and the names must be attributed to Faujas de Saint Fond. In this case, these taxa have been attributed to Faujas de Saint Fond by all subsequent authors, including Lamarck. On the other hand, Brander (1766) clearly stated that the descriptions of the species in his work were supplied by Solander, and the names can be attributed to Solander. All examples are not as clear. The taxon *Triton antiquatus* first appeared in print in Reeve (June, 1844), attributed by Reeve to Hinds' "Zoology of the Sulphur vol. ii, pl.4, fig.78", a work not published until July, 1844. It is obvious that Reeve had access to a "preprint" of Hinds' work, or that some copies were distributed prior to the stated publication date. Thus authorship is attributed to Hinds as "Hinds in Reeve".

The bibliography lists, alphabetically by senior author, all works referred to in either of the indices or in the introduction. We have attempted to provide the correct dates of publication for all of the references cited, but some of the dates may eventually be shown to be incorrect. A number of scientific papers [primarily 19th century] were published in two forms: as a paper in a journal or other scientific publication, and as a separate or part of a series of works on a given topic or by a single author. In most cases the journal publication appeared first, but on several occasions the separates or collected works were distributed prior to the publication of the journal articles. Dating of such works is difficult, as publication dates printed within these works may be in error by as much as several years. In some cases, only a range of dates is given. An Appendix discusses two works that may potentially create nomenclatural problems.

Conventions used in the genus-group list

Genus-group taxa are listed alphabetically, followed by the author(s) and an abbreviated bibliographic citation. Full citations appear in the Literature Cited section that comprises the third part of this catalogue. The type species is then listed, followed by the geological horizon and the geographical locality for the type species. In some cases, our annotations follow the geographical range.

This is a non-critical list with subjective synonyms being shown only for a few taxa. A critical review of these taxa is currently in preparation.

Conventions used in the species-group list

The entries are listed alphabetically by species-group name, followed by the genus in which the taxon was first proposed (in parentheses), then by the author(s), date and an abbreviated citation. As in the genus list, full citations are provided in the Literature Cited section. If the taxon was proposed as a subspecies, variety or other infra-subspecific form, that information follows the reference. If the taxon is proposed as a replacement name, the abbreviation n.n. (new name or *nomen novum*) is followed by the citation on which the replacement name (either of a homonym or an incorrectly identified figure) is based. The geological horizon and geographic locality are then listed. Objective synonyms are indicated by "=". Subjective synonyms, indicated by "?=", are given only where the listed taxon is a junior homonym, where the name has a confused history, or where the subjective synonymy is thought to be helpful to users of this compilation.

Taxa incorrectly attributed are shown with the supposed author's name in single quotes followed by the citation for the reference containing the incorrect usage. Incorrect usages are generally not attributed, except when this information is thought to be particularly useful. Sources for misspellings are omitted in many cases, as are many misspellings. Only those that could cause confusion have been included.

If the genus-group taxon cited is not currently included in Cancellarioidea, the current placement of the species is given in square brackets [ ]. Conversely, if the species was originally proposed in a genus referable to Cancellarioidea, but is not now considered a cancellarioidean, current placement, if known, is also given in square brackets [ ].

ACKNOWLEDGMENTS

Publication of these lists of taxa in the Cancellarioidea is the culmination of a bibliographic search begun in 1964 when Mr. Druid Wilson, U.S. Geological Survey, gave one of us (REP) a notebook containing notes he had made on cancellariid genera over a period of many years. We are indebted to him not only for being responsible for starting this project, but also for his continued assistance and encouragement.

Mr. André Verhecken, Mortsel, Belgium, reviewed a draft of the list of species-group taxa and compared it with a list he had compiled. He graciously furnished us with references to a number of taxa that we would otherwise have overlooked.

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Compilation of these lists would not have been possible without assistance from many people who brought to our attention obscure references to cancellarioideans, and also who supplied copies of pertinent literature. At the risk of omitting some who rendered assistance, and to whom we apologize for such omission, we thank:

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Genus-group Taxa

A

Admete Kröyer in Möller, 1842:88 (ex Kröyer MS.) Type species, by monotypy, *Admete crispa* Möller, 1842 (?= *Tritonium viridulum* Fabricius, 1780). Recent, North Atlantic.

Admetopsis Meek, 1873:501. Type species, by subsequent designation of Cossmann (1895:753), *Admete gregaria* Meek, 1873. Cretaceous, Utah, U.S.A. A careful reading of Meek's text indicates that he considered his *Admete rhomboides* to be the type of the new genus. This is particularly evident in the discussion following the description of *Admete subfusiformis* where he states that *A. subfusiformis* and *A. gregaria* "may have to take the generic name *Turricula*." Although Cossmann (1899a:7) removed *Admetopsis* from the Cancellariidae, the genus appears to be cancellariid.

Admetula Cossmann, 1889:228. Type species, by original designation, *Cancellaria evulsa* (Solander, 1766) (= *Buccinum evulsa* Solander, 1766). Eocene, England.

Africostoma Eames, 1957:49. Type species, by original designation, *Trigonostoma decorata* Newton, 1922. Eocene, Nigeria.

Africosveltia Eames, 1957:48. Type species, by original designation, *Cancellaria multiplicis* Newton, 1922. Eocene, Nigeria.

Africotriton Beu and Maxwell, 1987:29. Type species, by original designation, *Epidromus crebriliratus* G.B. Sowerby III, 1903. Recent, South Africa.

Agatrix Petit, 1967:218. Type species, by original designation, *Trigonostoma agassizii* Dall, 1889. Recent, western Atlantic.

Anapepta Finlay, 1930b:241. Type species, by original designation, *Admete anomala* Marshall and Murdoch, 1920. Eocene, New Zealand.

Aneurystoma Cossmann, 1899a:23. Type species, by original designation, *Cancellaria dufourii* Grateloup, 1832. Miocene, France.

Antepepta Finlay and Marwick, 1937:82. Type species, by original designation, *Antepepta nasuta* Finlay and Marwick, 1937. Paleocene, New Zealand.

Aphera H. Adams and A. Adams, 1854:277. Type species, by monotypy, *Cancellaria tessellata* Sowerby, 1832. Recent, Panamic-Pacific.

Arizelostoma Iredale, 1936:318. Type species, by original designation, *Arizelostoma laseroni* Iredale, 1936. Recent, Australia.

Axelella Petit, 1988:130. Type species, by original designation of *Olssonella* Petit, 1970, *Cancellaria smithii* Dall, 1888. Recent, western Atlantic. Replacement name for *Olssonella* Petit, 1970, *non* Glibert and Van de Poel, 1967.

B

Babylonella Conrad, 1865a:32. Type species, by subsequent designation of Cossmann (1889:231), *Cancellaria elevata* Lea, 1833. Eocene, Alabama, U.S.A.

Barkeria Addicott, 1970:118. Type species, by original designation, *Cancellaria sanjosei* Anderson and Martin, 1914. Miocene, California, U.S.A.

Benthobia Dall, 1889a:131. Type species, by original designation, *Benthobia tryonii* Dall, 1889. Recent, North Carolina, U.S.A. Originally described in Cancellariidae, *Benthobia* was transferred to Olividae by Bouchet and Warén (1985:249).

Bivetia Jousseaume, 1887a:163. Type species, by monotypy, *Bivetia mariei* Jousseaume, 1887 (?= *Cancellaria indentata* Sowerby, 1832). Recent, Panamic-Pacific.

Bivetia Jousseaume, 1887b:193. Type species, by original designation, *Cancellaria similis* Sowerby, 1833. Recent, northwestern Africa. This usage and designation is invalid due to the prior (by one month) monotypic usage of *Bivetia* in the binomen *Bivetia mariei* Jousseaume.

Bivetiella Wenz, 1943:1356. Type species, by original designation of *Bivetia* Jousseaume, 1887b, *Cancellaria similis* Sowerby, 1833. Recent, northwestern Africa. Replacement name for *Bivetia* Jousseaume, 1887b:193, non 1887a:163.

Bivetiella Marks, 1949:456. Type species, by original designation, *Cancellaria similis* Sowerby, 1833. Recent, northwestern Africa. This is a junior objective synonym and a junior homonym of *Bivetiella* Wenz, 1943.

Bivetopsia Jousseaume, 1887b:193. Type species, by subsequent designation of Cossmann (1888:784), *Cancellaria chrysostoma* Sowerby, 1832. Recent, Panamic-Pacific.

Bivetopsis Jousseaume. Unnecessary emendation of *Bivetopsia* by Cossmann (1899a:9).

Bonellitia Jousseaume, 1887b:223. Type species, by original designation, *Cancellaria bonellii* Bellardi, 1841. Miocene/Pliocene, Italy.

Brocchinia Jousseaume, 1887b:221. Type species, by subsequent designation of Sacco (1894:68), *Brocchinia mitraeformis* (Brocchi) (= *Voluta mitraeformis* Brocchi, 1814, *non* Lamarck, 1811; ?= *Brocchinia parvula tauroparva* Sacco, 1894). Pliocene, Italy. See Petit, 1986.

Buccinella Perry, 1811:plate 27. Type species, by subsequent designation of Abbott (1950:203), *Buccinella caerulea* Perry, 1811 (?= *Turbinella pyrum* (Linne, 1767)). *Buccinella* is included here as it has traditionally been placed in the synonymy of *Cancellaria s.s.* until recent years. Among authors who cited *Buccinella* as a synonym of *Cancellaria* are H. Adams and A. Adams (1854:275), Thiele (1929:352) and almost all other cataloguers and monographers. This placement was due to the fact that Perry's first figured species, *Buccinella cannulata*, probably represents *Cancellaria reticulata* (Linné). Although *Buccinella* was often listed, no type was designated until Abbott's designation of *B. caerulea*, which is presumed to be a synonym of *Turbinella pyrum* (Linné). Unaware of Abbott's designation, Eames (1952:115) designated *Buccinella canulata* as type, placing *Buccinella* in the synonymy of *Cancellaria* had his designation been valid.

C

Calcarata Jousseaume, 1887b:214. Type species, by original designation, *Calcarata calcarata* (Brocchi) (= *Voluta calcarata* Brocchi, 1814). Pliocene, Italy.

Cancellaphera Iredale, 1930:80. Type species, by monotypy, *Cancellaphera amasia* Iredale, 1930. Recent, Australia.

Cancellaria Lamarck, 1799:71. Type species, by monotypy, *Voluta reticulata* Linné, 1767. Recent, Caribbean.

Cancellariella G. Martin, 1904:168. Type species, by original designation, *Cancellaria* (*Cancellariella*) *neritoidea* G. Martin, 1904. Miocene, Maryland, U.S.A.

Cancellarius Montfort, 1810:562. Type species, by original designation, *Voluta reticulata* Linné, 1767. A junior objective synonym of *Cancellaria*.

Cancelrana Palmer, 1937:455. Type species, by original designation, *Pleurotoma* (*Taranis*) *finexa* Harris, 1895. Eocene, Texas, U.S.A.

Caveola Stephenson, 1941:363. Type species, by original designation, *Cancellaria acuta* Wade, 1926. Cretaceous, Tennessee, U.S.A.

Charcolleria Olsson, 1942:61. Type species, by original designation, *Cancellaria* (*Charcolleria*) *perdiciana* Olsson, 1942. Miocene, Colombia.

Contortia Sacco, 1894:48. Type species, by original designation, *Cancellaria contorta* Basterot, 1825. Tertiary, France.

Coptostoma Cossmann, 1899a:34. Type species, by original designation, *Cancellaria quadrata* J. Sowerby, 1822. Eocene, England.

Coptostomella Finlay and Marwick, 1937:83. Type species, by original designation, *Coptostomella pupa* Finlay and Marwick, 1937. Paleocene, New Zealand.

Crawfordia Dall, 1918:138. Type species, by original designation, *Cancellaria crawfordiana* Dall, 1891. Recent, California, U.S.A. Not *Crawfordia* Pierce, 1908 (Coleoptera). Renamed *Crawfordina* Dall, 1919.

Crawfordina Dall, 1919:306. Type species, by monotypy, *Cancellaria crawfordiana* Dall, 1891. Recent, California, U.S.A. Although obviously a replacement name for the preoccupied *Crawfordia*, that fact is not mentioned. As no type designation is made, and it is not stated that this is a replacement name, type designation is by monotypy.

D

Daguinia Magne, 1966:127. Type species, by monotypy, *Daguinia vigneauxi* Magne, 1966. Miocene, France.

Dellina Beu, 1970:223. Type species, by original designation, *Waipaoa munida* Ponder, 1968 (?= *Antizafra aoteana* Dell, 1956). Recent, New Zealand.

E

Egerea Gábor, 1936:7. Type species, by monotypy, *Egerea collectiva* Gábor, 1936. Oligocene, Hungary.

Emmonsella Olsson and Petit, 1964:541. Type species, by original designation, *Trigonostoma tenerum* (Philippi, 1848) (= *Cancellaria tenera* Philippi, 1848). Recent, Caribbean. A junior subjective synonym of *Ventrilia*.

Esbelta Sarasúa, 1975:2. Type species, by original designation, *Ranella lanceolata* Menke, 1828. Recent, Caribbean.

Euclia H. Adams and A. Adams, 1854:277. Type species, by subsequent designation of Cossmann (1899a:10), *Cancellaria cassidiformis* Sowerby, 1832. Recent, Panamic-Pacific.

Exechoptychia Cossmann, 1903b:189. Type species, by original designation, *Cancellaria conradiana* Dall, 1890. Pliocene, Florida and the Carolinas, U.S.A. A junior subjective synonym of *Cancellaria*.

Extractrix Korobkov, 1955:138. Type species, by original designation, *Pseudomalaxis extractrix* (Boettger, 1906) (= *Discohelix extractrix* Boettger, 1906). Miocene, Romania.

F

Fusiaphera Habe, 1961a:72, Appendix p. 27. Type species, by original designation, *Fusiaphera macrospira* Adams and Reeve) (= *Cancellaria macrospira* Adams and Reeve, 1850). Recent, Japan.

G

Gerdiella Olsson and Bayer, 1972:876. Type species, by original designation, *Gerdiella gerda* Olsson and Bayer, 1972. Recent, Caribbean.

Gergovia Cossmann, 1899a:16. Type species, by original designation, *Cancellaria platypleura* Tate, 1898 (= *Cancellaria laticostata* Tenison-Woods, 1879). Eocene, Australia.

Gulia Jousseaume, 1887b:194. Type species, by subsequent designation of Cossmann (1888:784), *Cancellaria acutangula* Faujas de Saint Fond, 1817. Miocene, France.

H

Habesolatia Kuroda, 1965:8. Type species, by original designation, *Cancellaria nodulifera* Sowerby, 1825. Recent, Japan.

Hertleinia Marks, 1949:457. Type species, by original designation, *Cancellaria mitriformis* Sowerby, 1832. Recent, Panamic-Pacific.

Hetereuclia 'Roverto' - Wenz, 1943:1357. Error for *Heteroeuclia* Rovereto.

Heteroeuclia Rovereto, 1899:103. Unnecessary replacement name for *Euclia* Adams and Adams, 1854, which Rovereto considered to be preoccupied by *Euclea* Hübner, 1816, and *Euclea* Newman, 1842.

I

Inermia Korobkov, 1955:328. Type species, by original designation, *Cancellaria inermis* Pusch, 1837. Tertiary, Poland. *Inermia* is preoccupied and a new name must be proposed if this is found to be a valid genus-level group.

Inglisella Finlay, 1924c:513. Type species, by original designation, *Ptychatractus pukeuriensis* Suter, 1917. Miocene, New Zealand.

Iphinoella Habe, 1958:34, 40. Type species, by monotypy, *Iphinoella choshiensis* Habe, 1958. Recent, Japan. Placed in synonymy of *Iphinopsis* Dall by Habe (1962:73) and Bouchet and Warén (1985:261).

Iphinopsis Dall, 1924:88. Type species, by original designation, *Iphinoe kelseyi* (Dall, 1908) (= *Trichotropis kelseyi* Dall, 1908). Recent, California, U.S.A. Transferred from Trichotropidae to Cancellariidae by Bouchet and Warén (1985:261).

J

Junghuhnia K. Martin, 1931:11. Type species, by monotypy, *Trigonostoma* (*Junghuhnia*) *ficus* K. Martin, 1931. Eocene, Indonesia.

K

Kapuatriton Beu and Maxwell, 1987:24. Type species, by original designation, *Kapuatriton kaitarus* Beu and Maxwell, 1987. Eocene, New Zealand.

L

Loxotaphrus G. F. Harris, 1897:165. Type species, by original designation, *Phos variciferus* Tate, 1888. Miocene, Australia.

M

Maorivetia Finlay, 1924c:513. Type species, by original designation, *Turbinella brevirostris* Hutton, 1877. Miocene, New Zealand.

Marianarona Petuch, 1988:27. Type species, by original designation, *Cancellaria alternata* Conrad, 1834. Miocene, Maryland, U.S.A.

Mariasveltia Petuch, 1988:34. Type species, by original designation, *Cancellaria lunata* Conrad, 1830. Miocene, Maryland, U.S.A.

Marksella Olsson, 1964:127. Type species, by original designation, *Admete* (*Marksella*) *jumala* Olsson, 1964. Pliocene, Ecuador.

Massyla H. Adams and A. Adams, 1854:278. Type species, by monotypy, *Cancellaria corrugata* Hinds, 1843. Recent, Panamic-Pacific.

Mataxa Wade, 1917:455. Type species, by original designation, *Mataxa elegans* Wade, 1917. Cretaceous, Tennessee, U.S.A.

Merica H. Adams and A. Adams, 1854:277. Type species, by subsequent designation of Cossmann (1899a:13), *Cancellaria melanostoma* Sowerby, 1849. Recent, Indian Ocean.

Mericella Thiele, 1929:352. Type species, by monotypy, *Cancellaria jucunda* Thiele, 1925. Recent, eastern Africa.

Microcancilla Dall, 1924:87. Type species, by original designation, *Admete microscopica* (Dall, 1889) (= *Cancellaria microscopica* Dall, 1889). Recent, Caribbean.

Microsveltia Iredale, 1925:265. Type species, by original designation, *Microsveltia recessa* Iredale, 1925. Recent, Australia.

Misteia Janssen, 1984:16. Type species, by original designation, *Cancellaria planispira* Nyst, 1845. Miocene, Netherlands.

Momoebora Habe and Kikuchi, 1960:51. *Nomen nudum.*

Momoebora 'Habe (MS)', Azuma, 1960:49. *Nomen nudum.*

Momoebora Kuroda and Habe, 1971:310 [Japanese], 202 [English]. Type species, by original designation, *Cancellaria sinensis* Reeve, 1856. Recent, Japan.

N

Narona H. Adams and A. Adams, 1854:277. Type species, by subsequent designation of Jousseaume (1887b:222), *Cancellaria clavatula* Sowerby, 1832. Recent, Panamic-Pacific.

Neadmete Habe, 1961a:73, Appendix p. 28. Type species, by I.C.Z.N. Opinion 1370, *Neadmete okutanii* Petit, 1974. Recent, Japan.

Nevia Jousseaume, 1887b:222. Type species, by original designation, *Cancellaria spirata* Lamarck, 1822. Recent, Australia.

Nipponaphera Habe, 1961a:72, Appendix p. 27. Type species, by I.C.Z.N. Opinion 1052, *Nipponaphera habei* Petit, 1972. Recent, Japan.

Nivitriton Iredale, 1929b:288. Type species, by original designation, *Triton antiquatus* Hinds in Reeve, 1844. Recent, Indo-Pacific.

Nothoadmete Oliver, 1982:15. Type species, by monotypy, *Nothoadmete tumida* Oliver, 1982. Recent, Antarctica.

O

Oamaruia Finlay, 1924c:514. Type species, by original designation, *Admete suteri* Marshall and Murdoch, 1920. Miocene, New Zealand.

Olssonella Petit, 1970:83. Type species, by original designation, *Cancellaria smithii* Dall, 1888. Recent, Caribbean. Not *Olssonella* Glibert and Van de Poel, 1967. Renamed *Axelella* Petit, 1988.

Ovilia Jousseaume, 1887b:193. Type species, by original designation, "*O. doliaris* Bast." (= *Cancellaria doliolaris* Basterot, 1825). Miocene, France.

P

Paladmete Gardner, 1916:412. Type species, by original designation, *Trichotropis cancellaria* Conrad, 1858. Cretaceous, Mississippi, U.S.A.

Palaeadmete 'Gardner' - Okutani, 1964:398. Error for *Paladmete* Gardner.

Palaeocancellaria Kollmann, 1976:199. Type species, by original designation, *Palaeocancellaria hoelleitenensis* Kollmann, 1976. Cretaceous, Austria.

Pallidonia Laseron, 1955:272. Type species, by original designation, *Pallidonia simplex* Laseron, 1955. Recent, Australia.

Panarona Petit, 1975:387. Type species, by original designation, *Cancellaria clavatula* Sowerby, 1832. Recent, Panamic-Pacific. An unnecessary name which is a junior objective synonym of *Narona*.

Paradmete Strebel, 1908:22. Type species, by indication (I.C.Z.N. Article 68c), *Paradmete typica* Strebel, 1908. Recent, Antarctica. Originally described in Cancellariidae, *Paradmete* is now placed in Volutomitridae.

Peptu Iredale, 1925:266. Type species, by monotypy, *Admete stricta* Hedley, 1907. Recent, Australia.

Perplicaria Dall, 1890:90. Type species, by monotypy, *Perplicaria perplexa* Dall, 1890. Pliocene, Florida, U.S.A.

Peruclia Pilsbry and Olsson, 1941:24. Error for *Pyruclia* Olsson, 1932.

Plesiocerithium Cossmann, 1889:232. Type species, by original designation, "*Cancellaria magloirei* Melleville, 1843" (= *C. maglorii* Melleville, 1843). Lower Eocene, France.

Plesiotriton Fischer, 1884:654. Type species, by original designation, *Cancellaria volutella* Lamarck, 1803. Eocene, France.

Plicaria Fabricius, 1823:74. Fabricius' work has been placed on the Official Index of Rejected and Invalid Works in Zoological Nomenclature by I.C.Z.N. Opinion 521. Prior to placement of this work on the Official Index, *Plicaria* was traditionally included in the synonymy of *Cancellaria*. Eames (1952:116) designated "*P. reticulata* (L.) (= *Cancellaria reticulata* (Linné))" as type.

Preangeria K. Martin, 1921:450. Type species, by subsequent designation of Wenz (1943:1356), *C.* (*P.*) *angsanana* (K. Martin) (= *Preangeria angsanana* K. Martin, 1921). Tertiary, Indonesia. Martin did not designate a type species and Wenz (1943:1356) shows type by monotypy. This is incorrect as Martin described two species in his new genus. However, Wenz' citation may be taken as a subsequent designation. *Preangeria* was originally described in Cancellariidae, but was transferred to Purpuridae by K. Martin (1928:124).

Pristimerica Finlay and Marwick, 1937:82. Type species, by original designation, *Pristimerica dolioides* Finlay and Marwick, 1937. Paleocene, New Zealand.

Procancellaria Wilckens, 1922:21. Type species, by monotypy, *Procancellaria parkiana* Wilckens, 1922. Cretaceous, New Zealand. Originally described in Cancellariidae, *Procancellaria* was transferred to Littorinidae by Finlay and Marwick (1937:81).

Progabbia Dall, 1918:138.] Type species, by original designation, *Cancellaria cooperi* Gabb, 1865. Recent, California, U.S.A.

Pyruclia Olsson, 1932:160. Type species, by original designation, *Cancellaria solida* Sowerby, 1832. Recent, Panamic-Pacific.

R

Rhomboidestoma K. Martin, 1931:12. Type species, by monotypy, *Rhomboidestoma oscitans* K. Martin, 1931. Eocene, Indonesia.

S

Scalptia Jousseaume, 1887b:213. Type species, by original designation, *Cancellaria obliquata* Lamarck, 1822. Recent, Indo-Pacific.

Semitriton Cossmann, 1903b:102. Type species, by original designation, *Plesiotriton dennanti* Tate, 1898. Eocene, Australia.

Solatia Jousseaume, 1887b:222. Type species, by original designation, "*Solatia solat* Adams (*Piscatorum* Chemn.)" (= *Buccinum piscatorium* Gmelin, 1791). Recent, western Africa. "Adams" as used by Jousseaume is an error for Adanson, whose non-binominal work referred to the type species as *Le Solat*.

Solutosveltia Habe, 1961b:433. Type species, by monotypy, *Solutosveltia abyssicola* Habe, 1961. Recent, Japan.

Sveltella Cossmann, 1889:226. Type species, by original designation, *Cancellaria quantula* Deshayes, 1864. Eocene, France.

Sveltia Jousseaume, 1887b:214. Type species, by original designation, "*Sveltia varicosa* Brocc." (= *Voluta varricosa* Brocchi, 1814). Pliocene, Italy.

Sydaphera Iredale, 1929a:341. Type species, by original designation, *Sydaphera renovata* Iredale, 1929. Recent, Australia.

T

Tatara Fleming, 1950:247. Type species, by original designation, *Cymatium pahiense* Marshall and Murdoch, 1921. Eocene, New Zealand.

Torellia Jeffreys, 1867:244. Type species, by monotypy, *Torellia vestita* Jeffreys, 1867. Recent, North Sea. Originally described in Cancellariidae, *Torellia* is now placed in Trichotropidae.

Tribia Jousseaume, 1887b:221. Type species, by original designation, "*Tribia angasi* Crosse" (= *Cancellaria angasi* Crosse, 1863). Recent, western Africa.

Trigona Perry, 1811:pl. 51. Type species, by monotypy, *Trigona pellucida* Perry, 1811. Not *Trigona* Jurine, 1807 (Hymenoptera). This preoccupied taxon is a subjective synonym of *Trigonostoma* Blainville.

Trigonaphera Iredale, 1936:319. Type species, by original designation, *Trigonostoma vinnulum* Iredale, 1925. Recent, Australia.

Trigonostoma Blainville, 1827:652. Type species, by monotypy, *Delphinula trigonostoma* Lamarck, 1822 (?= *Buccinum scalare* Gmelin, 1791). Recent, Indo-Pacific.

Tritonoharpa Dall, 1908:319. Type species, by original designation, *Tritonoharpa vexillata* Dall, 1908. Recent, Galapagos Islands.

Turehua Marwick, 1943:189. Type species, by original designation, *Latirus dubius* Marshall, 1919. Eocene, New Zealand.

U

Unitas Palmer, 1947:413. Type species, by original designation of *Uxia* Jousseaume, *Cancellaria costulata* Lamarck, 1803. Eocene, France. Replacement name for *Uxia* Jousseaume, 1887, non Walker, 1866.

Uxia Jousseaume, 1887b:222. Type species, by original designation, *Cancellaria costulata* Lamarck, 1803. Eocene, France. Not *Uxia* Walker, 1866 (Lepidoptera). Renamed *Unitas* Palmer, 1947.

V

Varicohilda Eames, 1957:40. Type species, by original designation, *Hilda turriculata* Newton, 1922. Eocene, Nigeria.

Ventrilia Jousseaume, 1887a:164. Type species, by monotypy, *Ventrilia ventrilia* Jousseaume, 1887 (= *Cancellaria tenera* Philippi, 1848). Recent, Caribbean.

Vercomaris Garrard, 1975:42. Type species, by original designation, *Cancellaria pergradata* Verco, 1904. Recent, Australia.

W

Waipaoa Marwick, 1931:122. Type species, by original designation, *Admete cristata* Marwick, 1926. Miocene, New Zealand.

Z

Zeadmete Finlay, 1926b:429. Type species, by original designation, *Cancellaria trailli* Hutton, 1873. Recent, New Zealand.

Species-Group Taxa

A

abnormis (*Cancellaria*) Gray, 1847:136. *Nomen nudum.*

abnormis (*Admete*) 'Morch & Poulson MS' – Harmer, 1918:408; in synonymy of *A. viridula* var. *couthouyi* (Jay). *Nomen nudum.*

abyssicola (*Solutosveltia*) Habe, 1961b:433, pl. 23, fig. 4. Recent, Japan.

acalypta (*Cancellaria*) Woodring, 1970:341, pl. 53, figs. 1-2. Tertiary, Panama.

aclinica (*Colubraria*) Tucker & Wilson, 1933:70, pl. 11, fig. 14. Pliocene, Florida, U.S.A. [?= *Tritonoharpa lanceolata* (Menke, 1828)]

acosticillata (*Cancellaria*) Sacco, 1894:10; as var. of *C. ampullaceum* (Brocchi); see Appendix, Note 2. Pliocene, Italy.

acuminata (*Cancellaria*) G. B. Sowerby I, 1832a:53; 1832b:fig. 5. Recent, Panamic-Pacific.

acuminata (*Cancellaria*) Bellardi, 1841:38, pl. 4, figs. 15-16. Tertiary, Europe. (= *C. subacuminata* d'Orbigny, 1852)

acuta (*Cancellaria*) Wade, 1926:108, pl. 35, figs. 4-5. Cretaceous, Tennessee, U.S.A.

acutangula (*Cancellaria*) Faujas de Saint Fond, 1817:197, pl. 10, figs. 1, 1a. Miocene, France.

acutangularis (*Cancellaria*) Lamarck, 1822b:116. Miocene, France. (= *C. acutangula* Faujas de Saint Fond, 1817)

acuticarinata (*Cancellaria*) Weisbord, 1929:51, pl. 6, fig. 7. Miocene, Colombia.

acutiplicata (*Cancellaria*) Shuto, 1962:74, pl. 10, figs. 4-5; as subsp. of *C. pristina* Yokoyama. Pliocene, Japan.

adami (*Cancellaria*) 'Eichwald' – Sherborn, 1922:70. Error for *Cassis adami* Eichwald, 1830.

adelae (*Cancellaria*) Pilsbry, 1940:54, pl. 3, fig. 1; as subsp. of *C. reticulata* (Linné). Recent, Florida, U.S.A.

adicana (*Cancellaria*) Pereira Da Costa, 1867:210, pl. 25, figs. 1a-b. Miocene, Portugal.

aegyptiaca (*Cancellaria*) Oppenheim, 1906:331, pl. 26, figs. 18a-b. Eocene, Egypt.

aequaeva (*Cancellaria*) Ryckholt, 1862:pl. 32, figs. 32-33. Cretaceous, Belgium.

aequicosticillata (*Cancellaria*) Sacco, 1894:44, pl. 3, fig. 10; as var. of *C. serrata* Bronn; see Appendix, Note 2. Miocene, Italy.

aequivaricosa (*Cancellaria*) Sacco, 1894:4, pl. 1, fig. 2; as var. of *C. oligolongum* Sacco; see Appendix, Note 2. Oligocene, Italy.

aethiopica (*Admete*) Thiele, 1925:201, pl. 22, fig. 23. Recent, eastern Africa. [not a cancellariid]

afasciata (*Cancellaria*) Sacco, 1894:63, pl. 3, fig. 67; as var. of *C. intermedia* Bellardi; see Appendix, Note 2. Miocene, Italy.

afenestrata (*Aphera*) Sacco, 1894:67; n.n. for "*C. dufourii* Grateloup" Hörnes, 1854:pl. 44, fig. 9; as var. of *A. bronni* (Bellardi). Miocene, Austria.

affectata (*Waipaoa*) Marwick, 1931:123, pl. 13, fig. 241. Miocene, New Zealand.

affinis (*Cancellaria*) C.B. Adams, 1852a:356. Recent, Panamic-Pacific. (?= *C. ventricosa* Hinds, 1843)

affinis (*Cancellaria*) Reeve, 1856:pl. 9, figs. 39a-b. Recent, Panamic-Pacific. (?= *C. indentata* Sowerby, 1832)

africana (*Cancellaria*) Petit, 1970:86; n.n. for *C. imbricata* Watson, 1882, *non* Hörnes, 1856. Recent, South Africa.

agalma (*Cancellaria*) Melvill & Standen, 1901:450, pl. 24, fig. 18. Recent, Gulf of Oman.

agassizii (*Trigonostoma*) Dall, 1889a:130, pl. 35, fig. 4. Recent, Carolinas to Gulf of Mexico.

agria (*Cancellaria*) Mansfield, 1930:48, pl. 3, fig. 1. Miocene, Florida, U.S.A.

alabamensis (*Cancellaria*) Gabb, 1860a:301, pl. 48, fig. 14. Cretaceous, Alabama, U.S.A. [*Turbinella*]

alaskensis (*Cancellaria*) B. L. Clark, 1932:832, pl. 20, figs. 10, 12, 16, 17. Oligocene, Alaska, U.S.A.

alba (*Cancellaria*) Webb, 1936:125; as var. of *C. reticulata* (Linné). *Nomen nudum.*

alba (*Cancellaria*) 'Sowerby' – Domenech, Espinosa, Marquina & Martinell, 1983:45; as subsp. of *C. similis* Sowerby. *Nomen nudum.*

alba (*Iphinopsis*) Bouchet & Warén, 1985:263, figs. 695-697. Recent, Bay of Biscay, Europe.

albida (*Cancellaria*) Hinds, 1843:47; 1844b:42, pl. 12, figs. 9-10. Recent, Panamic-Pacific.

albrechtina (*Cancellaria*) Mayer, 1861b:118. Oligocene, Europe.

aldrichi (*Cancellaria*) Gardner, 1937:372, pl. 45, fig. 2. Miocene, Florida, U.S.A.

allophyla (*Inglisella*) Maxwell, 1988:70, pl. 11, figs. m-o. Miocene, New Zealand.

alta (*Paladmete*) Stephenson, 1941:367, pl. 71, figs. 12-13. Cretaceous, Texas, U.S.A.

altavillae (*Cancellaria*) Aradas, 1846:173, pl. 1, figs. 10a-b. Tertiary, Italy.

altavillae (*Cancellaria*) Libassi, 1859:38, fig. 15; as *altavill.* [*sic*]; as var. of *C. labrosa* Bellardi. Tertiary, Italy.

altavillae (*Cancellaria*) Libassi, 1859:40, fig. 25; as var. of *C. contorta* Basterot. Tertiary, Italy.

alternata (*Cancellaria*) Conrad, 1834:155. Miocene, Maryland, U.S.A.

alternicostula (*Cancellaria*) Sacco, 1894:19, pl. 1, fig. 53; see Appendix, Note 2. Miocene, Italy.

altispira (*Cancellaria*) Gabb, 1869:50, pl. 14, fig. 7. Pliocene, California, U.S.A.

alumensis (*Cancellaria*) Mansfield, 1930:49, pl. 4, fig. 5; as subsp. of *C. perspectiva* Conrad. Miocene, Florida, U.S.A.

alvaniopsis (*Cancellaria*) 'Harris' – Cossmann, 1899a:34. *Nomen nudum.*

alveata (*Cancellaria*) Conrad, 1833:45; 1835:44, pl. 16, fig. 19. Eocene, Alabama, U.S.A.

alveolata (*Cancellaria*) Tate, 1889:154, pl. 10, figs. 7a-b. Miocene, Australia.

amakusana (*Trigonaphera*) Petit, 1974:112, text-fig. 4. Recent, Japan.

amasia (*Cancellaphera*) Iredale, 1930:80, pl. 9, fig. 8. Recent, Australia.

ambigua (*Admete*) Hutton, 1885:320, pl. 18, fig. 18. Pliocene, New Zealand. [*Acteon*]

ameghinoi (*Cancellaria*) von Ihering, 1897:310, pl. 3, fig. 12; pl. 4, fig. 15. Tertiary, Argentina.

amekiensis (*Bonellitia*) Eames, 1957:49, pl. 7, figs. 5a-c. Eocene, Nigeria.

amoena (*Cancellaria*) Olsson & Harbison, 1953:179, pl. 28, fig. 7. Pliocene, Florida, U.S.A.

ampla (*Inglisella*) Laws, 1935:37, pl. 6, fig. 16. Miocene, New Zealand.

ampleumbilicata (*Cancellaria*) Sacco, 1894:33, pl. 2, fig. 42; as var. of *C. calcarata* (Brocchi); see Appendix, Note 2. Miocene, Italy.

ampulla (*Cancellaria*) 'Broc.'. Error for *C. ampullacea* Brocchi.

ampullacea (*Voluta*) Brocchi, 1814:313, pl. 3, figs. 9a-b. Pliocene, Italy. [*Trigonostoma s.l.*]

ampullacera (*Cancellaria*) Lesson, 1841b:253. Recent, ? New Zealand. *Nomen dubium.*

anachoreta (*Cancellaria*) Mayer, 1876:45, pl. 4, fig. 18. Tertiary, Europe.

ancycla (*Cancellaria*) Gardner, 1937:374, pl. 45, figs. 6-7. Miocene, Florida, U.S.A.

andaluciensis (*Trigonostoma*) Landau, 1984:151, pl. 2, figs. 12-17. Pliocene, Spain.

andersoni (*Cancellaria*) Arnold, 1909:60, pl. 9, fig. 5. Miocene, California, U.S.A.

andersoni (*Cancellaria*) B. L. Clark, 1918:80, 82, 97, pl. 23, fig. 4. Oligocene, California, U.S.A. (?= *C. oregonensis* Conrad, 1865)

angasi (*Cancellaria*) Crosse, 1863:64, pl. 2, fig. 8. Recent, northwestern Africa.

angasi (*Tritonium*) Brazier, 1877:174. Recent, Australia. [*Tritonoharpa*]

angelana (*Cancellaria*) G. D. Hanna, 1924:159; n.n. for *C. quadrata* Moody, 1916, *non* Sowerby, 1822. Pliocene, California, U.S.A.

anglica (*Cancellaria*) Sacco, 1894:9; n.n. for "*C. umbilicaris* (Brocchi)" Wood, 1874:Add. pl., fig. 10; as var. of *C. ampullaceum* (Br.); see Appendix, Note 2. Pliocene, England.

angosturana (*Cancellaria*) Marks, 1949:463, pl. 78, figs. 1-2. Miocene, Ecuador.

angulata (*Cancellaria*) Eichwald, 1830:222. Tertiary, Europe.

angulata (*Cancellaria*) 'Watelet' – Jousseaume, 1887b:222. Error for *C. angusta* Watelet.

angulata (*Cancellaria*) Sieber, 1936:98; as var. of *C. inermis* Pusch. Miocene, Austria.

angulatina (*Cancellaria*) Sacco, 1894:40, pl. 2, fig. 64; as var. of *C. dertonensis* Bellardi; see Appendix, Note 2. Miocene, Italy.

angulifera (*Cancellaria*) Deshayes, 1864:107, pl. 73, figs. 13-15. Middle Eocene, France.

angulifera (*Cancellaria*) von Koenen, 1885:10, pl. 1, figs. 6a-b. Paleocene, Denmark. (= *Narona ravni* Glibert, 1960)

angulopusilla (*Admete*) Sacco, 1894:71; n.n. for "*C. pusilla* (Phil.)" Beyrich, 1856:pl. 28, fig. 1; as var. of *A. exilis* (Philippi). Tertiary, Germany.

angulosior (*Admete*) Sacco, 1894:71; n.n. for "*C. subangulosa* Wood" Speyer, 1867:pl. 11 [*sic*; error for pl. 16], fig. 11; as var. of *A. exilis* (Philippi). Tertiary, Germany.

angulovaricosa (*Cancellaria*) Sacco, 1894:57, pl. 3, figs. 53a-b; see Appendix, Note 2. Miocene, Italy.

angusta (*Cancellaria*) Watelet, 1851:124, pl. 2, figs. 3-4. Lower Eocene, France.

angusta (*Cancellaria*) Almera & Bofill, 1884:46, pl. D, figs. 21-22; as var. of *C. lyrata* (Brocchi). Tertiary, Spain.

annosa (*Cancellaria*) Aldrich, 1898:97. Eocene, Alabama, U.S.A.

annulata (*Cancellaria*) Stoliczka, 1867:162, pl. 13, fig. 11. Cretaceous, India.

anodosomagna (*Brocchinia*) Sacco, 1894:69, pl. 3, fig. 84; as var. of *B. mitraeformis* (Brocchi). Pliocene, Italy.

anomala (*Admete*) Marshall & Murdoch, 1920:132, pl. 6, fig. 6. Eocene, New Zealand.

anomoia (*Cancellaria*) Woodring, 1970:334, pl. 52, figs. 1-2. Miocene, Panama.

ansonae (*Tritonoharpa*) Beu & Maxwell, 1987:35, pls. 13, figs. e-i; pl. 14, figs. h-k, m-p. Recent, western Australia.

antarctica (*Admete*) Strebel, 1908:21, pl. 4, figs. 44a-c. Recent, Antarctic.

antiqua (*Cancellaria*) 'Wagner' – Bronn, 1848:208. *Nomen nudum.*

antiqua (*Cancellaria*) Dall, 1897:11, pl. 3, fig. 3; *ex* Wagner MS. Tertiary, southeastern U.S.A.

antiquata (*Cancellaria*) Hinds, 1843:49; 1844b:43, pl. 12, figs. 17-18. Recent, Indo-Pacific.

antiquata (*Cancellaria*) 'Edwards MS' – Wrigley, 1935:372; in synonymy of *Bonellitia clarendonensis* Wrigley. *Nomen nudum.*

antiquatus (*Triton*) Hinds in Reeve, 1844:pl. 18, fig. 80. Recent, Indo-Pacific. [*Tritonoharpa*]

anxifer (*Cancellaria*) Iredale, 1925:264; as subsp. of *C. purpuriformis* Kuster [*sic*]. Recent, Australia.

aoteana (*Antizafra*) Dell, 1956:111, pl. 11, fig. 110. Recent, New Zealand. [?= *Dellina*]

apater (*Cancellaria*) Ryckholt, 1861:pl. 30, figs. 24-25. Cretaceous, Belgium.

apenninensis (*Cancellaria*) Sacco, 1894:54, pl. 3, fig. 41; as var. of *C. varicosa* (Br.); see Appendix, Note 2. Tertiary, Italy.

aperta (*Cancellaria*) Beyrich, 1856:586, pl. 28, figs. 5a-d. Miocene, Germany.

aphrogenia (*Colubraria*) Pilsbry & Lowe, 1932:62, pl. 4, fig. 10. Recent, Panamic-Pacific. [*Tritonoharpa*]

apimela (*Cancellaria*) Woodring, 1970:337, pl. 52, figs. 5-6. Miocene, Panama.

aqualica (*Cancellaria*) Petit & Harasewych, 1986:440, figs. 7-8. Recent, Philippines.

araeostyla (*Oamaruia*) Maxwell, 1988:71, pl. 11, figs. d, h, l. Miocene, New Zealand.

aquilara (*Buccinum*) Watson, 1882b:359. [a turrid; incorrectly placed in Cancellariidae by several authors]

arctica (*Cancellaria*) Middendorff, 1849:112, pl. 9, figs. 11-12, 15. Recent, Bering Strait.

arenaria (*Sveltella*) Wrigley, 1935:363, pl. 32, figs. 10-11. Paleocene, England.

arnoldi (*Cancellaria*) Dall, 1909a:29, pl. 14, fig. 7. Pliocene, California, U.S.A.

articularis (*Cancellaria*) G. B. Sowerby I, 1832b:fig. 32. Recent, Sri Lanka.

asheri (*Marianarona*) Petuch, 1988:27, pl. 5, figs. 9-10. Miocene, Maryland, U.S.A.

aspera (*Cancellaria*) Millet de la Turtaudière, 1866:10. Tertiary, France.

aspera (*Cancellaria*) 'Edwards MS' – Newton, 1891:169. *Nomen nudum.*

aspercella (*Cancellaria*) 'Lamarck'. Error for *asperella* Lamarck.

asperella (*Cancellaria*) Lamarck, 1822b:112. Recent, Indo-Pacific.

asperula (*Cancellaria*) Deshayes, 1830:187. Recent, Indo-Pacific. (?= *C. obliquata* Lamarck, 1822)

asprella (*Merica*) 'Lamarck' – Habe, 1961b:434; *et al.* Error for *C. asperella* Lamarck.

assimile (*Cancellaria*) 'Sowerby'. Error for *similis* Sowerby.

assimilis (*Cancellaria*) 'Sowerby'. Error for *similis* Sowerby.

astensis (*Cancellaria*) Bellardi, 1840:344; as var. of *C. cancellata* Lam. [*sic*]. *Nomen nudum.*

astensis (*Cancellaria*) Bellardi, 1841:28, pl. 3, figs. 17-18; as var. of *C. cancellata* Lam. [*sic*]. Tertiary, Italy.

atjehense (*Trigonostoma*) Oostingh, 1938:109, pl. 6, figs. 118-120. Pliocene, Indonesia.

atopodonta (*Cancellaria*) Petit & Harasewych, 1986:440, figs. 5-6, 15-16. Recent, Philippines.

atraktoides (*Cancellaria*) Gardner, 1937:376, pl. 45, figs. 13-14. Miocene, Florida, U.S.A.

aturensis (*Sveltia*) Peyrot, 1928:228, pl. 13, figs. 46-47. Miocene, France.

aturensis (*Tritonidea*) Peyrot, 1926:242, pl. 4, figs. 50-52. Miocene, France. [*Loxotaphrus*]

aupouria (*Zeadmete*) Powell, 1940:243, pl. 29, fig. 13. Recent, New Zealand.

auriculaperta (*Cancellaria*) Vokes, 1938:22, figs. 19-20. Pliocene, Trinidad.

auriculoides (*Cancellaria*) Millet de la Turtaudière, 1854:160. Tertiary, France.

aurorae (*Trigonostoma*) Palmer, 1937:445, pl. 73, figs. 14-16. Eocene, South Carolina, U.S.A.

australis (*Cancellaria*) G. B. Sowerby I. 1832b:fig. 23. Recent, Australia.

australis (*Cancellaria*) Philippi, 1855:208; 1856a:164; 1856b:99. Recent, Strait of Magellan. (= *Admete philippi* von Ihering, 1907).

austriaca (*Cancellaria*) Hoernes & Auinger, 1890:275, pl. 33, figs. 15a-c. Miocene, Austria.

avara (*Columbella*) Say, 1822. [incorrectly placed in *Cancellaria* by several authors]

aveniformis (*Cancellaria*) 'Edwards MS' – Newton, 1891:170. *Nomen nudum.*

awakinoensis (*Inglisella*) Laws, 1935:38, pl. 6, fig. 18. Miocene, New Zealand.

azorica (*Admete*) Bouchet & Warén, 1985:260, fig. 690. Recent, Azores.

azumai (*Cancellaria*) 'Habe MS' – Azuma, 1960:48. *Nomen nudum.*

azumai (*Fusiaphera*) Habe, 1961a:72, Appendix p. 28, pl. 35, fig. 20. Recent, Japan.

B

babylonica (*Cancellaria*) I. Lea, 1833:138, pl. 5, fig. 134. Eocene, Alabama, U.S.A.

badensis (*Cancellaria*) Sacco, 1894:60; n.n. for "*C. lyrata* (Brocchi)" Hörnes, 1854:pl. 34, fig. 4; as var. of *C. lyrata* (Brocchi); see Appendix, Note 2. Miocene, Austria.

badrii (*Cancellaria*) Abbass, 1972:59, pl. 4, fig. 14. Paleocene, Saudi Arabia.

bahia (*Cancellaria*) Pilsbry & Olsson, 1941:24, pl. 3, fig. 3. Pliocene, Ecuador.

balboae (*Cancellaria*) Pilsbry, 1931:439, pl. 41, figs. 7-8. Recent, Panama Bay.

bantamense (*Trigonostoma*) Oostingh, 1938:110, pl. 6, figs. 122a-c. Pliocene, Indonesia.

barjonae (*Cancellaria*) Pereira Da Costa, 1867:201, pl. 25, figs. 9-13. Miocene, Portugal.

barkeri (*Fossarus*) F. M. Anderson in G. D. Hanna, 1924:165; unnecessary n.n. for *Fossarus dalli* Anderson & Martin, 1914. [Cancellariidae]

barkeri (*Zeadmete*) Powell, 1952:184, pl. 36, fig. 1. Recent, New Zealand.

barnardi (*Trigonostoma*) Janssen, 1984:19, pl. 3, figs. 9-14; pl. 6, fig. 3. Miocene, Netherlands.

barretti (*Cancellaria*) Guppy, 1866:289, pl. 17, fig. 11. Pliocene, Jamaica.

bartonensis (*Bonellitia*) Wrigley, 1935:368, pl. 33, fig. 16. Eocene, England.

barystoma (*Cancellaria*) Woodring, 1970:342, pl. 53, figs. 5-6. Miocene, Panama.

basicosticillata (*Cancellaria*) Sacco, 1894:34, pl. 2, fig. 46; as var. of *C. calcarata* (Brocchi); see Appendix, Note 2. Pliocene, Italy.

basilaevis (*Tritonoharpa*) Beu & Maxwell, 1987:37, pl. 16, figs. a-i, k-l. Recent, western Pacific.

basisulcata (*Sveltia*) Peyrot, 1928:237, pl. 12, figs. 39-40; as "mut." of *S. calcarata* (Brocchi). Miocene, France.

basteroti (*Cancellaria*) Deshayes, 1864:104; n.n. for "*C. buccinula* Lam." Basterot, 1825. Miocene, France.

bastropensis (*Cancellaria*) G. D. Harris, 1895a:66, pl. 6, fig. 5. Eocene, Texas, U.S.A.

bathyalis (*Palaeadmete* [*sic*]) Okutani, 1964:398, pl. 6, fig. 7. Recent, Japan. [? *Iphinopsis*]

battersbyi (*Cancellaria*) Bell, 1870b:345; n.n. for "*C. hirta* (Brocc.)" Grateloup, 1847:pl. 25, fig. 25. Tertiary, France. (= *C. subhirta* d'Orbigny, 1852)

bayeri (*Admetula*) Petit, 1976:38, pl. 1, fig. 4. Recent, Gulf of Mexico.

baylei (*Cancellaria*) Bezançon, 1870:316, pl. 10, fig. 3. Tertiary, France.

bearnensis (*Cancellaria*) Peyrot, 1928:206, pl. 12, fig. 1; as var. of *C. barjonae* Pereira da Costa. Miocene, France.

bearnensis (*Sveltia*) Peyrot, 1928:219, pl. 13, fig. 8; as "mut." of *S. varicosa* (Brocchi). Miocene, France.

beata (*Cancellaria*) Jung, 1965:554, pl. 75, figs. 12-14. Miocene, Venezuela.

beatrix (*Admete*) Olsson, 1964:128, pl. 22, fig. 9. Pliocene, Ecuador.

beatum (*Trigonostoma*) Pilsbry & Harbison, 1933:108, pl. 3, fig. 1. Miocene, New Jersey, U.S.A.

behmi (*Cancellaria*) Beyrich, 1856:584, pl. 28, figs. 6a-b. Oligocene, Germany.

bella (*Cancellaria*) Aldrich, 1898:98; as var. of *C. graciloides* Aldrich. Eocene, Alabama, U.S.A.

bellardii (*Cancellaria*) Michelotti, 1846:55. *Nomen nudum.*

bellardii (*Cancellaria*) Michelotti, 1847:225. Miocene, Italy.

bellardii (*Trigonostoma*) de Stefani & Pantanelli, 1878:116. Pliocene, Italy. (= *C. exumbilicaris* Sacco, *q.v.*)

bellardii (*Trigonostoma*) Venzo & Pelosio, 1963:111, pl. 39, figs. 3, 3a-c, 4; n.n. for "*C. ampullacea* (Br.)" Bellardi, 1841:pl. 4, figs. 7-8; as subsp. of *T. ampullacea* (Brocchi). Tertiary, Italy.

bellsana (*Caveola*) Stephenson, 1953:190, pl. 42, figs. 26-28. Cretaceous, Texas, U.S.A. [? Fasciolariidae]

benedeni (*Voluta*) Müller, 1851:41, pl. 6, figs. 5a-b. Cretaceous, Germany. [Cancellariidae]

benoisti (*Trigonostoma*) Peyrot, 1928:245, pl. 14, fig. 31. Miocene, France.

beraudiana (*Cancellaria*) Millet de la Turtaudière, 1854:160. *Nomen nudum.*

beraudiana (*Cancellaria*) Millet de la Turtaudière, 1866:10. Tertiary, France.

bernardii (*Cancellaria*) Mayer, 1861a:371, pl. 15, figs. 3-4. Tertiary, France.

bernayi (*Cancellaria*) Cossmann, 1889:230, pl. 7, fig. 29. Middle Eocene, France.

berolinensis (*Cancellaria*) Beyrich, 1847:162. *Nomen nudum.*

betsiae (*Trigonostoma*) Olsson & Petit, 1964:544, pl. 80, figs. 1, 1a. Pliocene, South Carolina, U.S.A.

bettina (*Cuma*) Semper, 1862:102. Oligocene, Germany. [?= *Turehua tuberculata* (Giebel, 1861)]

beyrichi (*Cancellaria*) Mayer, 1859:391, pl. 11, fig. 8. Tertiary, Europe.

bezanconi (*Cancellaria*) de Raincourt, 1884:345, pl. 12, fig. 10. Upper Eocene, France.

bezanconi (*Cancellaria*) Morlet, 1885a:49, pl. 3, figs. 3, 3a. Eocene, France. (= *C. multienensis* Morlet, 1885b).

bezanconi (*Cancellaria*) 'de Boury' – Meyer, 1886:74. [Error for *Scalaria bezanconi* de Boury]

bicarinata (*Cancellaria*) Hoernes & Auinger, 1890:281, pl. 33, figs. 16a-c. Miocene, Austria.

bicincta (*Admete*) 'von Koenen' – Chavan, 1947:142. Error for *Cancellaria tricincta* von Koenen.

bicolor (*Cancellaria*) Hinds, 1843:48; 1844b:43, pl. 12, figs. 13-14. Recent, Indo-Pacific.

bicosticillata (*Cancellaria*) Sacco, 1894:56, pl. 3, fig. 45; as var. of *C. varicosa* (Br.); see Appendix, Note 2. Pliocene, Italy.

bicosticillata (*Cancellaria*) Sacco, 1894:35, pl. 2, fig. 50; as var. of *C. uniangulata* Deshayes; see Appendix, Note 2. Pliocene, Italy.

bifasciata (*Cancellaria*) Deshayes, 1830:181. Recent, Indo-Pacific. (?= *C. oblonga* Sowerby, 1825)

bifoliata (*Cancellaria*) Aldrich, 1903:101, pl. 4, fig. 24. Miocene, Florida, U.S.A.

bifurcoplicata (*Cancellaria*) Cossmann, 1896b:213, pl. 6, fig. 30. Middle Eocene, France.

bilineata (*Bonellitia*) Wrigley, 1935:367, pl. 33, fig. 15. Middle Eocene, England.

binckhorsti (*Cancellaria*) Nyst, 1881:8; n.n. for *C. reticulata* Binkhorst, 1861, *non* Linné, 1767. Cretaceous, Belgium.

binkhorsti (*Cancellaria*) Cossmann, 1899c:178; n.n. for *C. reticulata* Binkhorst, 1861, *non* Linné, 1767. Cretaceous, Belgium. (= *C. binckhorsti* Nyst, 1881)

biperspinosa (*Cancellaria*) Sacco, 1894:61, pl. 3, fig. 61; as var. of *C. lyrata* (Br.); see Appendix, Note 2. Pliocene, Italy.

biplex (*Cancellaria*) G. B. Sowerby I, 1822:fig. 4. Plate legend only; = *C. suturalis* G. B. Sowerby I, 1822.

biplicata (*Cancellaria*) Briart & Cornet, 1870:12, pl. 1, fig. 7. Paleocene, Belgium.

biplicatum (*Tritonium*) Ravn, 1902:228, pl. 2, figs. 11, 12, 13a-b. Tertiary, Europe. [? *Admete*]

biplicatus (*Fusus*) Lamarck, 1803:388. Eocene, France. [?= *Admetula evulsa* (Solander, 1766)]

biplicifera (*Cancellaria*) Conrad, 1841:31. Miocene, Maryland, U.S.A.

birchi (*Cancellaria*) Addicott, 1970:118, pl. 16, figs. 12-16. Miocene, California, U.S.A.

birmanica (*Cancellaria*) Vredenburg, 1921:140, pl. 15, figs. 10a-b. Tertiary, Burma.

birmanicum (*Trigonostoma*) Vredenburg, 1921:141, pl. 15, figs. 11a-b. Tertiary, Burma.

bistriata (*Cancellaria*) von Koenen, 1889:116, pl. 8, figs. 5a-d. Oligocene, Germany.

bivet (*Bivetia*) Jousseaume, 1887b:193; *ex* Adanson. Recent, western Africa. (= *Cancellaria similis* Sowerby, 1833)

blountiana (*Cancellaria*) Mansfield, 1935:27, pl. 2, fig. 4. Miocene, Florida, U.S.A.

bocageana (*Cancellaria*) Crosse, 1863:63. *Nomen nudum.*

bocageana (*Cancellaria*) Crosse & Debeaux, 1863a:77; 1863b:263, pl. 9, fig. 3. Recent, China.

bocagei (*Cancellaria*) Crosse & Debeaux – Dautzenberg & Fischer, 1907:149. Emendation of *bocageana*.

boettgeri (*Pseudomalaxis*) Cossmann, 1915:143, pl. 12, figs. 22-24; n.n. for *Discohelix calculiformis* Boettger, 1906, *non* Dunker, 1847. Miocene, Romania. [*Trigonostoma s.l.*]

bofilli (*Cancellaria*) Cossmann, 1899b:102; n.n. for *C. pulcherrima* Almera & Bofill, 1898, *non* Lea, 1841. Pliocene, Spain.

boivini (*Cancellaria*) Dareste de la Chavanne, 1910:23, pl. 4, fig. 7. Eocene, Algeria.

bonacorsi (*Cancellaria*) 'Doderlein MS' – Davoli, 1982:69. *Nomen nudum.*

bonellii (*Cancellaria*) Bellardi, 1840:344. *Nomen nudum.*

bonellii (*Cancellaria*) Bellardi, 1841:24, pl. 3, figs. 3-4. Miocene, Italy.

bonneti (*Sveltella*) Cossmann, 1902:56, pl. 4, fig. 4. Middle Eocene, France.

bonneti (*Trigonostoma*) Cossmann, 1903a:110, pl. 3, figs. 10-11. Pliocene, India.

borealis (*Admete*) A. Adams, 1855:122. Recent, Arctic Ocean. (?= *A. viridula* (Fabricius, 1780))

boreobsoleta (*Trigonostoma*) Kautsky, 1925:142, pl. 10, figs. 12-13. Miocene, Germany.

boucheti (*Cancellaria*) Petit & Harasewych, 1986:436, figs. 1-4, 9-14. Recent, Philippines.

boucheti (*Tritonoharpa*) Beu & Maxwell, 1987:37, pl. 6, figs.i-o; pl. 7, figs. a-h. Recent, Mozambique.

bouczeki (*Turbinella*) Ržehak, 1896:250; in synonymy of *Cancellaria bouczeki* Oppenheim, *q.v. Nomen nudum.*

bouczeki (*Cancellaria*) Oppenheim, 1922:81, pl. 5, figs. 14, 14a-b; *ex* Ržehak list. Tertiary, Czechoslovakia.

bourdoti (*Uxia*) Cossmann & Pissarro, 1901:20, pl. 8, fig. 6. Middle Eocene, France.

bournei (*Cancellaria*) M. A. Hanna, 1927:323, pl. 55, figs. 1, 3, 4, 6. Eocene, California, U.S.A.

boutillieri (*Cancellaria*) Cossmann, 1889:223, pl. 7, fig. 28. Middle Eocene, France.

bradleyi (*Cancellaria*) Nelson, 1870:192, pl. 6, figs. 8-9. Miocene, Peru.

brandenburgi (*Cancellaria*) Boettger, 1902:38. Miocene, Romania.

brauneana – error for *brauniana*.

brauniana (*Cancellaria*) 'Nyst' – Braun, 1851:1131; *et al. Nomen nudum.*

brauniana (*Cancellaria*) Sandberger, 1859:pl. 15, figs. 7, 7a; 1862:258; *ex* Braun; *ex* Nyst *in litt.* Tertiary, Germany.

breve (*Coptostoma*) Wrigley, 1935:359, pl. 32, fig. 4. Middle Eocene, England.

breviplicata (*Voluta*) Forbes, 1846:132, pl. 12, figs. 7a-b. Cretaceous, India. [placed in *Cancellaria* by Stoliczka, 1867:163; not a cancellariid]

brevirostris (*Turbinella*) Hutton, 1877:596, pl. 16, fig. 10. Tertiary, New Zealand. [*Maorivetia*]

brevis (*Cancellaria*) G. B. Sowerby I, 1832a:52; 1832b:fig. 33. Recent, Panamic-Pacific.

brocchii (*Cancellaria*) Crosse, 1861:248; n.n. for "*V. piscatoria* L." Brocchi, 1814:308, pl. 3, fig. 12. Pliocene, Italy. (= *C. hirta minor* Bronn, 1848)

bronnii (*Cancellaria*) Bellardi, 1840:344. *Nomen nudum.*

bronnii (*Cancellaria*) Bellardi, 1841:31, pl. 4, figs. 11-12. Miocene, Italy.

brueckneri (*Tritonium*) Boll, 1846:162, pl. 2, fig. 9; as *brücknerii*. Oligocene, Germany. [?= *Admetula evulsa* (Solander, 1766)]

brunnea (*Tritonoharpa*) Beu & Maxwell, 1987:38, pl. 15, figs. a-e, g-h. Recent, Indonesia.

bruuni (*Admete*) Knudsen, 1964:132, figs. 9-10. Recent, Kermadec Trench.

buccinea (*Cancellaria*) 'Basterot' – Bronn, 1848:209. Error for *C. buccinula* Lamarck.

buccinoides (*Cancellaria*) G. B. Sowerby I, 1832a:54; 1832b:fig. 11. Recent, Panamic-Pacific.

buccinoides (*Cancellaria*) Couthouy, 1838:105, pl. 3, fig. 3. Recent, North Atlantic. (= *C. couthouyi* Jay, 1839).

buccinoides (*Cancellaria*) von Koenen, 1889:106, pl. 10, figs. 9a-b, 10a-c. Oligocene, Germany.

buccinoides (*Triton*) K. Martin, 1879:60, pl. 14, fig. 11. Tertiary, Indonesia. [= *Cancellaria neglecta* K. Martin, 1895; = *Bivetia martini* Cossmann, 1899]

buccinovula (*Cancellaria*) Sacco, 1894:45; n.n. for "*C. evulsa* (Sol.)" Speyer, 1867:pl. 11 [*sic*; error for 16], fig. 2; as var. of *C. evulsa* (Sol.); see Appendix, Note 2. Tertiary, Germany.

buccinula (*Cancellaria*) Lamarck, 1822b:117. Tertiary, France. (?= *Admetula evulsa* (Solander, 1766))

bulbrooki (*Cancellaria*) 'Mansfield' – Marks, 1949:459. Error for *C. bullbrooki* Mansfield.

bulbulus (*Cancellaria*) G. B. Sowerby I, 1832a:55. Recent, Panamic-Pacific.

bullata (*Cancellaria*) G. B. Sowerby I, 1832a:51; 1832b:fig. 35. Recent, Panamic-Pacific.

bullbrooki (*Cancellaria*) Mansfield, 1925:31, pl. 5, fig. 3. Miocene, Trinidad.

burdigalense (*Cancellaria*) Peyrot, 1928:253, pl. 14, figs. 29, 34-35. Miocene, France.

burdigalensis (*Sveltia*) Peyrot, 1928:221, pl. 14, figs. 1-2. Miocene, France.

C

cacellensis (*Cancellaria*) Pereira Da Costa, 1867:209, pl. 26, figs. 3a-b. Miocene, Portugal.

cacellotransiens (*Cancellaria*) Sacco, 1894:52; n.n. for "*C. dufourii* Grat." Pereira Da Costa, 1867:pl. 24, fig. 7; as var. of *C. callosa* Partsch; see Appendix, Note 2. Miocene, Portugal.

cacellowestiana (*Cancellaria*) Sacco, 1894:26; n.n. for "*C. westiana* Gr." Pereira Da Costa, 1867:pl. 25, figs. 3-5; as var. of *C. mutinensis* Foresti; see Appendix, Note 2. Miocene, Portugal.

calais (*Trigonostoma*) Kautsky, 1925:140, pl. 10, figs. 7-8. Miocene, Germany.

calcarata (*Voluta*) Brocchi, 1814:309, pl. 3, fig. 7. Pliocene, Italy. [*Calcarata*]

calculiformis (*Discohelix*) Boettger, 1906:138. [= *Pseudomalaxis boettgeri* Cossmann, 1915, *q.v.*]

californica (*Cancellaria*) Dall, 1908:296, pl. 4, fig. 4. Recent, California, U.S.A.

callosa (*Cancellaria*) 'Partsch' – M. Hörnes, 1848:20. *Nomen nudum.*

callosa (*Cancellaria*) M. Hörnes, 1854:314, pl. 34, figs. 14-16; *ex* Partsch MS. Miocene, Austria.

caloosahatchiensis (*Cancellaria*) Tucker & Wilson, 1932:7, pl. 1, fig. 4. Pliocene, Florida, U.S.A.

calvatula (*Cancellaria*) 'Sowerby' – Grant & Gale, 1931:942. Plate caption error for *C. clavatula* Sowerby.

calvertensis (*Cancellaria*) G. C. Martin, 1904:167, pl. 43, fig. 12. Miocene, Maryland, U.S.A.

calvulata (*Cancellaria*) Tate, 1889:153, pl. 9, fig. 3. Miocene, Australia.

calypso (*Cancellaria*) White, 1887:124, pl. 10, figs. 23-24. Cretaceous, Brazil.

camdeo (*Voluta*) Forbes, 1846:131, pl. 12, figs. 5a-b. Cretaceous, India. [? Cancellariidae]

camdio (*Voluta*) Forbes, 1846:pl. 12, figs. 5a-b; plate legend error for *V. camdeo.*

campbelli (*Trigonostoma*) Shasky, 1961:20, pl. 4, fig. 5. Recent, western Mexico.

canaliculata (*Cancellaria*) M. Hörnes, 1854:324, pl. 35, figs. 9a-c, 10a-b. Miocene, Austria.

canaliculata (*Cancellaria*) Deshayes, 1864:97, pl. 72, figs. 26-28. Eocene, France. (= *C. rhabdota* Bayan, 1873)

canaliculata (*Narona*) Janssen, 1972:40, pl. 7, figs. 8-9. Miocene, Netherlands.

cancellangulosa (*Admete*) Sacco, 1894:71; n.n. for "*C. subangulosa* Wood" Speyer, 1867:pl. 11 [*sic*; error for 16], fig. 10; as var. of *A. minuta* Braun. Tertiary, Germany.

cancellaria (*Trichotropis*) Conrad, 1858:333, pl. 35, fig. 8. Cretaceous, Mississippi, U.S.A. [*Paladmete*]

cancellata (*Voluta*) Linné, 1767:1191; n.n. for *Murex scabriculus* Linné, 1758, *non Voluta scabriculus* Linné, 1758. Recent, northwestern Africa. [*Cancellaria*]

cancellata (*Admete*) Kobelt, 1887a:12; 1887b:105, pl. 24, fig. 14. Recent, Japan.

cancellata (*Lora*) Otuka, 1937:1020; n.n. for "*Admete viridula* Fabricius" Yokoyama, 1920:45, pl. 2, fig. 5. Pliocene, Japan. [= *Admete yokoyamai* Oyama, 1954]

cancellatina (*Cancellaria*) Sacco, 1894:45; n.n. for "*C. evulsa* (Sol.)" Speyer, 1867:pl. 11 [*sic*; error for 16], fig. 4; as var. of *C. evulsa* (Solander); see Appendix, Note 2. Tertiary, Germany.

cancellatina (*Cancellaria*) Sacco, 1894:12, pl. 1, fig. 30; as var. of *C. taurolaevigatum* Sacco; see Appendix, Note 2. Miocene, Italy.

cancellatula (*Cancellaria*) Sacco, 1894:43, pl. 3, fig. 4; as var. of *C. bonellii* (Bellardi); see Appendix, Note 2. Miocene, Italy.

cancellatum (*Pleurotoma*) Eichwald, 1830:225. Tertiary, U.S.S.R. [= *Cancellaria notabilis* Eichwald, 1851]

cancellosa (*Oamaruia*) Marwick, 1965:40, pl. 11, figs. 6, 7. Tertiary, New Zealand.

candeana (*Cancellaria*) d'Orbigny, 1842:pl. 21, figs. 23-25. Recent, Caribbean. (see *C. candei* d'Orbigny) [*Antillophos*]

candei (*Cancellaria*) d'Orbigny, 1853:129. Error for, or emendation of, *C. candeana* d'Orbigny. Recent, Caribbean. [*Antillophos*]

candida (*Cancellaria*) G. B. Sowerby I, 1832b:fig. 1. Recent,? Panamic-Pacific.

canulata (*Buccinella*) Perry, 1811:pl. 27, fig. 1. Recent, locality unknown. [?= *Cancellaria reticulata* (Linné, 1767)]

caperata (*Cancellaria*) Tate, 1889:158, pl. 9, fig. 7. Miocene, Australia.

capillata (*Cancellaria*) Tate, 1889:158, pl. 10, fig. 10. Miocene, Australia.

carinapex (*Africotriton*) Beu & Maxwell, 1987:30, pl. 6, figs. a-h. Recent, Australia.

carinata (*Cancellaria*) Briart & Cornet, 1877:14, pl. 14, figs. 5a-c. Paleocene, Belgium.

carinata (*Cancellaria*) Watson, 1882a:327; 1886:275, pl. 18, fig. 9. Recent, Kerguelen Islands. (= *Zeadmete watsoni* Petit, 1970)

carinata (*Sveltella*) Wrigley, 1935:362, pl. 32, fig. 8. Eocene, England.

carinatum (*Coptostoma*) Wrigley, 1935:359, pl. 32, fig. 3; as form of *C. quadratum* (Sowerby). Eocene, England.

carolinensis (*Cancellaria*) Emmons, 1858:254, fig. 118. Tertiary, North Carolina, U.S.A.

carolinensis (*Cancellaria*) Conrad, 1863:567; n.n. for "*C. reticulata* Lam." Emmons, 1858:255, fig. 119. Tertiary, North Carolina, U.S.A.

casicalva (*Cancellaria*) Marks, 1949:464, pl. 78, figs. 3, 10. Miocene, Ecuador.

cassidea (*Voluta*) Brocchi, 1814:314, pl. 3, figs. 13a-b. Pliocene, Italy. [*Trigonostoma s.l.*]

cassidiformis (*Cancellaria*) G. B. Sowerby I, 1832a:53; 1832b: fig. 22. Recent, Panamic-Pacific.

cassiniana (*Cancellaria*) 'Edwards MS' – Newton, 1891:170. *Nomen nudum.*

cassiniana (*Bonellitia*) Wrigley, 1935:372, pl. 33, fig. 26. Lower Eocene, England.

castexi (*Sveltia*) Peyrot, 1928:234, pl. 13, figs. 55-56. Miocene, France.

cathalai (*Pisanella*) Doncieux, 1908:73, pl. 4, figs. 7a-b. Eocene, France. [Cancellariidae]

caudatior (*Admete*) Sacco, 1894:73; n.n. for *C. dregeri* Hoernes & Auinger, 1890, pl. 33, fig. 19 (only); as var. of *A. nassiformis* (Seguenza). Miocene, Austria.

caveola (*Paladmete*) Stephenson, 1947:184, pl. 33, figs. 33-36. Cretaceous, Texas, U.S.A.

ceden (*Tritonium*) 'Gardner' – Sohl, 1964a:269. Error for *T. cedri* Gardner.

cedri (*Tritonium*) Gardner, 1935:262, pl. 21, figs. 9-10. Paleocene, Texas, U.S.A. [*Plesiotriton*]

centrota (*Cancellaria*) Dall, 1896:13; 1908:295, pl. 1, fig. 8. Recent, Panamic-Pacific.

cerithea (*Cancellaria*) Olsson, 1964:125, pl. 22, figs. 4, 4a. Tertiary, Ecuador.

cerithiopsis (*Cancellaria*) Almera & Bofill, 1898:18, pl. 11, figs. 22, 22a. Pliocene, Spain.

chainei (*Admete*) Peyrot, 1928:262, pl. 13, figs. 19-20. Miocene, France.

chalmasi (*Triton*) Quaas, 1902:272, pl. 32, figs. 44-46. Cretaceous, Libya. [? *Plesiotriton*]

chalmsi (*Triton*) 'Quass [*sic*]' – Beu & Maxwell, 1987:51. Error for *T. chalmasi* Quaas.

charapota (*Cancellaria*) Olsson, 1942:60, pl. 8, fig. 3. Miocene, Ecuador.

charlesworthii (*Cancellaria*) Wood, 1872:48, pl. 3, figs. 22a-b. Tertiary, England.

chaussyensis (*Cancellaria*) Cossmann, 1889:231, pl. 8, fig. 36. Middle Eocene, France.

chavani (*Trigonostoma*) Palmer, 1937:442, pl. 70, figs. 4, 10; as var. of *T. pulcherrima* (Lea). Eocene, South Carolina, U.S.A.

chinenensis (*Cancellaria*) MacNeil, 1960:99, pl. 14, fig. 12. Pliocene, Okinawa.

choshiensis (*Iphinoella*) Habe, 1958:34, 40, fig. 7. Recent, Japan.

choshiensis (*Admete*) 'Shikama MS' – Habe, 1961b:436, pl. 24, figs. 16, 17. *Nomen nudum.*

choshiensis (*Admete*) Shikama, 1962:47, pl. 2, figs. 13a-b, 14a-b. Recent, Japan.

christiei (*Trigonostoma*) Finlay, 1924b:466, pl. 49, fig. 5. Oligocene, New Zealand.

chrysostoma (*Cancellaria*) G. B. Sowerby I, 1832a:54; 1833:fig. 39. Recent, Panamic-Pacific.

chui (*Trigonostoma*) Yen, 1936:246, pl. 22, fig. 58. Recent, China.

cibarcola (*Cancellaria*) F. M. Anderson, 1929:116, pl. 14, figs. 1-3. Miocene, Colombia.

ciliata (*Cancellaria*) Michaelis & Scherk, 1847:115; *ex* Kröyer label. *Nomen nudum.*

ciliata (*Cancellaria*) 'Kröyer' – Mörch, 1869:22; Paetel, 1888:329; *et al. Nomen nudum.*

cincta (*Clathurella*) Hutton, 1885:327. Miocene, New Zealand. [*Inglisella*]

cingens (*Cancellaria*) 'Sandberger' – Semper, 1861:250. Error for *C. ringens* Sandberger.

cingulata (*Cancellaria*) Kaunhowen, 1898:105, pl. 13, figs. 3, 3a-b. Cretaceous, Belgium.

cingulata (*Gerdiella*) Olsson & Bayer, 1972:879, figs. 7-9. Recent, Caribbean.

circumcarinata (*Cancellaria*) 'Dall' – Dall, 1905:124. Error for *C. circumcincta Dall.*

circumcincta (*Cancellaria*) Dall, 1873:59, pl. 2, fig. 2. Recent, off northwestern North America.

circumspinosa (*Cancellaria*) Addicott, 1970:110, pl. 14, figs. 1-2, 6-7, 16. Miocene, California, U.S.A.

citharella (*Cancellaria*) Lamarck, 1822b:114. [not a cancellariid]

citharella (*Voluta*) Brongniart, 1823:64, pl. 6, fig. 9. Tertiary, Poland. [= *Cancellaria puschi* Semper, 1861]

clarendonensis (*Cancellaria*) 'Edwards MS' – Newton, 1891:170. *Nomen nudum.*

clarendonensis (*Bonellitia*) Wrigley, 1935:372, pl. 34, fig. 39. Lower Eocene, England.

clarki (*Perplicaria*) M. Smith, 1947:55, pl. 2, fig. 9. Recent, Panamic-Pacific.

clathrata (*Cancellaria*) Lamarck, 1822b:116. Tertiary, France.

clathrata (*Cancellaria*) A. Adams, 1855:123. Recent, Panamic-Pacific. (?= *C. jayana* Keen, 1958)

clatskaniensis (*Admete*) Anderson & Martin, 1914:88, pl. 8, figs. 3a-b. Tertiary, Oregon, U.S.A.

clavatula (*Cancellaria*) G. B. Sowerby I, 1832a:52; 1832b:fig. 12. Recent, Panamic-Pacific.

clenchi (*Brocchinia*) Petit, 1986:24, figs. 1-4. Recent, eastern Atlantic.

clewistonensis (*Cancellaria*) Olsson & Harbison, 1953:178, pl. 28, fig. 2; as subsp. of *C. conradiana* Dall. Pliocene, Florida, U.S.A.

cloezi (*Cancellaria*) Cossmann, 1892:74, pl. 3, fig. 16. Paleocene, France.

coaetana (*Cancellaria*) Ryckholt, 1862:pl. 33, fig. 1. Cretaceous, Belgium.

coaeva (*Cancellaria*) Ryckholt, 1862:pl. 33, figs. 3-4. Cretaceous, Belgium.

coctilis (*Cancellaria*) Reeve, 1856:pl. 17, fig. 79. Recent, Indo-Pacific.

codazzii (*Cancellaria*) F. M. Anderson, 1929:116, pl. 14, figs. 4-7. Miocene, Colombia.

coensis (*Cancellaria*) Mansfield, 1930:49, pl. 3, figs. 3-4; as *coënsis*. Miocene, Florida, U.S.A.

collectiva (*Egerea*) Gábor, 1936:7, pl. 1, fig. 13. Oligocene, Hungary.

colligens (*Cancellaria*) Sacco, 1894:22, n.n. for "*C. inermis* Pusch" Hörnes, 1854:pl. 34, figs. 11-13; as var. of *C. inermis* Pusch; see Appendix, Note 2. Miocene, Austria.

colligens (*Cancellaria*) Sacco, 1894:30, pl. 2, fig. 31; as var. of *C. hirta* (Brocchi); see Appendix, Note 2. Pliocene, Italy.

colombiana (*Cancellaria*) Olsson, 1942:63, pl. 9, fig. 4. Miocene, Colombia.

colpodes (*Sveltia*) Cossmann, 1899a:21, 192, pl. 2, figs. 18-19. Miocene, France.

cominella (*Cancellaria*) Pilsbry & Olsson, 1941:23, pl. 3, fig. 7. Pliocene, Ecuador.

complicata (*Cancellaria*) Handmann, 1882:264. Miocene, Austria.

compressa (*Cancellaria*) Sacco, 1894:25; n.n. for "*C. westiana* Grat." Hörnes, 1854:pl. 35, fig. 13; as var. of *C. exwestiana* Sacco; see Appendix, Note 2. Miocene, Austria.

compressohirta (*Cancellaria*) Sacco, 1894:23, pl. 2, fig. 11; as var. of *C. geslini* Basterot; see Appendix, Note 2. Miocene, Italy.

compressospira (*Cancellaria*) Sacco, 1894:40, pl. 2, fig. 63; as var. of *C. dertonensis* (Bellardi); see Appendix, Note 2. Miocene, Italy.

compressula (*Cancellaria*) Sacco, 1894:44, pl. 3, fig. 9; as var. of *C. serrata* Bronn; see Appendix, Note 2. Miocene, Italy.

compressula (*Cancellaria*) Sacco, 1894:15, pl. 1, figs. 38a-b; as var. of *C. michelinii* Bellardi; see Appendix, Note 2. Miocene, Italy.

concava (*Oamaruia*) Marwick, 1931:120, pl. 13, fig. 237. Pliocene, New Zealand.

concinna (*Cancellaria*) Wood, 1842:538. *Nomen nudum.*

condoni (*Cancellaria*) F. M. Anderson, 1905:200, pl. 15, figs. 49-50. Miocene, California, U.S.A.

confirmans (*Cancellaphera*) Ludbrook, 1958:78, pl. 6, fig. 5. Pliocene, Australia.

conoidea (*Cancellaria*) von Koenen, 1885:9, pl. 1, figs. 3a-c. Paleocene, Denmark.

conradiana (*Cancellaria*) Dall, 1889a:129; 1889b:104. *Nomen nudum.*

conradiana (*Cancellaria*) Dall, 1890:42, pl. 3, fig. 13. Tertiary, southeastern U.S.A.

consobrina (*Admete*) Powell, 1951:167, pl. 10, fig. 63. Recent, South Georgia Islands.

constantinensis (*Uxia*) Cossmann & Pissarro, 1901:21, pl. 8, figs. 7-9. Middle Eocene, France.

contabulata (*Cancellaria*) G. B. Sowerby I, 1832b:fig. 28. Recent, Indo-Pacific.

contabulata (*Admete*) Friele, 1879:276. Recent, North Atlantic. (?= *A. viridula* (Fabricius, 1780))

continua (*Cancellaria*) 'Tate' – Tate & Dennant, 1893:221. *Nomen nudum.*

contorta (*Cancellaria*) Basterot, 1825:47, pl. 2, fig. 3. Tertiary, France.

convexior (*Cancellaria*) Sacco, 1894:31, pl. 2, fig. 38; as var. of *C. doderleini* Mayer; see Appendix, Note 2. Miocene, Italy.

convexior (*Cancellaria*) Sacco, 1894:17, pl. 1, fig. 44; as var. of *C. subacuminata* d'Orbigny; see Appendix, Note 2. Miocene, Italy.

convexosimplex (*Cancellaria*) Sacco, 1894:55; n.n. for "*C. varicosa* (Br.)" Fontannes, 1880:pl. 9, fig. 6; as var. of *C. varicosa* (Brocchi); see Appendix, Note 2. Tertiary, France.

cooperii (*Cancellaria*) Gabb, 1865:186. Recent, California, U.S.A.

corbicula (*Cancellaria*) Dall, 1908:294, pl. 1, fig. 4. Recent, California, U.S.A.

corbula (*Cancellaria*) Conrad, 1843:308; printed in some copies as *corbulu.* Miocene, Maryland, U.S.A. *Species inquirendum.*

corbuliformis (*Paladmete*) Stephenson, 1941:366, pl. 71, figs. 9-11. Cretaceous, Texas, U.S.A.

corbulu (*Cancellaria*) Conrad, 1843. See *corbula.*

cordensis (*Fasciolaria*) Stanton, 1920:43, pl. 8, figs. 8a-b, 9-10. Paleocene, North Dakota, U.S.A. [Cancellariidae]

cornidei (*Admete*) Altimira, 1978:170, fig. 1. Recent, northwestern Africa.

cornigera (*Cancellaria*) Braun, 1851:1131. *Nomen nudum.*

coronadosensis (*Cancellaria*) Durham, 1950:102, pl. 26, figs. 2, 8. Pleistocene, Mexico.

coronata (*Cancellaria*) Hoeninghaus, 1831:145. *Nomen nudum.*

coronata (*Cancellaria*) Scacchi, 1835:5, pl. 1, fig. 15. Tertiary/Recent, Italy.

corrosa (*Cancellaria*) Reeve, 1856:pl. 14, fig. 64. Recent, Panamic-Pacific.

corrugata (*Cancellaria*) Hinds, 1843:48; 1844b:42, pl. 12, figs. 1-2. Recent, Panamic-Pacific.

corrugata (*Voluta*) Binkhorst, 1861:14, pl. 5, figs. 1a-b. Cretaceous, Belgium. [? Cancellariidae]

cossmanni (*Cancellaria*) Morlet, 1888:209, pl. 9, figs. 10, 10a-b. Upper Eocene, France.

cossmanni (*Cancellaria*) Olsson, 1922:81, pl. 6, figs. 9, 11. Pliocene, Costa Rica. (= *C. petiti* Olsson, 1967)

cossmanni (*Plesiotriton*) Oppenheim, 1906:311, pl. 24, figs. 23a-b. Eocene, Egypt.

costata (*Cancellaria*) G. B. Sowerby I, 1822:fig. 2. Recent, northwestern Africa. (?= *C. cancellata* (Linné, 1767)).

costata (*Cancellaria*) G. B. Sowerby I, 1833:fig. 42, *ex* Gray MS. Recent, western Africa. (?= *Scalptia scala* (Gmelin, 1791))

costata (*Cancellaria*) I. Lea, 1833:141, pl. 5, fig. 140. Eocene, Alabama, U.S.A. (?= *C. gemmata* Conrad, 1833)

costata (*Cancellaria*) Calcara, 1845:281. Not newly described; transfer of *Buccinum costulatus* Calcara, 1840 to *Cancellaria.*

costata (*Brocchinia*) Harmer, 1918:397, pl. 39, fig. 41; as var. of *B. mitraeformis* (Brocchi). Pliocene, England.

costatissima (*Cancellaria*) Sacco, 1894:15, pl. 1, fig. 41; as var. of *C. michelinii* Bellardi; see Appendix, Note 2. Miocene, Italy.

costatonodosa (*Cancellaria*) Sacco, 1894:47, pl. 3, fig. 19; as var. of *C. evulsa* (Solander); see Appendix, Note 2. Oligocene, Italy.

costellata (*Cancellaria*) 'Nyst' – Glibert, 1952a:131. Error for *C. costulata* Lamarck.

costellifer (*Murex*) J. Sowerby, 1818:225, pl. 199, fig. 3. Pliocene, England. [?= *Admete viridula* (Fabricius, 1780)]

costicillatina (*Cancellaria*) Sacco, 1894:14, pl. 1, fig. 36; as var. of *C. scrobiculatum* Hörnes; see Appendix, Note 2. Miocene, Italy.

costicillatissima (*Cancellaria*) Sacco, 1894:38, pl. 2, fig. 56; as "anom." of *C. cancellata pleuricosticillata* Sacco; see Appendix, Note 2. Pliocene, Italy.

costicillatissima (*Cancellaria*) Sacco, 1894:64, pl. 3, fig. 73; as var. of *C. tribulus* (Brocchi); see Appendix, Note 2. Pliocene, Italy.

costifera (*Cancellaria*) G. B. Sowerby I, 1832b:fig. 31. Recent, Indo-Pacific.

costigera (*Trigonostoma*) 'Sowerby' – Oliver, 1982:16, 19. Error for *T. costifera* (Sowerby).

costulata (*Cancellaria*) Lamarck, 1803:63. Middle Eocene, France.

costulatior (*Cancellaria*) Sacco, 1894:17, pl. 1, fig. 43; as var. of *C. subacuminatum* d'Orbigny; see Appendix, Note 2. Miocene, Italy.

costulatus (*Buccinum*) Calcara, 1840:50. Tertiary, Italy. [transferred to *Cancellaria* by Calcara, 1845:281, under the incorrect spelling *costata*]

couthonyi (*Admete*) 'Jay' – Habe, 1961a:72; 1961b:436. Error for *A. couthouyi* (Jay).

couthouyi (*Cancellaria*) Jay, 1839:77; n.n. for *C. buccinoides* Couthouy, 1838, *non* Sowerby, 1832. Recent, North Atlantic. (?= *Admete viridula* (Fabricius, 1780))

couturieauxi (*Admete*) Glibert, 1938:118, pl. 4, fig. 9, text-fig. 33. Oligocene, Belgium.

couvana (*Cancellaria*) Vokes, 1938:20, fig. 21. Miocene, Trinidad.

coxi (*Triton*) Brazier, 1872:22, pl. 4, fig. 9. Recent, Australia. [*Tritonoharpa*]

crassa (*Cancellaria*) Nomland, 1917:237, pl. 12, figs. 7, 7a. Pliocene, California, U.S.A.

crassa (*Cancellaria*) Waring, 1917:66, pl. 9, fig. 5. Cretaceous, California, U.S.A. (= *C. simiana* Hanna, 1924)

crassevaricosa (*Cancellaria*) Sacco, 1894:46, pl. 3, fig. 16; as var. of *C. evulsa* (Solander); see Appendix, Note 2. Miocene, Italy.

crassicosta (*Cancellaria*) Bellardi, 1841:23, pl. 2, figs. 7-8. Miocene, Italy.

crassicostata (*Narona*) Nordsieck, 1972:88; as form of *N. fusiformis* (Cantraine). Miocene, Europe.

crassicosticillata (*Admete*) Sacco, 1894:72, pl. 3, fig. 96; as var. of *A. costellifera* [*sic*] (Sowerby). Pliocene, Italy.

crassicosticillata (*Cancellaria*) Sacco, 1894:27, pl. 2, fig. 21; as var. of *C. piscatoria* (Gmelin); see Appendix, Note 2. Pliocene, Italy.

crassinodosa (*Brocchinia*) Sacco, 1894:70, pl. 3, figs. 90a-b. Miocene, Italy.

crassispiralis (*Turehua*) Beu & Maxwell, 1987:18, pl. 1, figs. k-l. Eocene, New Zealand.

crassistria (*Cancellaria*) von Koenen, 1889:112, pl. 8, figs. 6a-c, 7a-d. Oligocene, Germany.

crassistriata (*Cancellaria*) Wood, 1879:22, pl. 3, figs. 16a-b. Tertiary, England.

crassocostata (*Cancellaria*) Sacco, 1894:13, pl. 1, fig. 32; as var. of *C. imbricatum* Hörnes; see Appendix, Note 2. Miocene, Italy.

crassonana (*Cancellaria*) Sacco, 1894:23, pl. 2, fig. 7; as var. of *C. geslini* Basterot; see Appendix, Note 2. Miocene, Italy.

crassopostica (*Cancellaria*) Sacco, 1894:23, pl. 2, fig. 10; as var. of *C. geslini* Basterot; see Appendix, Note 2. Miocene, Italy.

crawfordiana (*Cancellaria*) Dall, 1891:182, pl. 6, fig. 1. Recent, California, U.S.A.

crebriliratus (*Epidromus*) G. B. Sowerby III, 1903:220, pl. 4, fig. 4. Recent, South Africa. [*Africotriton*]

cremata (*Cancellaria*) Hinds, 1843:48; 1844b:42. Recent, Panamic-Pacific.

crenata (*Cancellaria*) M. Hörnes, 1856:679, pl. 52, figs. 4a-b. Miocene, Austria.

crenifera (*Cancellaria*) G. B. Sowerby I, 1832b:fig. 29. Recent, Indo-Pacific.

crenulata (*Cancellaria*) Deshayes, 1835:501, pl. 79, figs. 31-33. Lower Eocene, France.

crenulata (*Cancellaria*) A. Adams, 1855:124. Recent, ? China.

crenulatus (*Triton*) 'Pease' – Carpenter, 1865:517; *ex* Pease MS, in synonymy of *Triton antiquatus* Hinds. *Nomen nudum.*

crepini (*Cancellaria*) Briart & Cornet, 1877:13, pl. 14, figs. 6a-c. Paleocene, Belgium.

cretacea (*Cancellaria*) Nyst, 1881:8; n.n. for *C. obtusa* Binkhorst, 1861, *non* Deshayes, 1830. Cretaceous, Belgium.

cretacea (*Cancellaria*) E. A. Smith, 1899b:245. Recent, India. (= *C. quasilla* Petit, 1987)

cretaceus (*Plesiotriton*) Sohl, 1960:128, pl. 18, figs. 35, 41-42. Cretaceous, Mississippi, U.S.A.

crispa (*Cancellaria*) G. B. Sowerby I, 1832b:fig. 30. Recent, Indo-Pacific.

crispa (*Admete*) Möller, 1842:88. Recent, North Atlantic. (?= *Admete viridula* (Fabricius, 1780))

crispata (*Admete*) 'Müller' – Nyst, 1881:12. Error for *A. crispa* Möller.

crispata (*Cancellaria*) 'Sowerby' – G. B. Sowerby II, 1849b:452; *et al.* Error for *C. crispa* G. B. Sowerby I.

crispata (*Cancellaria*) Seguenza, 1880:110; as var. of *C. italica* D'Ancona. Tertiary, Italy.

cristata (*Admete*) Marwick, 1926:323, pl. 73, fig. 16. Miocene, New Zealand.

crossei (*Cancellaria*) Semper, 1861:257; n.n. for *C. serrata* Reeve, 1856, *non* Bronn, 1831. Recent, Indo-Pacific.

crossletensis (*Cancellaria*) Covacevich & Frassinetti, 1986:45, pl. 2, figs. 1a-c, 2a-c, 3a-c, text-figs. 5-6. Miocene, Chile.

cruzialis (*Cancellaria*) von Ihering, 1907:214; n.n. for "*C. medinae* Philippi" Ortmann, 1902:236, pl. 36, figs. 4a-b. Tertiary, Argentina.

cubapatriae (*Colubraria*) Sarasúa, 1975:4, figs. 1-2. Recent, Cuba. [*Tritonoharpa*]

culminata (*Inglisella*) Beu, 1970:223, pl. 1, figs. 4-5. Miocene, New Zealand.

cumingiana (*Cancellaria*) Petit de la Saussaye, 1844:pl. 112. Recent, Panamic-Pacific.

cumingii (*Trigonostoma*) 'Sowerby' – H. Adams & A. Adams, 1854:276; *et al.* Error for *C. cuminigiana* Petit de la Saussaye.

curta (*Cancellaria*) von Koenen, 1885:12, pl. 1, figs. 8a-b. Paleocene, Denmark.

cytharella (*Cancellaria*) 'Brongniart' – Pusch, 1837:pl. 11, fig. 16; plate caption error for *citharella.*

D

dalli (*Fossarus*) Anderson & Martin, 1914:70, pl. 7, figs. 13a-b. Miocene, California, U.S.A. [Cancellariidae; see *F. barkeri* F. M. Anderson, 1924]

dalli (*Cancellaria*) Bartsch, 1915:33, pl. 4, fig. 2. Recent, "South Africa". (?= *C. bullata* Sowerby, 1832)

dalliana (*Cancellaria*) F. M. Anderson, 1905:199, pl. 15, figs. 39-42. Miocene, California, U.S.A.

dampierensis (*Fusiaphera*) Garrard, 1975:17, pl. 2, fig. 8. Recent, Australia.

danieli (*Cancellaria*) Morlet, 1885a:51, pl. 3, figs. 2, 2a. Middle Eocene, France.

dariena (*Cancellaria*) Toula, 1909:703, pl. 25, fig. 13; pl. 28, fig. 2. Miocene, Panama.

darienensis (*Cancellaria*) Toula – Cossmann, 1913a:51. Emendation of *dariena*.

darwini (*Cancellaria*) Petit, 1970:85, pl. 1, figs. 4a-c. Recent, Galapagos Islands.

dautzenbergi (*Cancellaria*) Cossmann, 1896b:210, pl. 4, figs. 34-35. Middle Eocene, France.

davidsoni (*Triton*) d'Archiac & Haime, 1854:312, pl. 30, figs. 3, 3a. Eocene, Burma. [placed in *Cancellaria* by Noetling, 1901:331; not a cancellariid]

decapensis (*Admete*) Barnard, 1960:439, fig. 1a. Recent, South Africa.

decaptyx (*Cancellaria*) Brown & Pilsbry, 1911:346, pl. 24, figs. 5-6. Miocene, Panama.

decorata (*Trigonostoma*) Newton, 1922:43, pl. 5, figs. 18-19. Eocene, Nigeria.

decussata (*Cancellaria*) G. B. Sowerby I, 1832a:55; 1832b:fig. 8. Recent, Panamic-Pacific.

decussata (*Cancellaria*) Nyst, 1838:115, pl. 1, fig. 5. ?Recent, unknown locality. (?= *C. oblonga* Sowerby)

decussata (*Cancellaria*) Bellardi, 1841:26. Tertiary, Europe.

decussata (*Cancellaria*) G. B. Sowerby I, 1847:421, pl. 20, fig. 27. Tertiary, Portugal.

decussata (*Cancellaria* 'Smith, 1847'. Error for *C. decussata* Sowerby, 1847.

decussata (*Cancellaria*) Grateloup, 1847:pl. 25, fig. 20; see Appendix, Note 1. Tertiary, France.

decussata (*Coralliophila*) de Loriol, 1882:19, pl. 2, figs. 22-25. ? Cretaceous, Europe. [? Cancellariidae]

defuniak (*Cancellaria*) Gardner, 1937:365, pl. 44, figs. 1-2. Miocene, Florida, U.S.A.

delecta (*Cancellaria*) Deshayes, 1864:99; n.n. for *C. elegans* Deshayes, 1835, *non* Sowerby, 1822. Middle Eocene, France.

deleta (*Oamaruia*) Finlay, 1930b:241, pl. 43, fig. 20. Recent, New Zealand.

delicatula (*Admete*) E. A. Smith, 1907:4, pl. 1, figs. 5, 5a. Recent, Antarctic.

deliciosa – error for *delicosa*.

delicosa (*Sydaphera*) Laseron, 1955:269, figs. 5, 5a. Recent, Australia.

delli (*Waipaoa*) Beu, 1970:224, pl. 4, fig. e. Miocene, New Zealand.

dennanti (*Plesiotriton*) Tate, 1898:383, pl. 19, fig. 1. Eocene, Australia.

densata (*Paladmete*) Wade, 1926:108, pl. 35, figs. 7-8. Cretaceous, Tennessee, U.S.A.

densestriata (*Sveltia*) Peyrot, 1928:226, pl. 13, fig. 44; as var. of *S. colpodes* Cossmann. Miocene, France.

dentifera (*Cancellaria*) Deshayes, 1864:98, pl. 73, figs. 8-10. Lower Eocene, France.

deperdita (*Cancellaria*) Michelotti, 1861:102, pl. 11, figs. 5-6. Oligocene, Italy.

depressa (*Cancellaria*) Tuomey & Holmes, 1856:143, pl. 28, fig. 17. Pliocene, South Carolina, U.S.A.

depressa (*Cancellaria*) Dall, 1915:48, pl. 10, fig. 4. Oligocene, Florida, U.S.A. (= *Trigonostoma tampaensis* Petit, 1967)

depresseplicata (*Brocchinia*) Sacco, 1894:69, pl. 3, fig. 85; as var. of *B. mitraeformis* (Br.). Pliocene, Italy.

depressicosta (*Cancellaria*) Sacco, 1894:22, pl. 2, fig. 2ter; as var. of *C. acutangula* Faujas de Saint Fond; see Appendix, Note 2. Miocene, Italy.

depressocostata (*Cancellaria*) Sacco, 1894:11, pl. 1, fig. 25; as var. of *C. fenestrata* Eichwald; see Appendix, Note 2. Miocene, Italy.

deroyae (*Agatrix*) Petit, 1970:85, pl. 1, figs. 3a-b. Recent, Galapagos Islands.

dertinflata (*Cancellaria*) Sacco, 1894:25, pl. 2, figs. 17a-c; as var. of *C. mutinensis* Foresti; see Appendix, Note 2. Miocene, Italy.

dertocacellensis (*Cancellaria*) Sacco, 1894:49; n.n. for "*C. contorta* Basterot" Pereira da Costa, 1867:pl. 24, fig. 6; as var. of *C. contorta* Basterot; see Appendix, Note 2. Miocene, Portugal.

dertocacellensis (*Cancellaria*) Sacco, 1894:30; n.n. for *C. barjonae* Pereira da Costa, 1867:pl. 25, fig. 9 only; as var. of *C. piscatoria* (Gmelin); see Appendix, Note 2. Miocene, Portugal.

dertocassideum (*Cancellaria*) Sacco, 1894:8, pl. 1, figs. 14a-b; see Appendix, Note 2. Miocene, Italy.

dertocontorta (*Cancellaria*) Sacco, 1894:49, pl. 3, figs. 27a-b; see Appendix, Note 2. Miocene, Italy.

dertoconvexula (*Cancellaria*) Sacco, 1894:60, pl. 3, fig. 59; as var. of *C. lyrata* (Br.); see Appendix, Note 2. Miocene, Italy.

dertoconvexulata (*Cancellaria*) Sacco, 1894:62, expl. to pl. 3; error for *dertoconvexula*.

dertocostatissima (*Cancellaria*) Sacco, 1894:60, pl. 3, fig. 60; as var. of *C. lyrata* (Br.); see Appendix, Note 2. Miocene, Italy.

dertocosticillata (*Cancellaria*) Sacco, 1894:13, pl. 1, figs. 31a-b; as var. of *C. imbricata* Hörnes; see Appendix, Note 2. Miocene, Italy.

dertocrenata (*Cancellaria*) Sacco, 1894:44, pl. 3, figs. 11a-b. Miocene, Italy; see Appendix, Note 2. [Ranellidae]

dertofusula (*Cancellaria*) Sacco, 1894:49; n.n. for "*C. contorta* Bast." Hörnes, 1854:pl. 34, fig. 7; as var. of *C. contorta* Basterot; see Appendix, Note 2. Miocene, Austria.

dertogranosa (*Bonellitia*) 'Sacco' – Ferrero Mortara, 1984:171. *Nomen nudum*.

dertolyratoides (*Cancellaria*) Sacco, 1894:36, pl. 2, fig. 54; as var. of *C. uniangulata* Deshayes; see Appendix, Note 2. Miocene, Italy.

dertonassoides (*Cancellaria*) Sacco, 1894:40, pl. 2, fig. 62bis; as var. of *C. dertonensis* Bellardi; see Appendix, Note 2. Miocene, Italy.

dertonensis (*Cancellaria*) Bellardi, 1840:344; as var. of *C. bonelli* Bellardi. *Nomen nudum.*

dertonensis (*Cancellaria*) Bellardi, 1840:344; as var. of *C. cancellata* Lk. [*sic*]. *Nomen nudum.*

dertonensis (*Cancellaria*) Bellardi, 1841:24, pl. 3, figs. 11-12; as var. of *C. bonellii* Bellardi. Tertiary, Italy.

dertonensis (*Cancellaria*) Bellardi, 1841:28, pl. 3, figs. 13-14; as var. of *C. cancellata* (Lamarck) [*sic*]. Tertiary, Italy.

dertoparva (*Cancellaria*) Sacco, 1894:7; n.n. for "*C. scabra* Desh." Hörnes, 1856:pl. 51 [*sic*; error for pl. 52], fig. 7; as var. of *C. scabra* Deshayes; see Appendix, Note 2. Miocene, Austria.

dertopercostata (*Cancellaria*) Sacco, 1894:34, pl. 2, fig. 47; as var. of *C. calcarata* (Brocchi); see Appendix, Note 2. Miocene, Italy.

dertopercostulata (*Cancellaria*) Sacco, 1894:36, pl. 2, fig. 53; as var. of *C. uniangulata* Deshayes; see Appendix, Note 2. Miocene, Italy.

dertopostica (*Cancellaria*) Sacco, 1894:12, pl. 1, fig. 27; as var. of *C. fenestrata* Eichwald; see Appendix, Note 2. Miocene, Italy.

dertoscalata (*Cancellaria*) Sacco, 1894:17, pl. 1, figs. 45a-b, 45bis a-b; see Appendix, Note 2. Miocene, Italy.

dertosimplex (*Cancellaria*) Sacco, 1894:30, pl. 2, fig. 32; as var. of *C. hirta* (Brocchi); see Appendix, Note 2. Miocene, Italy.

dertosuturata (*Cancellaria*) Sacco, 1894:56, pl. 3, fig. 46; as var. of *C. varicosa* (Brocchi); see Appendix, Note 2. Miocene, Italy.

dertoturrita (*Cancellaria*) Sacco, 1894:30, pl. 2, fig. 33; as var. of *C. barjonae* Pereira da Costa; see Appendix, Note 2. Miocene, Italy.

dertovaricosa (*Cancellaria*) Sacco, 1894:57, pl. 3, figs. 49a-b; see Appendix, Note 2. Miocene, Italy.

dertumbilicata (*Cancellaria*) Sacco, 1894:10, pl. 1, fig. 21; as var. of *C. gradata* Hörnes; see Appendix, Note 2. Miocene, Italy.

dertumbilicatior (*Trigonostoma*) 'Sacco' – Ferrero Mortara, 1984:160. *Nomen nudum.*

deshayesana (*Cancellaria*) Grateloup, 1832:338. Tertiary, France. (incorrectly attributed to Desmoulins by later authors, including Grateloup)

deshayesi (*Cancellaria*) 'Desm.' – Cossmann, 1899a:16. Error for *C. deshayesana* Grateloup.

deshayesiana (*Cancellaria*) 'de Moulins' – Crosse, 1861:248; *et al.* Error for *deshayesana* Grateloup.

deshayesianus (*Plesiotriton*) Beu & Maxwell, 1987:25, pl. 23, figs. a-e, h; n.n. for *Triton turriculatum* Deshayes, 1835, *non* 1833. Eocene, France.

deshayesii (*Cassidaria*) Duval, 1841:278. Recent, Senegal. [*Loxotaphrus*]

desmotis (*Cancellaria*) Gardner, 1937:373, pl. 45, fig. 5. Miocene, Florida, U.S.A.

desori (*Cancellaria*) Mayer, 1876:44, pl. 4, fig. 10. Tertiary, Europe.

deucalionis (*Cancellaria*) 'Eichwald' – Sherborn, 1922:1888. Error for *Cassis deucalionis* Eichwald, 1830.

dewalquei (*Cancellaria*) 'Nyst' – Dewalque, 1868:419. *Nomen nudum.*

deydieri (*Cancellaria*) Fontannes, 1878:78, pl. 1, figs. 4a-b; 1879a:515, pl. 5, figs. 4a-b. Tertiary, France.

diadela (*Cancellaria*) Woodring, 1970:338, pl. 53, figs. 7, 9. Pliocene, Panama.

diadema (*Cancellaria*) Watelet, 1853:22, pl. 2, fig. 12. Middle Eocene, France.

diamantina (*Trigonostoma*) Garrard, 1975:22, pl. 3, fig. 4. Recent, Australia.

dictyella (*Cancellaria*) Cossmann, 1899a:24. *Nomen nudum.*

dingdensis (*Narona*) H. J. Anderson, 1964:274, pl. 30, fig. 216. Miocene, Germany.

dingdensis (*Pseudomalaxis*) H. J. Anderson, 1964:203, pl. 15, figs. 109a-c. Miocene, Germany. [*Trigonostoma*]

dinota (*Cancellaria*) Woodring, 1970:340, pl. 54, figs. 1-2; pl. 56, figs. 5-6. Miocene, Panama.

disparstriata (*Cancellaria*) Hölzl, 1958:257, pl. 21, fig. 11; as var. of *C. trochlearis* Faujas de Saint Fond. Miocene, Germany.

disticha (*Inglisella*) Marwick, 1965:41, pl. 11, figs. 9-10. Pliocene, New Zealand.

distincta (*Admete*) Leche, 1878:48, pl. 1, figs. 14a-b; as var. of *A. viridula* (Fabricius). Recent, North Atlantic.

distincta (*Cancellaria*) Mayer, 1876:44, pl. 4, fig. 11. Tertiary, Europe.

distinguenda (*Charcolleria*) Petit, 1970:84, pl. 1, figs. 2a-b. Miocene, Florida, U.S.A.

doboi (*Chrysodomus*) Noszky, 1936:66, pl. 5, fig. 5. Oligocene, Hungary. [*Turehua*]

doderleini (*Cancellaria*) Mayer, 1868:108, pl. 2, fig. 5. Tertiary, Italy.

doderleini (*Cancellaria*) Moroni, 1958:74, pl. 1, figs. 1, 1a. Miocene, Italy. (?= *C. barjonae* Pereira da Costa, 1867)

doliaris – error for *doliolaris*.

dolioides (*Cancellaria*) Pilsbry & Olsson, 1941:22, pl. 3, fig. 5. Pliocene, Ecuador.

dolioides (*Pristimerica*) Finlay & Marwick, 1937:82, pl. 11, figs. 2-3. Paleocene, New Zealand.

doliolaris (*Cancellaria*) Basterot, 1825:46, pl. 2, fig. 17. Miocene, France.

doncieuxi (*Cancellaria*) Dareste de la Chavanne, 1910:24, pl. 4, figs. 8a-b. Eocene, Algeria.

dregeri (*Cancellaria*) Hoernes & Auinger, 1890:280, pl. 33, figs. 18a-c, 19a-c. Miocene, Austria.

druentica (*Cancellaria*) Fontannes, 1878:76, pl. 1, fig. 2; 1879a:514, pl. 5, fig. 2. Tertiary, France.

druidarum (*Cancellaria*) Gardner, 1937:367, pl. 44, figs. 7-8. Miocene, Florida, U.S.A.

druidi (*Trigonostoma*) Olsson & Petit, 1964:544, pl. 80, figs. 6, 6a; pl. 82, fig. 8. Pliocene, Florida, U.S.A.

dubia (*Cancellaria*) Deshayes, 1864:105, pl. 73, figs. 25-27. Eocene, France.

dubia (*Cancellaria*) 'Edwards MS' – Wrigley, 1935:379. *Nomen nudum.*

dubius (*Latirus*) Marshall, 1919:229, pl. 16, fig. 6. Eocene, New Zealand. [*Turehua*; see *Latirus marshalli* Finlay]

dubusi (*Uxia*) Cossmann & Pissarro, 1901:19, pl. 15, figs. 19-20. Middle Eocene, France.

dufourii (*Cancellaria*) Grateloup, 1832:342. Miocene, France.

dumasi (*Sveltella*) Cossmann, 1899a:30, 194, pl. 2, fig. 12. Miocene, France.

dunkeri (*Cancellaria*) Holzapfel, 1888:93, pl. 9, figs. 2a-c. Cretaceous, Germany.

duponti (*Cancellaria*) Briart & Cornet, 1877:12, pl. 14, figs. 4a-c. Paleocene, Europe.

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eburnaeformis (*Cancellaria*) Reeve, 1856:pl. 5, fig. 21. Recent, locality unknown. (?= *C. obesa* Sowerby, 1832)

echinata (*Cancellaria*) 'Doderlein' – Sacco, 1894:7. *Nomen nudum.*

ecuadoriana (*Trigonostoma*) Pilsbry & Olsson, 1941:25, pl. 3, figs. 8-9; pl. 5, fig. 2. Pliocene, Ecuador.

effosa (*Cancellaria*) Handmann, 1882:263. Miocene, Austria.

egregia (*Cancellaria*) von Koenen, 1889:142, pl. 12, figs. 13a-c. Oligocene, Germany.

elata (*Cancellaria*) Hinds, 1843:48; 1844b:42, pl. 12, figs. 3-4. Recent, Panamic-Pacific.

elatior (*Cancellaria*) von Koenen, 1889:135, pl. 12, figs. 5a-c; as var. of *C. nitens* Beyrich. Oligocene, Germany.

elatocostata (*Cancellaria*) Sacco, 1894:37; as subvar. of *C. cancellata pluricosticillata* Sacco; see Appendix, Note 2. Tertiary, Italy.

elatocosticillata (*Cancellaria*) Sacco, 1894:38; as subvar. of *C. cancellata pluricosticillata* Sacco; see Appendix, Note 2. Tertiary, Italy.

elegans (*Cancellaria*) G. B. Sowerby I, 1822:fig. 3. Recent, Indo-Pacific.

elegans (*Cancellaria*) 'Bonelli' – Sacco, 1894:35; *et al.*; in synonymy of *C. uniangulata* Deshayes. *Nomen nudum.*

elegans (*Cancellaria*) 'Gené' – Michelotti, 1838:396; *et al.*; in synonymy of *C. uniangulata* Deshayes. *Nomen nudum.*

elegans (*Cancellaria*) Deshayes, 1835:502, pl. 79, figs. 24-26. Middle Eocene, France. (= *C. delecta* Deshayes, 1864)

elegans (*Cancellaria*) Karsten, 1849:25. Oligocene, Germany. (?= *Babylonella pusilla* (Philippi, 1843))

elegans (*Mataxa*) Wade, 1917:456, pl. 23, figs. 1-3. Cretaceous, Tennessee, U.S.A.

elegans (*Paladmete*) Stephenson, 1941:368, pl. 71, figs. 16-17. Cretaceous, Texas, U.S.A.

elegantula (*Oamaruia*) Beu, 1970:222, pl. 3, fig. f. Miocene, New Zealand.

elegantula (*Trigonostoma*) M. Smith, 1947:54, pl. 2, fig. 3. Recent, Panamic-Pacific.

elevata (*Cancellaria*) I. Lea, 1833:141, pl. 5, fig. 139. Eocene, Alabama, U.S.A.

elevata (*Admetopsis*) D. W. Johnson, 1903:203, pl. 1, fig. 14. Cretaceous, New Mexico, U.S.A.

elizabethae (*Trigonostoma*) Olsson & Petit, 1964:543, pl. 80, figs. 2, 2a. Pliocene, South Carolina, U.S.A.

ellapsa (*Cancellaria*) Conrad, 1865d:212, pl. 20 [*sic*; error for pl. 21], fig. 8. ? Eocene, Texas, U.S.A. (?= *Paladmete cancellaria* (Conrad, 1858))

ellipsis (*Cancellaria*) Pilsbry, 1922:333, pl. 22, figs. 8-9. Tertiary, Dominican Republic.

elodiae (*Cancellaria*) Carson, 1926:49, pl. 1, fig. 1. Pliocene, California, U.S.A.

elongata (*Admete*) Leche, 1878:48, pl. 1, figs. 13a-b; as var. of *A. viridula* (Fabricius). ? Tertiary, Novaya Zemlya.

elongata (*Cancellaria*) Nyst, 1845:476, pl. 12, figs. 21a-b. Tertiary, Europe.

elongata (*Cancellaria*) Wood, 1847:354. *Nomen nudum.*

elongata (*Cancellaria*) Grateloup, 1847:index p. 2, pl. 25, fig. 31; as var. of *C. geslini* Basterot. Tertiary, France.

elongata (*Cancellaria*) 'Karsten' – Semper, 1861:255; in synonymy of *C. pusilla* (Philippi). Error for *C. elegans* Karsten.

elongata (*Cancellaria*) 'Sowerby' – Cossmann, 1903a:108. Error for *C. oblonga* Sowerby.

elongata (*Cancellaria*) Kobelt, 1904:210, pl. 79, figs. 3-4; as var. of *C. cancellata* (L.). Recent, northern Africa.

elongata (*Uxia*) Cuvillier, 1935:66, pl. 5, figs. 22-23. Eocene, Egypt.

elongata (*Unitas*) Traub, 1979:114, pl. 16, figs. 4a-b. Paleocene, Austria. (= *U. oichingensis* Traub, 1984)

elongata (*Olssonella*) Dockery in MacNeil & Dockery, 1984:163, pl. 21, figs. 10, 12. Oligocene, Mississippi, U.S.A.

elsmerensis (*Cancellaria*) English, 1914:216, pl. 23, fig. 8. Pliocene, California, U.S.A.

emmae (*Admete*) Albrecht & Valk, 1943:75, pl. 19, figs. 725-728. Oligocene, Netherlands.

emydis (*Cancellaria*) Dall & Ochsner, 1928:105, pl. 2, fig. 7. Pleistocene, Galapagos Islands.

enderbyensis (*Admete*) Powell, 1958:201, pl. 1, fig. 10. Recent, Antarctic.

engonata (*Cancellaria*) Conrad, 1841:32. Miocene, Maryland, U.S.A.

eocaenica (*Uxia*) 'Cossmann' – Cossmann & Pissarro, 1913:pl. 47, fig. 212-11; see *infraeocaenica* Cossmann.

eogassinense (*Cancellaria*) Sacco, 1904:119, pl. 25, fig. 1; see Appendix, Note 2. Eocene, Italy.

eoreticosa (*Cancellaria*) Cossmann, 1899c:178. Unnecessary n.n. for *C. reticulata* 'Newton', a *nomen nudum.*

epidromiformis (*Cancellaria*) Tate, 1889:154, pl. 8, fig. 9. Miocene, Australia.

epistomifera (*Cancellaria*) Guppy, 1876:520, pl. 28, fig. 9. Miocene, Dominican Republic.

epomis (*Tribia*) Woodring, 1928:223, pl. 12, fig. 10. Pliocene, Jamaica.

errata (*Cancellaria*) Sacco, 1894:15; n.n. for "*C. michelinii* Bell." Pereira da Costa, 1867:pl. 25, fig. 8; as var. of *C. michelinii* Bellardi; see Appendix, Note 2. Miocene, Portugal.

esi (*Cancellaria*) Koperberg, 1931:66, pl. 2, fig. 19. Tertiary, Indonesia.

esmeralda (*Cancellaria*) Olsson, 1964:119, pl. 21, figs. 6, 6a-b. Pliocene, Ecuador.

etheridgei (*Cancellaria*) Johnston, 1880:32. Miocene, New Zealand.

eucheea (*Cancellaria*) Gardner, 1947:636, pl. 52, fig. 43. Miocene, Florida, U.S.A.

euclethra (*Cancellaria*) Maury, 1925b:188, pl. 9, fig. 13. Miocene, Brazil.

eudeli (*Cancellaria*) G. B. Sowerby III, 1893:27, text. fig. Recent, ? Malaysia. (?= *C. angasi* Crosse)

euetrios (*Cancellaria*) Barnard, 1959:14, text-fig. 3. Recent, South Africa.

eufaulensis (*Cancellaria*) Gabb, 1860b:390, pl. 68, fig. 8. Cretaceous, Alabama, U.S.A.

eutaeniata (*Cancellaria*) Cossmann, 1896b:212, pl. 6, figs. 23-24. Middle Eocene, France.

euthymei (*Cancellaria*) Barnard, 1960:438, text-fig. 1b. Recent, South Africa.

eva (*Fusiaphera*) Petit, 1980:215, figs. 5-6. Recent, Mozambique.

evulsum (*Buccinum*) Solander, 1766:13, pl. 1, fig. 14. Eocene, England. [*Admetula*]

exaltata (*Cancellaria*) Tate, 1889:154, pl. 8, fig. 10. Miocene, Australia.

exampullacea (*Cancellaria*) Sacco, 1894:10; n.n. for "*C. ampullacea* (Br.)" Hörnes, 1854:pl. 35, fig. 4; as var. of *C. gradata* Hörnes; see Appendix, Note 2. Miocene, Austria.

exbellardi (*Cancellaria*) Sacco, 1894:46; n.n. for "*C. bellardi* [*sic*] Mich." Wood, 1872:pl. 3, fig. 25; as var. of *C. evulsa* (Solander); see Appendix, Note 2. Tertiary, England.

excassidea (*Cancellaria*) Sacco, 1894:8; n.n. for *C. cassidea* (Br.)" Hörnes, 1856:pl. 52, fig. 8; as var. of *C. cassidea* (Brocchi); see Appendix, Note 2. Miocene, Austria.

excavata (*Cancellaria*) G. B. Sowerby II, 1849a:137; 1849b:449, pl. 93, fig. 18. Recent, Australia. (?= *C. spirata* Lamarck, 1822)

excellens (*Cancellaria*) Beyrich, 1856:566, pl. 25, figs. 5a-b. Oligocene, Germany.

exdecussata (*Aphera*) Sacco, 1894:66; n.n. for "*C. decussata* Smith [*sic*]" Pereira da Costa, 1867:pl. 26, fig. 5. Miocene, Portugal.

exgeslini (*Cancellaria*) Sacco, 1894:22; n.n. for "*C. geslini* Bast." Hörnes, 1854:pl. 25 [*sic*; error for 35], fig. 3; as var of *C. geslini* Basterot; see Appendix, Note 2. Miocene, Austria.

exigua (*Cancellaria*) E. A. Smith, 1891:439, pl. 34, fig. 11. Recent, Australia.

exiliplex (*Sveltella*) Hickman, 1980:73, pl. 9, figs. 7-9. Oligocene, Oregon, U.S.A.

exilis (*Fusus*) Philippi, 1843:25, 60, pl. 4, fig. 12. Oligocene, Germany. [?= *Babylonella pusilla* (Philippi, 1843)]

eximbricata (*Cancellaria*) Sacco, 1894:50, pl. 3, fig. 28; as var. of *C. dertocontorta* Sacco; see Appendix, Note 2. Miocene, Italy.

eximia (*Narona*) Stoliczka, 1867:166, pl. 13, figs. 15-16. Cretaceous, India.

eximia (*Cancellaria*) 'Edwards MS.' – Newton, 1891:171. *Nomen nudum.*

exopleura (*Cancellaria*) Dall, 1908:294. Recent, Panamic-Pacific.

expidea (*Cancellaria*) – Tate, 1889:153. ? Error for *C. cassidea* (Brocchi). *Nomen nudum.*

explicata (*Anapepta*) Laws, 1935:38, pl. 6, fig. 20. Miocene, New Zealand.

expusilla (*Admete*) Sacco, 1894:71; n.n. for "*C. pusilla* (Phil.)" Beyrich, 1856:pl. 28, fig. 2; as var. of *A. minuta* Braun. Tertiary, Germany.

exquisita (*Cancellaria*) Preston, 1905:3, pl. 1, fig. 9. Recent, Sri Lanka.

exscrobiculata (*Cancellaria*) Sacco, 1894:17; n.n. for "*C. scrobiculata* Hörnes" Pereira da Costa, 1867:pl. 26, fig. 2; as var. of *C. dertoscalata* Sacco; see Appendix, Note 2. Miocene, Portugal.

extractrix (*Discohelix*) Boettger, 1906:138. Miocene, Romania. [*Extractrix*]

exumbilicaris (*Cancellaria*) Sacco, 1894:6; ? n.n. for *C.* [*sic*] *bellardii* de Stefani & Pantanelli, 1878, *non* Michelotti, 1847; as var. of *C. umbilicaris* (Br.); see Appendix, Note 2. Pliocene, Italy.

exvaricosa (*Cancellaria*) Sacco, 1894:58; n.n. for "*C. varicosa* (Br.)" Beyrich, 1856:pl. 27, fig. 6; as var. of *C. taurinia* Bellardi; see Appendix, Note 2. Tertiary, Germany.

exwestiana (*Cancellaria*) Sacco, 1894:24; n.n. for "*C. westiana* Grat." Hörnes, 1854:pl. 35, figs. 11-12; see Appendix, Note 2. Miocene, Austria.

F

farafrense (*Triton*) Quaas, 1902:273, pl. 32, fig. 47. Cretaceous, Libya. [?= *Plesiotriton*]

fenestrata (*Cancellaria*) Eichwald, 1830:222. Tertiary, Europe.

fenollerae (*Ovilia*) Landau, 1984:149, pl. 2, figs. 1-5. Pliocene, Spain.

fergusoni (*Cancellaria*) Carson, 1926:53, pl. 1, figs. 7-8. Pleistocene, California, U.S.A.

fernandoensis (*Cancellaria*) Arnold, 1907a:535, pl. 50, fig. 4. Pliocene, California, U.S.A.

fetzaraensis (*Cancellaria*) Dareste de la Chavanne, 1910:24, pl. 4, figs. 9a-d. Eocene, Algeria.

fictilis (*Triton*) Hinds, 1844a:21; 1844b:12, pl. 4, figs. 11-12. Recent, South Africa. [*Africotriton*]

ficus (*Trigonostoma*) K. Martin, 1931:11, pl. 2, figs. 5, 5a. Eocene, Indonesia.

finexa (*Pleurotoma*) G. D. Harris, 1895a:64, pl. 5, fig. 13. Eocene, Texas, U.S.A. [*Cancelrana*]

finlayi (*Anapepta*) Marwick, 1931:122, pl. 13, fig. 238. Miocene, New Zealand.

finlayi (*Zeadmete*) Powell, 1940:242, pl. 29, fig. 12. Recent, New Zealand.

fischeri (*Cancellaria*) A. Adams, 1860:411. Recent, Indo-Pacific.

flemingi (*Tatara*) Beu & Maxwell, 1987:53, pl. 27, figs. a-e. Eocene/Oligocene, New Zealand.

floridana (*Cancellaria*) Olsson & Petit, 1964:540, pl. 82, fig. 6; as subsp. of *C. rotunda* Dall. Pliocene, Florida, U.S.A.

floridensis (*Colubraria*) Tucker & Wilson, 1932:11, pl. 4, figs. 3-4. Pliocene, Florida, U.S.A. [*Tritonoharpa*]

fontinalis (*Cancellaria*) 'Tate' – Tate & Dennant, 1893:221. *Nomen nudum.*

forestieri (*Cancellaria*) Montrouzier in Souverbie & Montrouzier, 1863:161, pl. 5, fig. 7. Recent, New Caledonia. (?= *C. contabulata* Sowerby, 1832)

fornicis (*Uxia*) Wrigley, 1935:376, pl. 34, fig. 31. Lower Eocene, England.

foveata (*Cancellaria*) Almera & Bofill, 1884:32, pl. C, figs. 10-12. Tertiary, Spain.

foveolata (*Cancellaria*) G. B. Sowerby II, 1849a:137; 1849b:455, pl. 93, figs. 30-31. Recent, South Africa.

fragilis (*Sveltella*) Wrigley, 1935:363, pl. 35, fig. 41. Lower Eocene, England.

frugosa (*Cancellaria*) Olsson, 1964:123, pl. 21, fig. 8. Miocene, Ecuador.

fresvillensis (*Uxia*) Cossmann & Pissarro, 1901:21, pl. 8, fig. 2. Midle Eocene, France.

frigida (*Admete*) Rochebrune & Mabille, 1885:104. Recent, Cape Horn.

frizzelli (*Cancellaria*) Marks, 1949:462, pl. 78, fig. 5. Miocene, Ecuador.

fugleri (*Cancellaria*) Arnold, 1907b:433, pl. 54, fig. 9; as var. of *C. crawfordiana* Dall. Pliocene, California, U.S.A.

fumiculata – error for *funiculata.*

fundata (*Bonellitia*) Marwick, 1931:120, pl. 13, fig. 235. Pliocene, New Zealand.

funerata (*Cancellaria*) Conrad, 1848a:287; 1848b:118, pl. 11, fig. 39. Oligocene, Mississippi, U.S.A.

funiculata (*Cancellaria*) Hinds, 1843:48; 1844b:43, pl. 12, figs. 5-6. Recent, Panamic-Pacific.

funiculifera (*Cancellaria*) Vincent in Vincent & Lefèvre, 1872:59, pl. 2, fig. 1. Oligocene, Belgium.

funigera (*Admete*) Staadt in Cossmann, 1913b:188, pl. 3, fig. 212-ter-9. Paleocene, France.

fusca (*Cancellaria*) G. B. Sowerby III, 1889:568, pl. 28, fig. 12. Recent, Hong Kong.

fuscoapicata (*Iphinopsis*) Bouchet & Warén, 1985:262, figs. 700-703. Recent, off British Isles.

fusiformis (*Cancellaria*) Cantraine, 1835:391. Tertiary, Italy.

fusiformis (*Cancellaria*) 'Philippi, 1845' – Sherborn, 1926:2610. Error for *Fasciolaria fusiformis* Philippi, 1845.

fusiformis (*Cancellaria*) Deshayes, 1864:102, pl. 72, figs. 31-32. Middle Eocene, France.

fusoasealaris (*Cancellaria*) Sacco, 1894:25, pl. 2, fig. 16; as var. of *C. exwestiana* Sacco; see Appendix, Note 2. Miocene, Italy.

fusoconvexa (*Admete*) Sacco, 1894:71, pl. 3, fig. 95; as var. of *A. costellifera* [*sic*] (Sowerby). Pliocene, Italy.

fusosimplex (*Cancellaria*) Sacco, 1894:49; n.n. for "*C. contorta* Bast." Hörnes, 1854:pl. 34, fig. 8; as var. of *C. contorta* Basterot; see Appendix, Note 2. Miocene, Austria.

fusospinosa (*Cancellaria*) Sacco, 1894:65, pl. 3, figs. 74a-b; see Appendix, Note 2. Miocene, Italy.

fusulus (*Cancellaria*) Bronn, 1831:43. Tertiary, Italy. (?= *C. uniangulata* Deshayes, 1830)

fusus (*Cancellaria*) 'Bronn' – Deshayes, 1843:423. Error for *C. fusulus* Bronn.

G

gabbiana (*Cancellaria*) Pilsbry & Johnson, 1917:163. Miocene, Dominican Republic.

gailleti (*Uxia*) Cossmann, 1913b:201, pl. 7, fig. 212-24. Eocene, France.

gainfarnensis (*Cancellaria*) Handmann, 1882:262. Miocene, Austria.

galei (*Cancellaria*) Addicott, 1970:119, pl. 16, figs. 6-10. Miocene, California, U.S.A.

gallica (*Sveltia*) Peyrot, 1928:229, pl. 14, figs. 11-14; as mut. of *S. inermis* (Pusch). Miocene, France.

galvestonensis (*Cancellaria*) G. D. Harris, 1895b:100, pl. 3, fig. 11. Miocene, Texas, U.S.A.

gardnerae (*Paladmete*) Wade, 1926:108, pl. 35, figs. 3, 6. Cretaceous, Tennessee, U.S.A.

garrardi (*Admetula*) Petit, 1974:109; n.n. for *C. nassoides* Schepman, 1911, *non* von Koenen, 1889. Recent, Indo-Pacific.

garvani (*Bonellitia*) Palmer, 1937:452, pl. 69, figs. 1-3. Eocene, southeastern U.S.A.

gaudryi (*Cancellaria*) Fontannes, 1878:77, pl. 1, figs. 3a-b; 1879a:514, pl. 5, figs. 3a-b. Tertiary, France.

gelriana (*Cancellaria*) Janssen, 1972:39, pl. 8, figs. 5a-b, 6; as subsp. of *C. contorta* Basterot. Miocene, Netherlands.

gemmata (*Cancellaria*) Conrad, 1833:35; 1835:44, pl. 16, fig. 10. Eocene, Alabama, U.S.A.

gemmata (*Oamaruia*) Maxwell, 1969:182. Oligocene, New Zealand.

gemmulata (*Cancellaria*) G. B. Sowerby I, 1832a:55; 1832b:fig. 7. Recent, Panamic-Pacific.

gerda (*Gerdiella*) Olsson & Bayer, 1972:877, figs. 1-3. Recent, Caribbean.

gerthi (*Merica*) K. Martin, 1931:10, pl. 2, figs. 4, 4a. Eocene, Indonesia.

geslini (*Cancellaria*) Basterot, 1825:46, pl. 2, fig. 5. Tertiary, France.

gibbera (*Oamaruia*) Marwick, 1931:120, pl. 13, fig. 236. Miocene, New Zealand.

gilberti (*Cancellaria*) Aldrich, 1921:13, pl. 1, fig. 29. Eocene, Alabama, U.S.A.

girauxi (*Admete*) Cossmann, 1913b:203, pl. 7, fig. 212-ter-10. Middle Eocene, France.

glabra (*Cancellaria*) Tesch, 1915:40, pl. 7, figs. 84a-b. Tertiary, Indonesia.

glabrata (*Cancellaria*) 'Bosquet' – Vincent, 1886:6. *Nomen nudum.*

glabricula (*Cancellaria*) von Koenen, 1894:1397, pl. 100, figs. 4a-c. Oligocene, Germany.

gladiator (*Cancellaria*) Petit, 1976:35, pl. 1, fig. 2. Recent, Galapagos Islands.

gliberti (*Unitas*) Dolin, Dolin & Le Renard, 1980:43, pl. 2, fig. 19. Middle Eocene, France.

gliberti (*Sveltia*) Janssen, 1984:15, pl. 2, figs. 14-15; pl. 5, fig. 6. Miocene, Belgium.

globularis (*Admete*) E. A. Smith, 1875:426. Recent, Japan. [? *Microglyphis*]

globularis (*Cancellaria*) 'Edwards MS' – Jones, 1878:236. *Nomen nudum.*

globulosa (*Cancellaria*) Holzapfel, 1888:93, pl. 9, figs. 1, 1a-b. Cretaceous, Germany.

goniostoma (*Cancellaria*) G. B. Sowerby I, 1832a:51; 1833:fig. 43. Recent, Panamic-Pacific.

govenderi (*Cancellaria*) King, 1953:67, 83, fig. 7. Miocene, Zululand.

gracilenta (*Cancellaria*) Wood, 1872:46, pl. 3, fig. 23. Tertiary, England.

gracilenta (*Cancellaria*) 'Edwards MS' – Newton, 1891:171. *Nomen nudum.*

gracilina (*Cancellaria*) Sacco, 1894:13, pl. 1, fig. 34; as var. of *C. crassicosta* Bellardi; see Appendix, Note 2. Miocene, Italy.

gracilior (*Cancellaria*) Carpenter in Gabb, 1869:50. Tertiary, California, U.S.A.

gracilis (*Cancellaria*) Philippi, 1845:450. *Nomen nudum.*

gracilis (*Cancellaria*) von Ihering, 1897:310, pl. 3, fig. 11. Tertiary, Argentina.

gracilis (*Merica*) Friedberg, 1914:243, pl. 15, fig. 6; as var. of *M. fenestrata* (Eichwald). Miocene, Poland.

graciloides (*Cancellaria*) Aldrich, 1898:98. Eocene, Alabama, U.S.A.

gradata (*Cancellaria*) M. Hörnes, 1854:319, pl. 35, figs. 2a-b. Miocene, Austria.

gradata (*Cancellaria*) Tate, 1889:155, pl. 10, fig. 12. Miocene, Australia. (= *Aneurystoma tatei* Cossmann, 1899)

grandis (*Admete*) Mörch, 1869:22; as var. of *A. viridula* (Fabricius). Recent, Arctic Ocean.

granifera (*Cancellaria*) Deshayes, 1830:183. Eocene, France.

granosa (*Cancellaria*) G. B. Sowerby I, 1832b:figs. 16-17. Recent, Australia.

granulata (*Cancellaria*) Wood, 1842:538; 1872:48. *Nomen nudum.*

granulata (*Cancellaria*) Nyst, 1845:479; 1845-46:pl. 39, fig. 14. Tertiary, Belgium.

granulosa (*Cancellaria*) 'Sow.' – Lesson, 1842:205. Error for *C. granosa* Sowerby.

grata (*Waipaoa*) Marwick, 1931:122, pl. 13, fig. 240. Miocene, New Zealand.

grateloupi (*Cancellaria*) d'Orbigny – Crosse, 1861:247. First emendation of *C. gratteloupi* d'Orbigny, here accepted as correct emendation.

gratteloupi (*Cancellaria*) d'Orbigny, 1852:10; n.n. for "*C. acutangula* Faujas" Grateloup, 1847, pl. 1, figs. 2 & 4 only; see *grateloupi*. Tertiary, France.

gravecostata (*Cancellaria*) Hölzl, 1958:257, pl. 21, figs. 12, 12a; as var. of *C. trochlearis* Faujas de Saint Fond. Miocene, Germany.

grayi (*Cancellaria*) Tryon, 1885:70, pl. 3, fig. 33. Recent, Philippines.

gregaria (*Admete*) Meek, 1873:501. Cretaceous, Utah, U.S.A.

greggi (*Cancellaria*) G. D. Harris, 1899:26, pl. 3, fig. 6; as var. of *C. quercollis* Harris. Lower Eocene, Alabama and Texas, U.S.A.

grossauensis (*Cancellaria*) Handmann, 1882:262. Miocene, Austria.

guppyi (*Cancellaria*) Gabb, 1873:236. Miocene, Dominican Republic.

gurabis (*Cancellaria*) Maury, 1917:65, pl. 10, fig. 11. Miocene, Dominican Republic.

guttoides (*Sveltella*) Staadt in Cossmann, 1913b:187, pl. 3, fig. 212-bis-7. Paleocene, France.

H

habei (*Nipponaphera*) Petit, 1972:103; n.n. for "*N. lyrata* (Adams & Reeve)" Habe, 1961a:72, pl. 35, fig. 18. Recent, Japan.

haemastoma (*Cancellaria*) G. B. Sowerby I, 1832a:54; 1833:fig. 40. Recent, Galapagos Islands.

haemostoma (*Cancellaria*) 'Sowerby'. Error for *haemastoma* Sowerby.

hamlini (*Cancellaria*) Carson, 1926:51, pl. 1, figs. 4, 6. Pliocene, California, U.S.A.

hampdenensis (*Bonellitia*) Marshall & Murdoch, 1923:124, pl. 12, fig. 4. Eocene, New Zealand.

harmeri (*Cancellaria*) Glibert, 1958:16. *Nomen nudum.*

harmeri (*Cancellaria*) Glibert, 1960a:2, pl. 4, fig. 1. Pliocene, Belgium.

harpa (*Cancellaria*) von Koenen, 1889:145, pl. 9, figs. 3a-d. Oligocene, Germany.

harpiformis (*Cancellaria*) Pilsbry & Olsson, 1941:23, pl. 3, figs. 1-2. Pliocene, Ecuador.

harpovoluta (*Admete*) Powell, 1957:143, pl. 1, fig. 3. Recent, Antarctic.

harrisi (*Cancellaria*) Maury, 1917:64, pl. 10, figs. 9-10. Miocene, Dominican Republic.

harrisi (*Trigonostoma*) Palmer, 1937:444, pl. 70, figs. 3-6. Eocene, Texas, U.S.A.

hartti (*Cancellaria*) Maury, 1925b:184, pl. 9, fig. 19. Miocene, Brazil.

haswelli (*Gergovia*) Garrard, 1975:36, pl. 4, fig. 7. Recent, Australia.

haweraensis (*Merica*) Laws, 1940:54, pl. 7, fig. 26. Pliocene, New Zealand.

hebertiana (*Cancellaria*) M. Hörnes, 1856:680, pl. 52, figs. 5a-b. Miocene, Austria.

helenae (*Trigonostoma*) Olsson & Petit, 1964:543, pl. 80, figs. 3, 3a. Pliocene, Florida, U.S.A.

hemphilli (*Cancellaria*) Dall, 1909a:30, pl. 14, fig. 5. Pliocene, California, U.S.A.

hettneri (*Cancellaria*) F. M. Anderson, 1929:114, pl. 10, figs. 5-6. Miocene, Colombia.

hidalgoi (*Narona*) Jousseaume, 1887a:164, fig. 3. Recent, western Mexico. (?= *Cancellaria clavatula* Sowerby, 1832)

hidasensis (*Cancellaria*) Hoernes & Auinger, 1890:276, pl. 33, figs. 13a-b, 14a-b. Miocene, Austria.

hillegondae (*Eutritonium*) K. Martin, 1914:150, pl. 4, figs. 111, 111a-c. Eocene/Oligocene, Indonesia. [*Plesiotriton*]

hirta (*Inglisella*) Laws, 1936:116, pl. 16, fig. 69. Pliocene, New Zealand.

hirta (*Voluta*) Brocchi, 1814:315, pl. 4, figs. 1a-b. Pliocene, Italy. [*Solatia*]

hirtissima (*Cancellaria*) Sacco, 1894:24; n.n. for "*C. spinifera* Grateloup" Hörnes, 1854:pl. 35, fig. 8; see Appendix, Note 2. Miocene, Austria.

hirtocostata (*Cancellaria*) Sacco, 1894:pl. 1, fig. 46; plate caption error for *C. dertoscalata* var. *tricostata* Sacco.

histrio (*Scalptia*) 'Reeve' – Jousseaume, 1887b:213. Error for *C. hystrix* Reeve.

hoelleitenensis (*Palaeocancellaria*) Kollmann, 1976:199, pl. 1, figs. 7-9. Cretacous, Austria.

hoerlei (*Trigonostoma*) Olsson, 1967:24, pl. 8, figs. 6, 6a. Pliocene, Florida, U.S.A.

hoernesi (*Cancellaria*) Kittl, 1887:246, pl. 8, fig. 9. Tertiary, Europe.

hoffmanni (*Neptunea*) Gabb, 1864:90, pl. 18, fig. 41. Cretaceous, California, U.S.A. [?= *Paladmete perforata* (Gabb, 1864)]

hordeola (*Cancellaria*) von Koenen, 1889:99, pl. 12, figs. 9a-c, 10a-c. Oligocene, Germany.

horii (*Sydaphera*) Masuda, 1967:10, pl. 2, figs. 16a-b, 17a-b, 18a-b, 19. Tertiary, Japan.

hukuiensis (*Admete*) Nomura & Niino, 1940:74, pl. 1, fig. 5. Recent, Japan.

hukusimana (*Cancellaria*) Nomura & Hatai, 1936:134, pl. 17, figs. 6a-b. Pliocene, Japan.

humerosa (*Admetopsis*) Stanton, 1893:160, pl. 33, figs. 4-5. Cretaceous, Utah, U.S.A.

hypermeces (*Cancellaria*) Cossmann, 1896a:42, pl. 3, figs. 19-20. Middle Eocene, France.

hystrix (*Cancellaria*) Reeve, 1856:pl. 14, fig. 67. Recent, Mauritius.

I

igarassuensis (*Cancellaria*) Penna, 1965:273, pl. 1, figs. 1-2, 4. Miocene, Brazil.

imbricata (*Cancellaria*) M. Hörnes, 1854:327, pl. 35, figs. 16a-b. Miocene, Austria.

imbricata (*Cancellaria*) Watson, 1882a:325; 1886:274, pl. 18, figs. 10a-c. Recent, South Africa. (= *C. africana* Petit, 1970)

imbricatum (*Tritonium*) Dareste de la Chavanne, 1910:23, pl. 4, fig. 6. Eocene, Algeria. [*Plesiotriton*]

imevborei (*Bonellitia*) Adegoke, 1977:206, pl. 31, figs. 16-19. Paleocene, Nigeria.

imperialis (*Cancellaria*) Michelin, 1832:[unnumbered page], pl. 16. Recent, locality unknown. (?= *C. cassidiformis* Sowerby, 1832)

impressa (*Cancellaria*) Conrad, 1865a:32. *Nomen nudum.*

impressa (*Cancellaria*) Conrad, 1865b:145, pl. 11, fig. 16. Eocene, Alabama, U.S.A. (?= *C. gemmata* Conrad, 1833)

inaequalis (*Paladmete*) Stephenson, 1941:368, pl. 71, figs. 14-15. Cretaceous, Texas, U.S.A.

incerta (*Bonellitia*) Harmer, 1918:405, pl. 40, fig. 9. Pliocene, England.

incompta (*Cancellaria*) Briart & Cornet, 1877:16, pl. 14, figs. 7a-c. Paleocene, Belgium.

indentata (*Cancellaria*) G. B. Sowerby I, 1832a:54; 1832b:figs. 9-10. Recent, Panamic-Pacific.

indicum (*Tritonium*) Spengler, 1923:37, pl. 3, figs. 19a-b. Cretaceous, India. [? Cancellariidae]

indicum (*Trigonostoma*) Vredenburg, 1921:139. *Nomen nudum.*

indicum (*Trigonostoma*) Vredenburg, 1925:96, pl. 12, figs. 4a-c. Tertiary, India.

indoceana (*Tritonoharpa*) Beu & Maxwell, 1987:40, pl. 19, figs. m-o; pl. 24, figs. m-p, s. Recent, Mozambique.

inermis (*Cancellaria*) Pusch, 1837:129, pl. 11, fig. 22; n.n. for *Buccinum mitraeforme* Pusch in Andrzejowski, 1830. Tertiary, Poland.

inflata (*Trichotropis*) Friele, 1879:275. Recent, North Atlantic. [*Iphinopsis*]

inflata (*Admetula*) Dockery in MacNeil & Dockery, 1984:164, pl. 21, figs. 8-9. Oligocene, Mississippi, U.S.A.

infracosticillata (*Cancellaria*) Sacco, 1894:38, pl. 2, fig. 59; as var. of *C. cancellata* (L.); see Appendix, Note 2. Pliocene, Italy.

infracosticillata (*Cancellaria*) Sacco, 1894:47, pl. 3, fig. 23; as var. of *C. tauroconvexula* Sacco; see Appendix, Note 2. Miocene, Italy.

infraeocaenica (*Cancellaria*) Cossmann, 1889:224, pl. 7, fig. 27.[1] Paleocene, France..

inopinatus (*Semitriton*) Cossmann & Pissarro, 1905:92, pl. 16, figs. 19-20. Eocene, France.

inornata (*Cancellaria*) Noetling, 1901:329, pl. 22, figs. 9a-c. Miocene, Burma.

insularis (*Cancellaria*) Pilsbry & Johnson, 1917:163. Tertiary, Dominican Republic.

intercedens (*Cancellaria*) Stoliczka, 1867:164, pl. 13, fig. 13. Cretaceous, India.

interlaevis (*Trigonaphera*) Laseron, 1955:270, figs. 9, 9a. Recent, Australia.

intermedia (*Cancellaria*) Bellardi, 1840:344. *Nomen nudum.*

intermedia (*Cancellaria*) Bellardi, 1840:344; as var. of *C. nodulosa* Lamarck. *Nomen nudum.*

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[1] Cossmann & Pissarro (1913:pl. 47, fig. 212-11) listed "*Uxia infraeocaenica* Cossmann" with the notation "err. typ. *eocaenica.*" No usage of "*eocaenica*" has been located, and we are unsure as to the meaning of this remark.

intermedia (*Cancellaria*) Bellardi, 1841:13, pl. 1, figs. 13-14. Tertiary, Italy.

intermedia (*Cancellaria*) Hölzl, 1958:258, pl. 21, fig. 13; as var. of *C. trochlearis* Faujas de Saint Fond. Miocene, Germany.

interrupta (*Cancellaria*) Deshayes, 1864:100, pl. 73, figs. 5-7. Lower Eocene, France.

interstrialis (*Cancellaria*) von Koenen,-889:130, pl. 11, figs. 3a-d. Oligocene, Germany.

io (*Cancellaria*) Dall, 1896:14; 1908:295, pl. 1, fig. 2. Recent, Panamic-Pacific.

iota (*Trigonostoma*) Garrard, 1975:23, pl. 3, fig. 3. Recent, Australia.

irelaniana (*Cancellaria*) Cooper, 1894:42, pl. 1, fig. 5. Cretaceous (? Eocene), California, U.S.A.

irregularisuturata (*Cancellaria*) Sacco, 1894:38; as 'anom.' of *C. cancellata pleuricosticillata* Sacco; see Appendix, Note 2. Pliocene, Italy.

islacolonis (*Cancellaria*) Maury, 1917:65, pl. 10, figs. 12, 12a-b. Miocene/Pliocene, Dominican Republic.

italica (*Cancellaria*) D'Ancona, 1872:112, pl. 12, figs. 5a-b, 6a-b. Pliocene, Italy.

iunior (*Cancellaria*) Bellardi, 1841:pl. 1, fig. 15; as var. of *C. intermedia* Bellardi; plate caption only; see *C. junior* Bellardi. Miocene, Italy.

iwaotakii (*Nipponaphera*) Habe, 1961b:431, pl. 24, fig. 22. Recent, Japan.

J

jacksonica (*Cancellaria*) Cooke, 1926:134, fig. 4. Eocene, Mississippi, U.S.A.

jadisi (*Cancellaria*) Olsson, 1964:123, pl. 21, fig. 7. Miocene, Ecuador.

japonica (*Cancellaria*) E. A. Smith, 1879b:216, pl. 20, fig. 54. Recent, Japan.

japonica (*Cancellaria*) 'Lischke'. Error for *C. japonica* Smith.

jasnini (*Cancellaria*) Glibert, 1952b:368, pl. 12, fig. 10. Miocene, Belgium.

jayana (*Cancellaria*) Keen, 1958:249, pl. 30, fig. 5. Recent, Panamic-Pacific.

jipijapana (*Cancellaria*) Pilsbry & Olsson, 1941:22, pl. 4, figs. 1, 4. Pliocene, Ecuador.

joachimi (*Cancellaria*) Handmann, 1882:261. Miocene, Austria.

jocosa (*Inglisella*) Maxwell, 1988:70, pl. 11, figs. i-k. Miocene, New Zealand.

joaquinensis (*Cancellaria*) F. M. Anderson, 1905:199, pl. 15, figs. 46-48. Miocene, California, U.S.A.

jogjacartensis (*Cancellaria*) K. Martin, 1914:128, pl. 2, fig. 57. Eocene, Indonesia.

jonkairiana (*Cancellaria*) Nyst, 1835:29, pl. 5, fig. 28. Tertiary, Europe. (see *C. lajonkairii* Nyst, 1853)

jonkeiriana (*Cancellaria*) 'Nyst' – Nyst, 1845:475; *et al*. Error for *C. jonkairiana* Nyst.

jonkeri (*Cancellaria*) Koperberg, 1931:65, pl. 2, fig. 18. Tertiary, Indonesia.

josephinae (*Trigonostoma*) Janssen, 1984:23, pl. 4, figs. 10-13; pl. 6, fig. 5; as subsp. of *T. geslini* (Basterot). Miocene, Netherlands.

jucunda (*Cancellaria*) Thiele, 1925:201, pl. 22, fig. 21. Recent, eastern Africa.

jumala (*Admete*) Olsson, 1964:127, pl. 22, figs. 3, 3a-c. Pliocene, Ecuador.

junior (*Sveltia*) 'Bellardi' – Ferrero Mortara, 1984:176; variant spelling of *iunior*, *q.v.*

junipera (*Cancellaria*) G. D. Harris, 1895a:65, pl. 6, fig. 3; as var. of *C. panones* Harris. Eocene, Texas, U.S.A.

K

kaiparaensis (*Merica*) Laws, 1939:496, pl. 65, fig. 50. Miocene, New Zealand.

kaitarus (*Kapuatriton*) Beu & Maxwell, 1987:24, pl. 2, figs. a-b, d-e. Upper Eocene, New Zealand.

karsteni (*Cancellaria*) F. M. Anderson, 1929:114, pl. 10, figs. 7-9, Miocene, Colombia.

kaunhoweni (*Uxia*) Cossmann, 1899a:38; n.n. for *C. minima* Kaunhowen, 1898, *non* Reeve, 1856. Cretaceous, Germany.

keaseyensis (*Sveltella*) Hickman, 1980:75, pl. 9, figs. 10-11. Oligocene, Oregon, U.S.A.

keenae (*Cancellaria*) Addicott, 1970:119, pl. 16, figs. 1-4, 18-19. Miocene, California, U.S.A.

keepingi (*Bonellitia*) Wrigley, 1935:368, pl. 33, fig. 17. Middle Eocene, England.

kelseyi (*Trichotropis*) Dall, 1908:254. Recent, California, U.S.A. [*Iphinopsis*]

kernensis (*Cancellaria*) Addicott, 1970:117, pl. 15, figs. 18-21. Miocene, California, U.S.A.

kilburni (*Africotriton*) Beu & Maxwell, 1987:31, pl. 8, figs. i-p; pl. 11, figs. m-q. Recent, South Africa.

kimikoae (*Cancellaria*) Hatai, 1940:115, figs. 1-2. Miocene, Japan.

kobayashii (*Mitra*) Yokoyama, 1927:173, pl. 47, fig. 5. Neogene, Japan. [*Merica*]

kobayasii (*Cancellaria*) Otuka, 1937:1020. *Nomen nudum*.

kochiensis (*Cancellaria*) Katto, 1960:110, pl. 1, fig. 5. Oligocene, Japan.

koreanica (*Cancellaria*) Hatai & Kotaka, 1952:83, pl. 7, figs. 3, 5; as subsp. of *C. spengleriana* Deshayes. Miocene, Japan.

kroyeri (*Trichotropis*) Philippi, 1849:175. Recent, North Pacific. [? *Iphinopsis*]

kugleri (*Cancellaria*) Rutsch, 1934:90, pl. 8, figs. 3-4. Neogene, Venezuela.

kulanda (*Zeadmete*) Garrard, 1975:44, pl. 3, fig. 15. Recent, Australia.

kumeroa (*Zeadmete*) Fleming, 1943:206, pl. 31, fig. 34. Pliocene/Pleistocene, New Zealand.

kunraedensis (*Cancellaria*) Kaunhowen, 1898:105, pl. 13, fig. 6. Cretaceous, Belgium.

kurodai (*Trigonostoma*) Makiyama, 1927:85, pl. 4, fig. 8. Pliocene, Japan.

L

labratula (*Cancellaria*) von Koenen, 1889:147, pl. 11, figs. 5a-d, 6a-b. Oligocene, Germany.

labrosa (*Cancellaria*) Bellardi, 1840:343. *Nomen nudum*.

labrosa (*Cancellaria*) Bellardi, 1841:10, pl. 1, figs. 3-4. Tertiary, Italy.

lacondamini (*Cancellaria*) Olsson, 1964:121, pl. 21, figs. 1, 1a-c. Miocene, Ecuador.

lactea (*Cancellaria*) Deshayes, 1830:180. Recent, Australia.

lacunosa (*Cancellaria*) Hutton, 1885:320. Pliocene/Pleistocene, New Zealand.

laddi (*Cancellaria*) Petit, 1987:154; n.n. for *C. petiti* Ladd, 1982, *non* Olsson, 1967. Pliocene, Fiji.

laekeniana (*Cancellaria*) Vincent in Vincent & Lefèvre, 1872:58, pl. 2, figs. 2-3. Eocene, Belgium.

laekeniensis – error for *laekeniana*.

laevescens (*Cancellaria*) Guppy, 1866:289, pl. 17, fig. 12. Pliocene, Jamaica.

laevicolligens (*Cancellaria*) Sacco, 1894:43, pl. 3, fig. 3; as var. of *C. bonellii* Bellardi; see Appendix, Note 2. Miocene, Italy.

laevicolumella (*Admete*) Sacco, 1894:72, pl. 3, fig. 97; as var. of *A. nassiformis* (Seguenza). Miocene, Italy.

laevicosta (*Cancellaria*) Wood, 1842:538. *Nomen nudum.*

laevifasciata (*Brocchinia*) Sacco, 1894:69, pl. 3, fig. 88; as var. of *B. mitraeformis* (Brocchi). Pliocene, Italy.

laevigata (*Cancellaria*) G. B. Sowerby I, 1832b:fig. 24. Recent, Australia. (?= *C. lactea* Deshayes, 1830)

laevigata (*Cancellaria*) von Koenen, 1865:472. Oligocene, Europe.

laevilabris (*Cancellaria*) 'Bon.' – Bellardi, 1840:344; as var. of *C. nodulosa* Lamarck. *Nomen nudum.*

laevilabris (*Cancellaria*) Bellardi, 1841:20; *ex* Bonelli MS, as var. of *C. nodulosa* Lamarck. Tertiary, Italy.

laevior (*Admete*) Leche, 1878:48; n.n. for "*C. viridula* (Fabr.)" Middendorff, 1849:pl. 9, figs. 1-2; as var. of *A. viridula* (Fabricius). Recent, Arctic Ocean.

laevior (*Cancellaria*) Sacco, 1894:30; n.n. for *C. barjonae* Pereira da Costa, 1867:pl. 25, fig. 13 (only); as var. of *C. barjonae* Pereira da Costa; see Appendix, Note 2. Miocene, Portugal.

laevior (*Cancellaria*) Sacco, 1894:12, pl. 1, fig. 29; as var. of *C. taurolaevigatum* Sacco; see Appendix, Note 2. Miocene, Italy.

laevis (*Paladmete*) Sohl, 1964a:273, pl. 45, figs. 35, 41, 42, 46-48. Cretaceous, Mississippi, U.S.A.

laeviuscula (*Cancellaria*) J. Sowerby, 1822:84, pl. 361, fig. 1. Lower Eocene, England.

lajonkairei (*Cancellaria*) 'Nyst' – Cossmann, 1899a:21; *et al.* Error for *C. lajonkairii* Nyst.

lajonkairii (*Cancellaria*) Nyst, 1853:592. Emendation of *C. jonkairiana* Nyst, 1835.

lamberti (*Cancellaria*) Souverbie in Souverbie & Montrouzier, 1870:428, pl. 14, fig. 2. Recent, New Caledonia.

lamellosa (*Cancellaria*) Hinds, 1843:49; 1844b:43, pl. 12, figs. 15-16. Recent, Indo Pacific. (?= *Scalptia nassa* (Gmelin, 1791))

lamyi (*Cancellaria*) Koperberg, 1931:69, pl. 2, fig. 20. Tertiary, Indonesia.

lanceolata (*Cancellaria*) Aldrich, 1897b:27, text-fig. Eocene, Alabama, U.S.A.

lanceolata (*Ranella*) Menke, 1828:87. Recent, Caribbean. [*Tritonoharpa*]

landesi (*Cancellaria*) Van Winkle, 1918:91, pl. 7, fig. 17. Oligocene, Washington, U.S.A.

laqua (*Cancellaria*) Mansfield, 1935:26, pl. 2, fig. 5. Miocene, Florida, U.S.A.

larkinii (*Cancellaria*) Nelson, 1870:192, pl. 6, fig. 7. Miocene, Peru.

laseroni (*Arizelostoma*) Iredale, 1936:318, pl. 24, fig. 9. Recent, Australia.

lateapertum (*Trigonostoma*) Peyrot, 1928:240, pl. 13, fig. 31; as var. of *T. geslini* (Basterot). Miocene, France.

latecostata (*Admete*) Traub, 1938:94, pl. 8, figs. 10a-b. Tertiary, Europe.

latecostata (*Cancellaria*) 'Löbbecke' – Löbbecke, 1887b:40. Error for *C. laticosta* Löbbecke, 1881.

latefasciata (*Cancellaria*) Sacco, 1894:64, pl. 3, fig. 70; as var. of *C. tribulus* (Brocchi). Pliocene, Italy.

laterinensis (*Inglisella*) Maxwell, 1988:70, pl. 11, figs. e-g. Miocene, New Zealand.

latesulcata (*Cancellaria*) von Koenen, 1885:8, pl. 1, figs. 2a-f. Paleocene, Denmark.

laticosta (*Cancellaria*) Löbbecke, 1881:12, pl. 2, figs. 7-9; as var. of *C. reeveana* Crosse. Recent, Indo-Pacific.

laticostata (*Cancellaria*) Tenison-Woods, 1880:17, pl. 2, fig. 8. Miocene, Australia. (see *C. platypleura* Tate)

laticostata (*Cancellaria*) 'Löbbecke' – Löbbecke, 1881:13. Error for *C. laticosta* Löbbecke, 1881.

laticostata (*Cancellaria*) Sacco, 1894:31, pl. 2, fig. 37; as var. of *C. doderleini* Mayer; see Appendix, Note 2. Miocene, Italy.

latilabris (*Cancellaria*) 'Bon.' – Michelotti, 1838:396. *Nomen nudum.*

lattorfensis (*Bonellitia*) Wrigley, 1935:369, pl. 33, fig. 19; n.n. for *C. ovata* von Koenen, 1889, *non* Sowerby, 1832. Oligocene, Germany.

latum (*Tritonium*) Dareste de la Chavanne, 1910:22, pl. 4, fig. 4; as var. of *T. turriculatum* Deshayes. Eocene, Algeria. [*Plesiotriton*]

laurensii (*Cancellaria*) Grateloup, 1832:341. Tertiary, France.

lauta (*Cancellaria*) 'Tate' – Tate & Dennant, 1893:221. *Nomen nudum.*

lavelana (*Cancellaria*) H. K. Hodson in Hodson & Hodson, 1931:44, pl. 24, fig. 12. Miocene, Venezuela.

lavescens (*Cancellaria*) 'Guppy' – Marks, 1949:460. Error for *C. laevescens* Guppy.

laviae (*Cancellaria*) 'Hoffmann' – Brugnone, 1880:103; as *La Viae*. *Nomen nudum.*

leai (*Cancellaria*) Crosse, 1861:255; n.n. for *C. tessellata* Lea, 1833, *non* Sowerby, 1832. Eocene, southeastern U.S.A. (?= *C. alveata* Conrad, 1833)

lebrosus (*Fusus*) Bellardi, 1839:31. *Nomen nudum.* [= *C. labrosa* Bellardi, 1841]

leioderma (*Mataxa*) Sohl, 1964b:382, pl. 56, figs. 2-3. Cretaceous, Mississippi, U.S.A.

leona (*Colubraria*) Mansfield, 1937:610, pl. 85, fig. 3. Pliocene, Florida, U.S.A. [?= *Plesiotriton lanceolata* (Menke, 1828)]

leonensis (*Cancellaria*) Mansfield, 1930:46, pl. 3, fig. 12; as subsp. of *C. reticulata* (Linné). Miocene, Florida, U.S.A.

leopoldinae (*Cancellaria*) Tournouër in Bouillé, 1876:90, pl. 1, fig. 7. Miocene, France.

lesbarritzensis (*Sveltia*) Vergneau-Saubade, 1968:206, text-fig. Oligocene, France.

leuzingeri (*Cancellaria*) Rutsch, 1934:89, pl. 7, figs. 10-11; pl. 8, figs. 1-2, 5; as subsp. of *C. reticulata* (Linné). Neogene, Venezuela.

levis (*Merica*) Peyrot, 1928:208, pl. 12, fig. 34; as var. of *M. contorta* (Basterot). Miocene, France.

lichana – error for *lickana*.

lickana (*Cancellaria*) Anderson & Martin, 1914:84, pl. 8, figs. 6a-d. Miocene, California, U.S.A.

ligeriana (*Cancellaria*) Glibert, 1952b:367, pl. 11, fig. 11b; as *forma* of *C. contorta* Basterot. Miocene, France.

ligustica (*Cancellaria*) Sacco, 1894:6, pl. 1, fig. 5; as var. of *C. umbilicaris* (Brocchi); see Appendix, Note 2. Pliocene, Italy.

lima (*Cancellaria*) Hoeninghaus, 1831:145. *Nomen nudum.*

lima (*Cancellaria*) von Koenen, 1889:126, pl. 11, figs. 1a-c. Oligocene, Germany.

limata (*Cancellaria*) Yokoyama, 1928:342, pl. 66, fig. 12. Pliocene, Japan.

limnaeaeformis (*Admete*) E. A. Smith, 1877:6, pl. 9, fig. 4; 1879a:172, pl. 9, fig. 4. Recent, Kerguelen Island. [not a cancellariid; ? *Toledonia*]

limnaeiformis (*Cancellaria*) 'Smith' – Tryon, 1885:85. Error for *C. limnaeaeformis* (Smith).

lindae (*Aphera*) Petuch, 1987:109, pl. 13, fig. 11. Recent, Barbados.

lindeni (*Trigonostoma*) Janssen, 1984:21, pl. 4, figs. 1-4; pl. 6, fig. 6. Miocene, Netherlands.

lipara (*Cancellaria*) Woodring, 1951:76, pl. 16, figs. 13-14. Tertiary, California, U.S.A.

lipara (*Cancellaria*) Woodring, 1970:337, pl. 52, figs. 7-8; as subsp. of *C. epistomifera* Guppy. Pliocene, Panama. (= *C. sathra* Woodring, 1973)

lirata (*Cancellaria*) Conrad, 1865a:32. *Nomen nudum.*

lirata (*Cancellaria*) Conrad, 1865b:145, pl. 11, fig. 3. Eocene, Texas, U.S.A. (?= *C. gemmata* Conrad, 1833)

lirata (*Cancellaria*) 'Brocchi'- de Stefani & Pantanelli, 1878:118. Error for *C. lyrata* (Brocchi).

lirisculpta (*Admete*) Cossmann, 1902:57, pl. 6, fig. 25; *ex* deBoury MS. Middle Eocene, France.

lisberi (*Cancellaria*) 'Risso' – Sacco, 1894:27. Error for *C. listeri* Risso.

lischkei (*Cancellaria*) Yokoyama, 1926a:264, pl. 32, figs. 16-17. Pliocene, Japan.

listeri (*Cancellaria*) Risso, 1826:188. Tertiary, Europe.

littorinaeformis (*Cancellaria*) 'Sowerby' – G. B. Sowerby II, 1849:450; *et al.* Error for *C. littoriniformis* G. B. Sowerby I.

littoriniformis (*Cancellaria*) G. B. Sowerby I, 1832b:fig. 18. Recent, Sri Lanka.

lividorupis (*Turehua*) Beu & Maxwell, 1987:19, text-fig. 2K; pl. 2, figs. c, f-j, m. Miocene, New Zealand.

lloydi (*Fasciolaria*) Stanton, 1920:42, pl. 8, figs. 11a-b. Paleocene, North Dakota, U.S.A. [Cancellariidae]

lobata (*Cancellaria*) Swainson, 1840:305, fig. 72f. ?Recent, locality unknown. (?= *C. tuberculosa* Sowerby, 1832)

loebbeckei (*Cancellaria*) – Kuroda & Habe, 1971:202 (English). Error for *C. laticosta* Löbbecke.

longispirata (*Cancellaria*) Yokoyama, 1926a:265, pl. 32, fig. 10. Pliocene, Japan.

longojuvenis (*Cancellaria*) Sacco, 1894:22, pl. 2, fig. 3; as var. of *C. acutangula* Faujas de Saint Fond; see Appendix, Note 2. Miocene, Italy.

longonassoides (*Cancellaria*) Sacco, 1894:52, pl. 3, fig. 34; as var. of *C. deshayesiana* Desm. [*sic*]; see Appendix, Note 2. Miocene, Italy.

losquemadica (*Cancellaria*) Maury, 1917:66, pl. 10, fig. 13. Miocene, Dominican Republic.

luffa (*Admete*) Olsson, 1929:27, pl. 8, figs. 3-4. Eocene, Peru.

lunata (*Cancellaria*) Conrad, 1830:222, pl. 9, fig. 4. Miocene, Maryland, U.S.A.

luscinia (*Cancellaria*) Melvill & Standen, 1903:319, pl. 23, figs. 14-15. Recent, Arabian Sea.

lyra (*Cancellaria*) – Deshayes, 1833:30. Error for *C. lyrata* (Brocchi).

lyrata (*Voluta*) Brocchi, 1814:311, pl. 3, fig. 6. Pliocene, Italy. [*Sveltia*]

lyrata (*Cancellaria*) Adams & Reeve, 1850:42, pl. 10, fig. 4. Recent, ? Panamic-Pacific. (?= *C. funiculata* Hinds, 1843)

M

macconkeyi (*Scalptia*) Jousseaume, 1894:201. Recent, Aden. (?= *Scalptia hystrix* (Reeve, 1856))

maccoyi (*Cancellaria*) Pritchard & Gatliff, 1899:182, pl. 20, fig. 6. Recent, Australia. (?= *C. purpuriformis* Kiener, 1841)

macnairyensis (*Cancellaria*) Sohl, 1964a:268, pl. 44, figs. 1-2. Cretaceous, Tennessee, U.S.A.

macneili (*Cancellaria*) Mansfield, 1937:609, pl.85, figs. 1, 4. Miocene, Florida, U.S.A.

macrospira (*Cancellaria*) Adams & Reeve, 1850:41, pl. 10, fig. 2. Recent, Indo-Pacific.

macrospiratoides (*Fusiaphera*) Habe, 1961b:433, pl.23, fig. 10; pl. 24, fig. 10. Recent, Japan.

macrostoma (*Cancellaria*) du Bois de Montpéreux, 1831:32, pl. 3, figs. 36-37. [not a cancellariid]

macrostoma (*Cancellaria*) Doderlein, 1863:21. *Nomen nudum.*

macrostoma (*Cancellaria*) 'Eichwald' – Sacco, 1894:25. ? Error for *C. macrostoma* du Bois de Montpéreux.

magellanica (*Admete*) Strebel, 1905:594, pl. 22, figs. 29a-d. Recent, Magellanic Province.

magloirei (*Plesiocerithium*) 'Melleville' – Cossmann, 1889:232; *et al.* Error for *P. maglorii* (Melleville).

maglorii (*Cancellaria*) Melleville, 1843:112, pl. 9, figs. 1-3. Lower Eocene, France.

magnoturrita (*Cancellaria*) Sacco, 1894:57, pl. 3, fig. 50; as var. of *C. dertovaricosa* Sacco; see Appendix, Note 2. Miocene, Italy.

maior (*Cancellaria*) Bellardi, 1841:19, pl. 2, figs. 1-2; as var. of *C. nodulosa* Lamarck. Pliocene, Italy.

major (*Cancellaria*) 'Bellardi' – Sacco, 1894:28; as var. of *C. hirta* (Br.). Variant spelling of *C. maior* Bellardi.

major (*Cancellaria*) Grateloup, 1847:2, pl. 1, fig. 29; as var. of *C. dufourii* Grateloup; see Appendix, Note 1. Tertiary, France.

major (*Cancellaria*) von Ihering, 1899:35, pl. 2, fig. 10; as var. of *C. gracilis* von Ihering. Tertiary, Argentina.

major (*Cancellaria*) Pallary, 1900:259; as var. of *C. scabriuscula* (Linné). *Nomen nudum.*

major (*Oamaruia*) Marwick, 1965:40, pl. 11, figs. 12, 15. Pliocene, New Zealand.

malachitensis (*Cancellaria*) Stanton, 1893:158, pl. 33, figs. 6-7. Cretaceous, Colorado, U.S.A.

malaisei (*Cancellaria*) Briart & Cornet, 1877:15, pl. 14, figs. 2a-c; as *malaisi* on p. 15, but as *malaisei* on p. 16 and in later publications by the authors, *et al.* Paleocene, Belgium.

malaisi (*Cancellaria*) 'Briart & Cornet' – Briart & Cornet, 1877:15. Error for *C. malaisei* Briart & Cornet.

maldonadoi (*Cancellaria*) Olsson, 1964:122, pl. 21, figs. 5, 5a. Miocene, Ecuador.

mangelioides (*Cancellaria*) Reeve, 1856:pl. 15, figs. 69a-b. Recent, Indo-Pacific.

mangyschlakica (*Cancellaria*) Bajarunas, 1912:46, pl. 3, figs. 5-7. Upper Oligocene, U.S.S.R.

maorium (*Admete*) Marshall & Murdoch, 1921:82, pl. 18, figs. 7-8. Miocene, New Zealand.

margaritata (*Cancellaria*) Vinassa de Regny, 1896:270, pl. 18, figs. 16-17. Tertiary, Italy.

mariae (*Bivetia*) 'Jousseaume' – Marks, 1949:456. Error for *B. mariei* Jousseaume.

marieana (*Cancellaria*) Aldrich, 1897a:179, pl. 1, fig. 6. Lower Eocene, Alabama, U.S.A.

mariei (*Bivetia*) Jousseaume, 1887a:163, fig. 1. Recent, locality unknown. (?= *C. indentata* Sowerby, 1832)

marksi (*Cancellaria*) Olsson, 1964:125, pl. 37, fig. 6. Pliocene, Ecuador.

marshalli (*Cerittudea* [*sic*]) Vignal in Cossmann, 1921:181; n.n. for *Cerithidea minuta* Marshall, 1919, *non* Gabb, 1873. Eocene, New Zealand. [*Brocchinia*]

marshalli (*Latirus*) Finlay, 1924a:102; unnecessary n.n. for *Latirus dubius* Marshall, 1919, *q.v.*

marshalli (*Uxia*) Allan, 1926:342, pl. 77, figs. 3a-b. Eocene, New Zealand.

marthae (*Trigonostoma*) Olsson, 1967:25, pl. 7, fig. 3. Pliocene, Florida, U.S.A.

martini (*Bivetia*) Cossmann, 1899a:10; n.n. for *C. neglecta* Martin, 1895, *non* Michelotti, 1861. Tertiary, Indonesia.

martiniana (*Cancellaria*) Noetling, 1901:332, pl. 22, figs. 11a-d, 12, 12a, 13a-c. Miocene, Burma. [not a cancellariid]

marwicki (*Waipaoa*) Dell, 1956:112, fig. 113. Recent, New Zealand.

marylandica (*Cancellaria*) G. C. Martin, 1904:165, pl. 43, fig. 8. Miocene, Maryland, U.S.A.

marylandica (*Marianarona*) Petuch, 1988:27, pl. 5, figs. 13-14. Miocene, Maryland, U.S.A.

marysvillensis (*Cancellaria*) Dickerson, 1916:442. *Nomen nudum.*

masferreri (*Cancellaria*) Almera & Bofill, 1884:30; as var. of *C. gradata* Hörnes. Tertiary, Spain.

matsoni (*Cancellaria*) Stephenson, 1941:362, pl. 69, figs. 4-5. Cretaceous, Texas, U.S.A.

mauryae (*Cancellaria*) Olsson, 1922:82, pl. 6, fig. 5. Miocene, Dominican Republic.

mediangulata (*Cancellaria*) Sacco, 1894:36; n.n. for "*C. uniangulata* Deshayes" Hörnes, 1853:pl. 32, fig. 2; see Appendix, Note 2. Miocene, Austria.

medicinensis (*Petersia*) Cragin, 1894:11. Cretaceous, Kansas, U.S.A. [? Cancellariidae]

medinae (*Cancellaria*) Philippi, 1887:63, pl. 7, fig. 4. Miocene, Chile.

megapex (*Bonellitia*) Vokes, 1939:129, pl. 18, figs. 4-5. Eocene, California, U.S.A.

megastoma (*Cancellaria*) Peyrot, 1928:206, pl. 12, fig. 7; as var. of *C. barjonae* Pereira da Costa. Miocene, France.

melanostoma (*Cancellaria*) G. B. Sowerby II, 1849a:137; 1849b:447, pl. 95, fig. 78. Recent, Indian Ocean.

menadensis (*Cancellaria*) Schepman, 1907:164, pl. 10, figs. 5, 5a. Post-Tertiary, Indonesia.

mercadoi (*Scalptia*) Old, 1968:286, pl. 43, figs. 1-3, text-figs. 1-2. Recent, Philippines.

mericana (*Cancellaria*) – Cossmann, 1899a:30. ? Error for *C. marieana* Aldrich.

mericoides (*Cancellaria*) Sacco, 1894:52, pl. 3, fig. 35; as var. of *C. deshayesiana* Desm. [*sic*]; see Appendix, Note 2. Miocene, Italy.

meridionalis (*Cancellaria*) Woods, 1906:326, pl. 40, figs. 10-11. Cretaceous, South Africa.

metuloides (*Cancellaria*) Olsson, 1964:119, pl. 37, figs. 7, 7a. Miocene, Ecuador.

michelinii (*Cancellaria*) Bellardi, 1841:37, pl. 4, figs. 5-6. Miocene, Italy.

micra (*Cancellaria*) Tate, 1889:158, pl. 10, fig. 8. Eocene, Australia.

microscopica (*Cancellaria*) Dall, 1889a:131. Recent, Caribbean.

microsoma (*Cancellaria*) Dall, 1908:296, pl. 11, fig. 10. Recent, western Mexico.

microstoma (*Cancellaria*) 'Dubois' – Bellardi, 1841:3. Error for *C. macrostoma* du Bois de Montpéreux.

microstoma (*Cancellaria*) 'Charlesworth MS' – Morris, 1854:239; Newton, 1891:171. *Nomen nudum.*

microstoma (*Cancellaria*) Newton, 1895:327, pl. 22, figs. 3-4; *ex* Charlesworth MS. Eocene, England.

middendorffiana (*Admete*) Dall, 1885:524; n.n. for "*Admete viridula* Fabricius" Middendorff, 1849:pl. 9, figs. 13-14. Recent, Alaska, U.S.A. (= *Admete laevior* Leche, 1878)

mihelici (*Cancelaria* [*sic*]) Šuklje, 1929:30, pl. 4, figs. 3a-b. Miocene, Yugoslavia.

milleri (*Trigonostoma*) Burch, 1949:3, text-figs. Recent, Panamic-Pacific.

milletii (*Cancellaria*) Deshayes, 1830:181. Tertiary, France.

minbuensis (*Cassidaria*) Noetling, 1895:28, pl. 6, figs. 4, 4a-b. Oligocene/Miocene, India. [*Loxotaphrus*]

minima (*Cancellaria*) Reeve, 1856:pl. 17, figs. 77a-b. Recent, Canary Islands.

minima (*Cancellaria*) Geinitz, 1874a:265, pl. 59, figs. 2a-b. Cretaceous, Germany.

minima (*Cancellaria*) Kaunhowen, 1898:104, pl. 7, figs. 9, 9a. Cretaceous, Belgium. (= *Uxia kaunhoweni* Cossmann, 1899)

minor (*Cancellaria*) Grateloup, 1847:2, pl. 1, fig. 26; as var. of *C. dufourii* Grateloup; see Appendix, Note 1. Tertiary, France.

minor (*Cancellaria*) Bronn, 1848:210; n. n. for "*V. piscatoria* (Gm.)" Brocchi, 1814:pl. 3, fig. 12; as var. of *C. hirta* (Br.). Pliocene, Italy. (= *C. brocchii* Crosse, 1861)

minor (*Cancellaria*) Beyrich, 1856:557; as var. of *C. evulsa* (Sol.). Tertiary, Europe.

minor (*Cancellaria*) Almera & Bofill, 1884:56, pl. E, figs. 31-32; as var. of *C. cancellata* (L.). Tertiary, Spain.

minor (*Cancellaria*) G. B. Sowerby III, 1889:568; as var. of *C. fusca* Sowerby. Recent, Hong Kong.

minor (*Cancellaria*) Almera & Bofill, 1892:12; as var. of *C. hirta* (Br.). *Nomen nudum.*

minor (*Cancellaria*) Pallary, 1900:259; as var. of *C. scabriuscula* (L.). *Nomen nudum.*

minor (*Cancellaria*) Pallary, 1920:27, fig. 15; as var. of *C. piscatoria* (Gmelin). Recent, Morocco.

minuta (*Cancellaria*) Nyst, 1845:482, pl. 12, figs. 23a-c. Tertiary, Belgium.

minuta (*Cancellaria*) Brown, 1849:253, pl. 33*, fig. 73. ? Tertiary, ? British Isles. *Nomen dubium.*

minuta (*Cancellaria*) Braun, 1851:1131. *Nomen nudum.*

minuta (*Cancellaria*) Sandberger, 1859:pl. 15, figs. 9, 9a; 1862:259; *ex* Braun. Tertiary, Germany. (= *C. moguntina* Crosse, 1861)

minuta (*Cancellaria*) 'Harris' – Kennedy, 1895:130. *Nomen nudum.*

minuta (*Cerithidea*) Marshall, 1919:226, pl. 15, fig. 11. Eocene, New Zealand. [= *Cerittudea marshalli* Vignal, *q.v.*]

miocaenica (*Cancellaria*) 'Doderl.' – Cossmann, 1899a:21. Error for *C. miocenica* Doderlein.

miocaenica (*Cancellaria*) Cossmann, 1913a:54, pl. 4, figs. 11-12. Miocene, Panama.

miocenica (*Cancellaria*) Doderlein, 1863:21; as var. of *C. lyrata* (Br.). *Nomen nudum.*

miocenica (*Cancellaria*) Doderlein, 1863:21; as var. of *C. varicosa* (Br.). *Nomen nudum.*

miocenica (*Cancellaria*) Doderlein, 1863:21; as var. of *C. cassidea* (Br.). *Nomen nudum.*

miocenica (*Cancellaria*) Sacco, 1894:61, pl. 3, fig. 62; as var. of *C. lyrata* (Brocchi); *ex* Doderlein; see Appendix, Note 2. Miocene, Italy.

miocenica (*Cancellaria*) Sacco, 1894:56, pl. 3, figs. 47a-b; as var. of *C. varicosa* (Brocchi); *ex* Doderlein; see Appendix, Note 2. Miocene, Italy.

miocenica (*Cancellaria*) Sacco, 1894:8, pl. 1, figs. 15a-b; as *miocenicum*; *ex* Doderlein; see Appendix, Note 2. Miocene, Italy.

miocenica (*Zeadmete*) Finlay, 1930a:78. Miocene, New Zealand.

mioconnectens (*Cancellaria*) Sacco, 1894:58, pl. 3, fig. 55; as var. of *C. taurinia* Bellardi; see Appendix, Note 2. Miocene, Italy.

miocrassa (*Cancellaria*) Sacco, 1894:7; n.n. for "*C. ampullacea* (Br.)" Grateloup, 1847:pl. 25, figs. 28, 32; see Appendix, Note 2. Tertiary, France.

miohirta (*Cancellaria*) Sacco, 1894:27; n.n. for "*C. hirta* (Br.)" Almera & Bofill, 1884:pl. B, figs. 6-7; see Appendix, Note 2. Tertiary, Spain.

miolonga (*Cancellaria*) Sacco, 1894:46, pl. 3, fig. 17; as var. of *C. evulsa* (Solander); see Appendix, Note 2. Miocene, Italy.

miolyrata (*Cancellaria*) Sacco, 1894:62; n.n. for "*C. lyrata* (Br.)" Beyrich, 1857:pl. 27, figs. 7-8; see Appendix, Note 2. Tertiary, Germany.

mioparva (*Cancellaria*) Sacco, 1894:33; n.n. for "*C. calcarata* (Br.)" Beyrich, 1857:pl. 28, fig. 3; see Appendix, Note 2. Tertiary, Germany.

mioquadrata (*Cancellaria*) Sacco, 1894:66; n.n for "*C. laurensii* Grat." Hoernes & Auinger, 1890:pl. 33, figs. 1-2; see Appendix, Note 2. Miocene, Austria.

mioscalaroides (*Cancellaria*) Sacco, 1894:54; n.n. for "*C. scalaroides* Wood" Beyrich, 1857:pl. 27, fig. 5; see Appendix, Note 2. Tertiary, Germany.

mirabilis (*Plesiotriton*) Beu & Maxwell, 1987:27, pl. 24, figs. a-l, q-r; text-figs. 2E-F. Recent, New Britain.

mississippiensis (*Cancellaria*) Conrad, 1848a:287; 1848b:118, pl. 11, fig. 38. Oligocene, Mississippi, U.S.A.

mistense (*Trigonostoma*) Janssen, 1984:16, pl. 3, figs. 4a-b. Miocene, Netherlands.

mitraeforme (*Buccinum*) Pusch in Andrzejowski, 1830:94, pl. 4, figs. 1a-b. Tertiary, Poland. [= *Cancellaria inermis* Pusch, 1837, *q.v.*]

mitraeformis (*Voluta*) Brocchi, 1814:645, pl. 15, fig. 13. Pliocene, Italy. [*non Voluta mitraeformis* Lamarck, 1811; ?= *Brocchinia parvula tauroparva* Sacco, 1894]

mitraeformis (*Cancellaria*) 'Eichwald' – Crosse, 1861:251. Error for *C. mitraeformis* (Pusch).

mitraeformis (*Cancellaria*) 'Sowerby' – Bellardi, 1841:9; *et al.* Error for *C. mitriformis* Sowerby.

mitriformis (*Cancellaria*) G. B. Sowerby I, 1832a:51; 1832b:fig. 14. Recent, Panamic-Pacific.

mitrodita (*Cancellaria*) Gardner, 1937:369, pl. 44, fig. 11. Miocene, Florida, U.S.A.

mitroides (*Cancellaria*) Fischer von Waldheim, 1807:173. Fossil, locality unknown. *Nomen inquirendum.*

modesta (*Cancellaria*) Carpenter, 1864:628, 660. Recent, northwestern coast of U.S.A.

modestina (*Cancellaria*) Tate, 1889:157, pl. 9, fig. 4. Miocene, Australia.

moguntina (*Cancellaria*) Crosse, 1861:252; n.n. for *C. minuta* Braun, *non* Nyst, with ref. to Sandberger, [1859]:pl. 15, fig. 9. Tertiary, Germany.

moharrami (*Cancellaria*) Abbass, 1972:58, pl. 4, fig. 15. Paleocene, Saudi Arabia.

montrouzieri (*Cancellaria*) Souverbie in Souverbie & Montrouzier, 1863:163, pl. 5, fig. 8. Recent, New Caledonia. (?= *C. contabulata* Sowerby, 1832)

montserratensis (*Cancellaria*) Maury, 1925a:194, pl. 35, figs. 6, 8. Miocene, Trinidad.

moorei (*Cancellaria*) Guppy, 1866:289, pl. 17, fig. 7. Pliocene, Jamaica.

moravica (*Cancellaria*) Oppenheim, 1922:80, pl. 5, figs. 15, 15a-b. Tertiary, Czechoslovakia.

morgani (*Sveltia*) Cossmann, 1903a:107, pl. 3, figs. 3-4. Pliocene, India.

mourloni (*Cancellaria*) Briart & Cornet, 1877:12, pl. 14, figs. 3a-c. Paleocene, Belgium.

mucronatum (*Trigonostoma*) Peyrot, 1928:256, pl. 14, figs. 9, 33. Miocene, France.

multicostata (*Cancellaria*) Bellardi & Michelotti, 1840:147; as var. of *C. uniangulata* Deshayes. Tertiary, Italy.

multicostata (*Cancellaria*) Bellardi, 1840:344; as var. of *C. uniangulata* Deshayes. *Nomen nudum.*

multicostata (*Cancellaria*) Bellardi, 1841:17, pl. 2, figs. 5-6; as var. of *C. uniangulata* Deshayes. Tertiary, Italy.

multicostata (*Cancellaria*) Bellardi, 1841:8; as var. of *C. ampullacea* (Br.). *Nomen nudum.*

multicostata (*Cancellaria*) Bellardi, 1841:20, pl. 2, figs. 13-14; as var. of *C. nodulosa* Lamarck. Tertiary, Italy.

multicostata (*Cancellaria*) Bellardi, 1841:31, pl. 4, figs. 19-20; as var. of *C. buccinula* Basterot [*sic*]. Tertiary, Italy.

multicostatum (*Triton*) Favre, 1869:89, pl. 10, fig. 15. Cretaceous, France. [*Plesiotriton*]

multienensis (*Cancellaria*) Morlet, 1885b:196; n.n. for *C. bezanconi* Morlet, 1885, *non* de Raincourt, 1884. Middle Eocene, France.

multiensis (*Cancellaria*) 'Morlet' – Cossmann, 1899:38. Error for *C. multienensis* Morlet.

multilinea (*Cancellaria*) 'Edwards MS' – Newton, 1891:171. *Nomen nudum.*

multilineata (*Bonellitia*) Wrigley, 1935:370, pl. 33, figs. 21-22. Middle Eocene, England.

multilira (*Mataxa*) Stephenson, 1941:366, pl. 70, figs. 6-7; as subsp. of *M. valida* Stephenson. Cretaceous, Texas, U.S.A.

multinodulatus (*Africotriton*) Beu & Maxwell, 1987:32, pl. 10, figs. a-s. Recent, South Africa.

multiplicata (*Cancellaria*) I. Lea, 1833:139, pl. 5, fig. 135. Eocene, Alabama, U.S.A.

multiplicata (*Cancellaria*) Lesson, 1841a:37. Recent, ? Panamic-Pacific. (?= *C. chrysostoma* Sowerby, 1832)

multiplicis (*Cancellaria*) Newton, 1922:42, pl. 3, fig. 26. Eocene, Nigeria.

multistriata (*Cancellaria*) Bellardi, 1840:344; as var. of *C. taurinia* Bellardi. *Nomen nudum.*

multistriata (*Cancellaria*) Beyrich, 1856:567, pl. 26, figs. 6a-d. Oligocene, Europe.

multistriata (*Sveltia*) Ravn, 1939:87, pl. 3, figs. 23a-b, 24a-b. Paleocene, Denmark.

munida (*Waipaoa*) Ponder, 1968:46, pl. 4, fig. 57. Recent, New Zealand. (?= *Dellina aoteana* (Dell, 1956))

muratana (*Cancellaria*) Nomura & Onisi, 1940:185, pl. 17, fig. 14. Neogene, Japan.

murayamai (*Cancellaria*) Yokoyama, 1926b:384, pl. 44, fig. 3. Pliocene, Japan.

muricata (*Cancellaria*) Risso, 1826:188. Tertiary, Europe.

muricata (*Cancellaria*) Wood, 1847:354. *Nomen nudum.*

mutica (*Cancellaria*) 'Basterot' – Grateloup, 1832:338. *Nomen nudum.*

mutinensis (*Cancellaria*) Foresti, 1884:302, pl. 1, figs. 1a-c. Tertiary, Italy.

mutsuana (*Cancellaria*) Hatai, Masuda & Suzuki, 1961:29, pl. 4, figs. 1a-b, 2a-b. Pliocene, Japan.

myrayamai (*Cancellaria*) 'Yok.' – Zoological Record for 1930, 67(8):72. Error for *C. murayamai* Yokoyama.

N

nakayamai (*Neadmete*) Habe, 1961a:73, Appendix p. 29, pl. 36, fig. 3. Recent, Japan.

namnetica (*Cancellaria*) Vasseur, 1881:249. *Nomen nudum.*

nana (*Cancellaria*) Deshayes, 1864:106, pl. 73, figs. 11-12. Eocene, France.

nana (*Cancellaria*) 'Doderlein' – Davoli, 1980:228. *Nomen nudum.*

nana (*Trigonostoma*) Ozaki, 1956:2, pl. 1, fig. 5. Miocene, Japan.

nancellaria (*Cancellaria*) Woodring, 1970:341, pl. 53, figs. 3-4. Miocene/Pliocene, Panama.

nanggulanensis (*Cancellaria*) K. Martin, 1914:126, pl. 2, fig. 55. Tertiary, Indonesia.

narica (*Uxia*) Vredenburg, 1925:99, pl. 7, fig. 7. Tertiary, India.

naroniformis (*Uxia*) Finlay, 1930a:80. Miocene, New Zealand.

nassa (*Voluta*) Gmelin, 1791:3464. Recent, Indo-Pacific. [*Scalptia*]

nassaeformis (*Cancellaria*) 'Wood MS' – Newton, 1891:171. *Nomen nudum.*

nassaeformis (*Uxia*) Wrigley, 1925:246, fig. 12. Eocene, England.

nassaeformis (*Egerea*) Noszky, 1936:73, pl. 5, fig. 12; as var. of *E. collectiva* Gabor. Oligocene, Hungary.

nassariformis (*Cancellaria*) Covacevich & Frassinetti, 1986:49, pl. 2, figs. 4a-c, 5a-c, text-fig. 9. Miocene, Chile.

nassiformis (*Cancellaria*) Lesson, 1842:204. Recent, western Mexico. [?= *Nassarius corpulentus* (C. B. Adams, 1852)]

nassiformis (*Cancellaria*) Seguenza, 1880:110, pl. 11, fig. 28. Tertiary, Italy. (?= *C. dregeri* Hoernes & Auinger, 1890)

nassoides (*Cancellaria*) von Koenen, 1889:149, pl. 12, figs. 13a-c. Oligocene, Germany.

nassoides (*Cancellaria*) Schepman, 1911:263, pl. 18, fig. 9. Recent, Indonesia. (= *Admetula garrardi* Petit, 1974)

nasuta (*Antepepta*) Finlay & Marwick, 1937:83, pl. 11, fig. 1. Paleocene, New Zealand.

nausorensis (*Neadmete*) Ladd, 1982:58, pl. 14, figs. 19-22. Pliocene, Fiji.

neavolutella (*Cancellaria*) Noetling, 1901:328, pl. 22, figs. 7a-b, 8, 8a. Miocene, Burma. [?= *Rimella javana* K. Martin, 1879]

neglecta (*Cancellaria*) Michelotti, 1861:104, pl. 11, figs. 9-10. Tertiary, Italy.

neglecta (*Cancellaria*) K. Martin, 1895:47, pl. 7, fig. 112; n.n. for *Triton buccinoides* K. Martin, 1880). Tertiary, Indonesia. (= *Bivetia martini* Cossmann, 1899)

neritoidea (*Cancellaria*) G. C. Martin, 1904:168, pl. 43, figs. 13a-b. Miocene, Maryland, U.S.A.

neudorfensis (*Cancellaria*) Oppenheim, 1922:82, pl. 6 [*sic*; error for pl. 5], figs. 13, 13a-b. Tertiary, Czechoslovakia.

neugeboreni (*Cancellaria*) M. Hörnes, 1856:680, pl. 52, figs. 6a-b. Miocene, Austria.

neuvillei (*Bivetia*) Peyrot, 1928:203, pl. 12, figs. 35-36. Miocene, France.

nevadensis (*Cancellaria*) Anderson & Martin, 1914:85, pl. 8, figs. 5a-d. Miocene, California, U.S.A.

newhallensis (*Cancellaria*) Carson, 1926:56, pl. 3, fig. 3. Pliocene, California, U.S.A.

nitens (*Cancellaria*) Beyrich, 1856:561, pl. 27, figs. 1a-c. Oligocene, Germany.

nitida (*Cancellaria*) A. Adams, 1855:123. Recent, Indo-Pacific.

nitida (*Cancellaria*) Reeve, 1856:pl. 17, figs. 78a-b; *ex* Adams MS. Recent, ? Indo-Pacific.

nitida (*Cancellaria*) von Koenen, 1889:100, pl. 12, figs. 11a-c, 12a-c. Oligocene, Germany.

nitida (*Scalptia*) 'Hinds' – Jousseaume, 1887b:214. Error for *S. nitida* (Adams).

nitidula (*Voluta*) Müller, 1851:41, pl. 5, figs. 25a-b. Cretacous, Germany. [Cancellariidae]

nodigera (*Cancellaria*) 'Edwards MS' – Newton, 1891:172. *Nomen nudum.*

nodosa (*Admete*) Verrill & Smith in Verrill, 1885:419, pl. 44, fig. 9. Recent, Delaware Bay, U.S.A.

nodosissima (*Cancellaria*) Sacco, 1894:47, pl. 3, fig. 20; as var. of *C. evulsa* (Solander); see Appendix, Note 2. Oligocene, Italy.

nodosivaricosa (*Agatrix*) Petuch, 1979:11, figs. 26-27. Recent, Philippines.

nodulatus (*Epidromus*) Tate, 1888:128, pl. 6, fig. 11. Eocene, Australia. [*Tritonoharpa*]

nodulifera (*Cancellaria*) G. B. Sowerby I, 1825:Appendix p. 15. Recent, Japan.

nodulifera (*Cancellaria*) Beyrich, 1856:569, pl. 27, figs. 3-4, 4a. Miocene, Austria. (= *C. rothi* Semper, 1861)

noduliformis (*Cancellaria*) 'Sowerby' – Otuka, 1937:1004. Error for *C. nodulifera* Sowerby.

nodulosa (*Cancellaria*) Lamarck, 1822b:113. Recent, western Africa. (= *C. piscatoria* (Gmelin, 1791))

nodulosissima (*Cancellaria*) Sacco, 1894:30, pl. 2, fig. 34; as var. of *C. barjonae* Pereira da Costa; see Appendix, Note 2. Miocene, Italy.

nodus (*Oamaruia*) Finlay, 1930a:78. Miocene, New Zealand.

notabilis (*Cancellaria*) Eichwald, 1851:103, pl. 8, figs. 14a-c. Tertiary, U.S.S.R.

nucleosa (*Anapepta*) Marwick, 1931:122, pl. 13, fig. 239. Miocene, New Zealand.

nuda (*Trichotropis*) Dall, 1927:104. Recent, Florida, U.S.A. [*Iphinopsis*]

nympha (*Inglisella*) Garrard, 1975:40, pl. 4, fig. 14. Recent, Australia.

nysti (*Cancellaria*) M. Hörnes, 1854:305, pl. 34, figs. 1a-c. Miocene, Austria.

nysti (*Pentadactylus*) Briart & Cornet, 1870:43, pl. 3, figs. 10a-c. Paleocene, Europe. [*Unitas*]

O

obesa (*Cancellaria*) G. B. Sowerby I, 1832a:52; 1832b:figs. 3-4. Recent, Panamic-Pacific.

obliqua (*Cancellaria*) 'Lamarck' – Crosse, 1861:233. Error for *C. obliquata* Lamarck.

obliquata (*Cancellaria*) Lamarck, 1822b:115. Recent, Indo-Pacific.

obliquata (*Cancellaria*) 'Kiener' – Sherborn, 1929:4461. Error for *C. obliquata* Lamarck.

oblita (*Cancellaria*) Michelotti, 1861:103, pl. 11, figs. 7-8. Tertiary, Italy.

oblonga (*Cancellaria*) G. B. Sowerby I, 1825:Appendix p. 15. Recent, Indo-Pacific.

obnixa (*Sydaphera*) Iredale, 1936:318, pl. 23, fig. 6. Recent, Australia.

observatoria (*Cancellaria*) von Ihering, 1907:214; n.n. for "*C. gracilis* Ihering" Ortmann, 1902:235, pl. 36, figs. 3a-b; as var. of *C. gracilis* von Ihering. Tertiary, Argentina.

obsoleta (*Cancellaria*) M. Hörnes, 1856:678, pl. 52, figs. 3a-b. Miocene, Austria.

obsoleta (*Cancellaria*) Brugnone, 1880:103, pl. 1, fig. 2; as var. of *C. hirta* (Br.). Tertiary, Italy.

obtusa (*Cancellaria*) Deshayes, 1830:187. Recent, Panamic-Pacific.

obtusa (*Cancellaria*) Binkhorst, 1861:5, pl. 2, figs. 2a-b. Cretaceous, Belgium. (= *C. cretacea* Nyst, 1881)

occulta (*Cancellaria*) Beyrich, 1856:576, pl. 28, figs. 7a-b. Oligocene, Germany.

ocoyana (*Cancellaria*) Addicott, 1970:110, pl. 14, figs. 4-5, 8-9; pl. 16, fig. 20. Miocene, California, U.S.A.

oichingensis (*Unitas*) Traub, 1984:6; n.n. for *U. elongata* Traub, 1979, *non U. elongata* (Cuvillier, 1935). Paleocene, Austria.

okinawana (*Merica*) Noda, 1980:37, pl. 5, figs. 5a-b; as subsp. of *Merica asprella* [*sic*] Lamarck. Pliocene, Okinawa.

okutanii (*Neadmete*) Petit, 1974:110, n.n. for "*Neadmete japonica* (Smith)" Habe, 1961a:73, Appendix p. 28, pl. 36, fig. 2. Recent, Japan.

oldroydia (*Cancellaria*) Carson, 1926:51, pl. 1, fig. 5. Pliocene, California, U.S.A.

oligocancellata (*Cancellaria*) Sacco, 1894:46, pl. 3, fig. 18; as var. of *C. evulsa* (Solander); see Appendix, Note 2. Oligocene, Italy.

oligoevulsa (*Cancellaria*) Sacco, 1894:45; n.n. for "*C. evulsa* Sow." von Koenen, 1889:pl. 10, figs. 1-3; see Appendix, Note 2. Tertiary, Germany. (= *C. evulsa* var. *parisiensis* Cossmann, 1889)

oligolongum (*Cancellaria*) Sacco, 1894:4, pl. 1, figs. 1a-b; see Appendix, Note 2. Oligocene, Italy.

oligopercostata (*Admete*) Sacco, 1894:71; n.n. for "*C. subangulosa* Wood" Speyer, 1867:pl. 11 [*sic*; error for 16], fig. 10. Tertiary, Germany.

olssoni (*Admete*) Rivera, 1957:186, pl. 4, fig. 27. Eocene, Peru.

onubensis (*Ovilia*) Landau, 1984:149, pl. 1, fig. 14; pl. 2, figs. 6-11. Pliocene, Spain.

oppenheimi (*Sveltella*) Cossmann & Pissarro, 1901:22, pl. 8, figs. 4-5. Middle Eocene, France.

orbignyana (*Cancellaria*) Briart & Cornet, 1868:21, pl. 2, figs. 9-10. Cretaceous, Belgium.

orbignyi (*Cancellaria*) 'Blainville,1829' – Sherborn, 1929:4602. Refers to transfer of *Buccinum d'orbignyi* Payraudeau to *Cancellaria* by Blainville. [*Cantharus*]

orcitans (*Trigonostoma*) 'Martin' – Marks, 1949:458. Error for *Rhomboidestoma oscitans* K. Martin.

oregonensis (*Cancellaria*) Conrad, 1865c:151. Miocene, Oregon, U.S.A.

oregonensis (*Cancellaria*) Dall, 1909a:28, pl. 2, fig. 7. Tertiary, Oregon, U.S.A. (?= *C. crawfordiana* Dall, 1891)

oregonsis (*Cancellaria*) 'Dall' – Dall, 1909a:pl. 2, fig. 7. Plate caption error for *C. oregonensis* Dall.

ornata (*Turbinella*) Watelet, 1853:21, pl. 2, fig. 17. Eocene, France. [?= *Cancellaria maglorii* Melleville, 1843]

ornata (*Cancellaria*) Deshayes, 1864:101, pl. 73, figs. 19-20. Lower Eocene, France.

ornata (*Cancellaria*) Ovechkin, 1954:82, pl. 12, fig. 14; pl. 13, figs. 4-5; *ex* Alekseyev MS. Paleogene, U.S.S.R.

ornata (*Admete*) Il'ina, 1955:78, pl. 30, fig. 16; *ex* Alekseyev MS. Paleogene, U.S.S.R.

ornata (*Cancellaria*) Alekseyev, 1963:124, pl. 22, figs. 11-12, 15-20. Paleogene, U.S.S.R.

ornatissima (*Cancellaria*) Boettger, 1906:50; as var. of *C. geslini* Basterot. Miocene, Romania.

oscitans (*Rhomboidestoma*) K. Martin, 1931:12, pl. 2, figs. 6, 6a. Tertiary, Indonesia.

otagoensis (*Zeadmete*) Dell, 1956:113, fig. 104. Recent, New Zealand.

ovalis (*Cancellaria*) 'Friele' – Paetel, 1888:331. ? Error for *Pleurotoma ovalis* Friele.

ovalis (*Borsonia*) Marshall, 1918:269, pl. 18, figs. 10, 10a. Miocene, New Zealand. [*Bonellitia*]

ovalis (*Zeadmete*) Dell, 1956:114, fig. 103. Recent, New Zealand.

ovata (*Admete*) E. A. Smith, 1875:426. Recent, ? Japan.

ovata (*Cancellaria*) G. B. Sowerby I, 1832a:53; 1832b:fig. 2. Recent, Panamic-Pacific.

ovata (*Cancellaria*) von Koenen, 1889:104, pl. 12, figs. 6a-c, 7a-b. Oligocene, Germany. (= *Bonellitia lattorfensis* Wrigley, 1935)

ovatocrassa (*Aphera*) Sacco, 1894:67, pl. 3, figs. 79a-b. Miocene, Italy.

ovatoventricosa (*Cancellaria*) Sacco, 1894:15; as var. of *C. michelinii* Bellardi; *ex* Grateloup, 1847:pl. 1, fig. 13; see Appendix, Note 2. Tertiary, France.

ovilia (*Ovilia*) 'Bast.' – Jousseaume, 1887b:194. *Nomen nudum.*

ovoidolaevis (*Cancellaria*) Sacco, 1894:18, pl. 1, fig. 47; see Appendix, Note 2. Tertiary, Italy.

ovulum (*Cancellaria*) Geinitz, 1874a:265, pl. 59, figs. 3a-b. Cretaceous, Germany.

ozawai (*Cancellaria*) Otuka, 1937:1004. *Nomen nudum.*

ozawai (*Cancellaria*) 'Otuka MS' – Hatai & Nisiyama, 1940:119, 131. *Nomen nudum.*

P

pabloensis (*Cancellaria*) B. L. Clark, 1915:503, pl. 68, figs. 9, 11. Miocene, California, U.S.A.

pachia (*Cancellaria*) M. Smith, 1940:45, pl. 2, fig. 2; as subsp. of *C. moorei* Guppy. Pleistocene, Florida, U.S.A.

pacifica (*Cancellaria*) F. M. Anderson, 1905:199, pl. 15, figs. 43-45. Miocene, California, U.S.A.

pacifica (*Cancellaria*) Pilsbry & Olsson, 1941:23, pl. 3, fig. 4. Pliocene, Ecuador. (= *C. surpacifica* Olsson, 1967)

pahiense (*Cymatium*) Marshall & Murdoch, 1921:81, pl. 18, fig. 5. Eocene, New Zealand. [*Tatara*]

pajana (*Cancellaria*) Pilsbry & Olsson, 1941:25, pl. 3, fig. 6. Pliocene, Ecuador.

pakistanicum (*Trigonostoma*) Eames, 1952:117, pl. 4, fig. 99. Eocene, Pakistan.

pallida (*Cancellaria*) E. A. Smith, 1899a:313, text-fig. Recent, Australia.

palmeri (*Cancellaria*) Carson, 1926:55, pl. 2, fig. 4. Pliocene, California, U.S.A.

panamensis (*Colubraria*) M. Smith, 1947:55, pl. 2, fig. 6. Recent, Panamic-Pacific. [*Tritonoharpa*]

panamica (*Olssonella*) Petit, 1976:35, pl. 2, fig. 1. Pliocene, Panama.

panamuna (*Cancellaria*) Garrard, 1975:14, pl. 2, fig. 7. Recent, Australia.

panones (*Cancellaria*) G. D. Harris, 1895a:65, pl. 6, fig. 1. Eocene, Texas, U.S.A.

papillosa (*Cancellaria*) Doderlein, 1863:21. *Nomen nudum.*

papillosa (*Cancellaria*) Coppi, 1872:17, pl. 1, figs. 29a-b; *ex* Doderlein. Tertiary, Italy. (?= *C. doderleini* Mayer, 1868)

papyracea (*Cancellaria*) Grateloup, 1832:344. Tertiary, France.

paraguanensis (*Cancellaria*) H. K. Hodson in Hodson & Hodson, 1931:44, pl. 24, fig. 10. Miocene, Venezuela.

paramoorei (*Cancellaria*) 'Gardner MS' – Mansfield, 1925:31. *Nomen nudum.*

paramoorei (*Cancellaria*) Gardner, 1937:372, pl. 45, figs. 3-4. Miocene, Florida, U.S.A.

parcestriata (*Cancellaria*) Bronn in Reiss & Bronn, 1862:27, pl. 1, fig. 7; as *parce-striata*. Tertiary, Azores.

parilis (*Bonellitia*) Palmer, 1937:453, pl. 70, figs. 21-25. Eocene, Louisiana and Texas, U.S.A.

parisiensis (*Cancellaria*) Cossmann, 1889:228; n.n. for "*C. evulsa* (Sol.)" von Koenen, 1889:117, pl. 10, figs. 1-3; as var. of *C. evulsa* (Sol.). Tertiary, Europe. (see *C. oligoevulsa* Sacco, 1894)

parnensis (*Cancellaria*) Cossmann, 1896a:42, pl. 3, figs. 21-22. Middle Eocene, France.

partschi (*Cancellaria*) M. Hörnes, 1854:307, pl. 34, figs. 3a-b. Miocene, Austria.

parva (*Cancellaria*) I. Lea, 1833:142, pl. 5, fig. 141. Eocene, southeastern U.S.A.

parva (*Cancellaria*) Philippi, 1860:187, pl. 7, fig. 18. Recent, Chile. (= *Sveltella philippii* Cossmann, 1899) [? *Engina*]

parva (*Cancellaria*) Brugnone, 1880:103; as var. of *C. hirta* (Br.). Tertiary, Italy.

parva (*Inglisella*) Laws, 1935:37, pl. 6, fig. 17. Miocene, New Zealand.

parvicarinata (*Sveltia*) Kautsky, 1925:139, pl. 10, fig. 4; as var. of *S. lyrata* (Br.). Miocene, Germany.

parvillima (*Admete*) Sacco, 1894:71; n.n. for "*C. pusilla* Phil." Beyrich, 1857[=1856]:pl. 27, fig. 9; as var. of *Admete minuta* (Braun). Tertiary, Germany.

parvocrassa (*Cancellaria*) Sacco, 1894:9; n.n. for "*C. ampullacea* (Br.)" Almera & Bofill, 1884:pl. C, figs. 13-14; as var. of *C. ampullacea* (Br.); see Appendix, Note 2. Miocene, Spain.

parvotriangula (*Cancellaria*) Sacco, 1894:6, pl. 1, fig. 6; as var. of *C. umbilicaris* (Br.); see Appendix, Note 2. Pliocene, Italy.

parvoturrita (*Cancellaria*) Sacco, 1894:58, pl. 3, fig. 56; as var. of *C. taurinia* Bellardi; see Appendix, Note 2. Miocene, Italy.

parvula (*Cancellaria*) Beyrich, 1856:576, pl. 28, figs. 8a-b. Tertiary, Germany.

paschalis (*Cancellaria*) Thiele, 1925:201, pl. 22, fig. 22. Recent, eastern Africa.

patricia (*Cancellaria*) Thiele, 1925:200, pl. 22, fig. 20. Recent, eastern Africa.

patula (*Cancellaria*) Mayer, 1858:80, pl. 3, fig. 8. Tertiary, France.

patuxentia (*Cancellaria*) G. Martin, 1904:167, pl. 43, figs. 11a-b. Miocene, Maryland, U.S.A.

paucicostata (*Cancellaria*) Sacco, 1894:8, pl. 1, fig. 13; as var. of *C. cassidea* (Brocchi); see Appendix, Note 2. Pliocene, Italy.

paucicostata (*Cancellaria*) G. B. Sowerby III, 1894:160, pl. 12, fig. 26. Recent, Persian Gulf.

paucicostata (*Merica*) Friedberg, 1914:243, pl. 15, fig. 5; as var. of *M. fenestrata* (Eichwald). Miocene, Poland.

paucicostata (*Sveltia*) Peyrot, 1928:218, pl. 14, fig. 7; as "mut." of *S. varicosa* (Brocchi). Miocene, France.

paucicostulata (*Brocchinia*) Sacco, 1894:69, pl. 3, fig. 86; as var. of *B. mitraeformis* (Brocchi). Pliocene, Italy.

pauciplicata (*Cancelrana*) Shuto, 1962:77, pl. 9, figs. 2, 6; pl. 11, figs. 5, 9; text-fig. 14; as subsp. of *C. lischkei* (Yokoyama). Tertiary, Japan.

pauciserrata (*Cancellaria*) Sacco, 1894:44, pl. 3, fig. 7; as var. of *C. serrata* Bronn; see Appendix, Note 2. Miocene, Italy.

paucivaricatum (*Tritonium*) Gabb, 1864:95, pl. 28, figs. 209, 209a. Eocene, California, U.S.A. [*Admetula*]

paytensis (*Admete*) Olsson, 1930:29, pl. 11, fig. 5. Eocene, Peru.

paytensis (*Plesiotriton*) Olsson, 1930:60, pl. 10, figs. 8, 10-11. Eocene, Peru.

pearlensis (*Cancellaria*) Meyer & Aldrich in Meyer, 1887:7, pl. 1, fig. 4. Eocene, Mississippi, U.S.A.

pellucida (*Trigona*) Perry, 1811:pl. 51, figs. 1, 2. Recent, Indo-Pacific. [?= *Trigonostoma scalare* (Gmelin, 1791)]

pemrosei (*Cancellaria*) 'Harris' – Cossmann, 1899:34. Error for *C. penrosei* Harris.

peninsularis (*Cancellaria*) Olsson, 1942:62, pl. 11, fig. 9. Pliocene, Costa Rica.

penita (*Cancellaria*) Olsson, 1942:59, pl. 8, figs. 4, 8. Pliocene, Costa Rica.

penrosei (*Cancellaria*) G. D. Harris, 1895a:66, pl. 6, fig. 4. Eocene, Texas, U.S.A.

peracuminata (*Cancellaria*) Sacco, 1894:29, pl. 2, fig. 26; as var. of *C. hirta* (Brocchi); see Appendix, Note 2. Pliocene, Italy.

percostata (*Cancellaria*) de Gregorio, 1890:48, pl. 3, figs. 21-22. Eocene, Alabama, U.S.A.

percostatoacuta (*Cancellaria*) Sacco, 1894:15, pl. 1, figs. 40a-b; as var. of *C. michelinii* Bellardi; see Appendix, Note 2. Miocene, Italy.

percostatula (*Cancellaria*) Sacco, 1894:14, pl. 1, figs. 35a-b; as var. of *C. crassicosta* Bellardi; see Appendix, Note 2. Miocene, Italy.

percrassulata (*Cancellaria*) Sacco, 1894:15, pl. 1, figs. 39a-b; as var. of *C. michelinii* Bellardi; see Appendix, Note 2. Miocene, Italy.

perdiciana (*Cancellaria*) Olsson, 1942:61, pl. 8, fig. 5. Miocene, Colombia.

perforata (*Neptunea*) Gabb, 1864:89, pl. 18, fig. 39. Cretaceous, California, U.S.A. [*Paladmete*]

pergradata (*Cancellaria*) Verco, 1904:142, pl. 26, fig. 19. Recent, Australia.

perhirta (*Cancellaria*) Sacco, 1894:30; n.n. for "*C. barjonae* Pereira da Costa" Almera & Bofill, 1884:pl. B, figs. 4-5; as var. of *C. barjonae* Pereira da Costa; see Appendix, Note 2. Tertiary, Spain.

perla (*Colubraria*) M. Smith, 1947:55, pl. 2, fig. 2. Recent, Panamic-Pacific. [*Tritonoharpa*]

perplexa (*Perplicaria*) Dall, 1890:90, pl. 3, fig. 1. Pliocene, Florida, U.S.A.

perproducta (*Cancellaria*) Sacco, 1894:25, pl. 2, fig. 15; as var. of *C. exwestiana* Sacco; see Appendix, Note 2. Miocene, Italy.

perrini (*Cancellaria*) Carson, 1926:56, pl. 3, fig. 4. Pliocene, California, U.S.A.

perscalarata (*Cancellaria*) Sacco, 1894:38, pl. 2, fig. 58; as var. of *C. cancellata* (L.); see Appendix, Note 2. Pliocene, Italy.

perscalaris (*Cancellaria*) Sacco, 1894:64, pl. 3, fig. 71; as var. of *C. tribulus* (Br.); see Appendix, Note 2. Pliocene, Italy.

perspectiva (*Cancellaria*) Conrad, 1834:136. Miocene, Virginia, U.S.A.

persuturata (*Cancellaria*) Sacco, 1894:56, pl. 3, fig. 44; as var. of *C. varicosa* (Br.); see Appendix, Note 2. Pliocene, Italy.

pertypica (*Cancellaria*) Sacco, 1894:54, pl. 3, fig. 42; as var. of *C. varicosa* (Br.); see Appendix, Note 2. Pliocene, Italy.

peruana (*Aphera*) Nelson, 1870:190, pl. 6, fig. 3. Miocene, Peru.

peruviana (*Cancellaria*) 'Strong & Hertlein' – Burch, 1945:5. *Nomen nudum.*

peruviana (*Cancellaria*) Strong, 1954:17; n.n. for *C. granosa* Sowerby, 1832b:fig. 16 (only). Recent, locality unknown. (?= *C. undulata* Sowerby, 1849)

peterana (*Trigonostoma*) Olsson & Harbison, 1953:181, pl. 28, figs. 6, 6a-b; as subsp. of *T. sericea* (Dall). Pliocene, Florida, U.S.A.

petiti (*Cancellaria*) Olsson, 1967:44; n.n. for *C. cossmanni* Olsson, 1922, *non* Morlet, 1888. Pliocene, Costa Rica.

petiti (*Cancellaria*) Ladd, 1982:57, pl. 14, figs. 16-18. Pliocene, Fiji. (= *C. laddi* Petit, 1987)

petiti (*Africotriton*) Beu & Maxwell, 1987:33, pl. 7, figs. i-m; pl. 8, figs. a-h. Recent, South Africa.

peyreirensis (*Sveltia*) Peyrot, 1928:235, pl. 13, figs. 9-10. Miocene, France.

pharaonica (*Admete*) Cuvillier, 1933:61, pl. 8, figs. 27, 33. Eocene, Egypt.

philippii (*Admete*) von Ihering, 1907:212; n.n. for *C. australis* Philippi, 1855, *non* Sowerby, 1832. Recent, Strait of Magellan.

philippii (*Admete*) Carcelles, 1950:65; n.n. for *C. australis* Philippi, 1855, *non* Sowerby, 1832. Recent, Strait of Magellan. (= *Admete philippii* von Ihering, 1907)

philippii (*Sveltella*) Cossmann, 1899a:30; n.n. for *Cancellaria parva* Philippi, 1860, *non* Lea, 1833. Recent, Chile. [? *Engina*]

pinguis (*Cancellaria*) Gardner, 1937:370, pl. 44, figs. 12-13. Miocene, Florida, U.S.A.

pinguis (*Caveola*) Stephenson, 1953:190, pl. 42, figs. 6-7. Cretaceous, Texas, U.S.A. [? Fasciolariidae]

pinolensis (*Cancellaria*) B. L. Clark, 1918:80. *Nomen nudum.*

pirabensis (*Cancellaria*) Maury, 1925b:186, pl. 9, fig. 7. Miocene, Brazil.

pisanelloides (*Tritonidea*) Cossmann, 1923:101, pl. 6, figs. 45-46. Eocene, France. [?= *Turehua*]

piscatorium (*Buccinum*) Gmelin, 1791:3496. Recent, western Africa. [*Solatia*]

plagiostoma (*Cancellaria*) Conrad, 1834:136. Miocene, Virginia, U.S.A.

planasuturata (*Trigonostoma*) Richards & Harbison, 1942:217, pl. 21, figs. 4-5. Miocene, New Jersey, U.S.A.

planispira (*Cancellaria*) Nyst, 1845:481, pl. 12, figs. 22a-b. Tertiary, Belgium.

planistria (*Cancellaria*) von Koenen, 1885:11, pl. 1, figs. 7a-c. Paleocene, Denmark.

planistria (*Cancellaria*) von Koenen, 1889:110, pl. 8, figs. 8a-c, 9a-d; as var. of *C. quadrata* Sowerby. Oligocene, Europe.

planospira (*Cancellaria*) 'Nyst' – Dewalque, 1868:419. Error for *C. planispira* Nyst.

planospira (*Cancellaria*) Grant & Gale, 1931:613, pl. 27, fig. 4; as var. of *C. obesa* Sowerby. Pliocene, California, U.S.A.

plateaui (*Sveltella*) Cossmann, 1902:56, pl. 4, fig. 5. Paleocene, France.

platypleura (*Cancellaria*) 'Tate' – Tate & Dennant, 1893:221. *Nomen nudum.*

platypleura (*Cancellaria*) Tate, 1898:389; unnecessary n.n. for *C. laticostata* Tenison-Woods.

plebeja (*Cancellaria*) Thiele, 1925:200, pl. 22, fig. 19. Recent, South Africa.

plicata (*Cancellaria*) I. Lea, 1833:139, pl. 5, fig. 136. Eocene, Alabama, U.S.A. (?= *C. gemmatum* Conrad)

pliocenica (*Cancellaria*) Sacco, 1894:24; n.n. for "*C. spinifera* Grateloup" D'Ancona, 1872:92, pl. 11, fig. 11; see Appendix, Note 2. Pliocene, Italy.

pliocenica (*Zeadmete*) Finlay, 1930a:77. Pleistocene, New Zealand.

plioligustica (*Cancellaria*) Sacco, 1894:63, pl. 3, fig. 68; as var. of *C. intermedia* Bellardi; see Appendix, Note 2. Pliocene, Italy.

pliopostica (*Cancellaria*) Sacco, 1894:19; n.n. for "*C. trochlearis* Faujas" Cocconi, 1873:170, pl. 4, figs. 9-11; see Appendix, Note 2. Pliocene, Italy.

plummeri (*Cancellaria*) Olsson, 1922:85, pl. 6, figs. 2-3. Miocene, Panama.

pluricarinata (*Brocchinia*) Sacco, 1894:70, pl. 3, fig. 92; as var. of *B. parvula* (Beyrich). Miocene, Italy.

pluricostata (*Trigonostoma*) Kautsky, 1925:140, pl. 10, fig. 6; as var. of *T. spinifera* (Grateloup). Miocene, Germany.

pluricostieillata (*Cancellaria*) Sacco, 1894:37, pl. 2, fig. 55; as var. of *C. cancellata* (L.); see Appendix, Note 2. Pliocene, Italy.

pluricostulata (*Cancellaria*) Sacco, 1894:36, pl. 2, fig. 52; as var. of *C. uniangulata* Deshayes; see Appendix, Note 2. Pliocene, Italy.

plurimixta (*Cancellaria*) de Gregorio, 1882:218. Tertiary, Italy.

poecilma (*Paladmete*) Harbison, 1945:87, pl. 3, figs. 17-18. Cretaceous, Mississippi, U.S.A.

poetzleinsdorfensis (*Cancellaria*) Sieber, 1936:91, pl. 3, figs. 5a-b; as *pötzleinsdorfensis*; as var. of *C. exwestiana* Sacco. Miocene, Austria.

polonica (*Cancellaria*) Pusch, 1837:128, pl. 11, figs. 17a-b; as var. of *C. acutangula* Faujas de Saint Fond. Tertiary, Poland.

polygona (*Cancellaria*) Bellardi, 1840:344. *Nomen nudum.*

ponderi (*Tritonoharpa*) Beu & Maxwell, 1987:42, pl. 18, figs. a-j, l. Recent, Australia.

ponseuspidis (*Turehua*) Beu & Maxwell, 1987:20, Pl. 2, figs. k-l, n-r ; text-fig. 2G. Eocene, New Zealand.

porrecta (*Cancellaria*) 'Edwards MS' – Newton, 1891:172. *Nomen nudum.*

porrectum (*Coptostoma*) Wrigley, 1935:358, pl. 32, fig. 2; as form of *Coptostoma quadrata* (Sowerby). Eocene, England.

portoricana (*Cancellaria*) Maury, 1920:69, pl. 7, fig. 10; as var. of *C. laevescens* Guppy. Miocene, Puerto Rico.

postera (*Cancellaria*) Beyrich, 1856:557, pl. 17, figs. 3a-b, 4a-c, 5a-b; as var. of *C. evulsa* (Solander). Oligocene, Europe.

posteror (*Cancellaria*) 'Beyrich' – Kuster-Wendenburg, 1973:126. Error for *C. postera* Beyrich.

postypica (*Cancellaria*) Sacco, 1894:58; n.n. for "*C. suessi* Hoernes" Hoernes & Auinger, 1890:pl. 25 [*sic*; error for pl. 35], fig. 9; see Appendix, Note 2. Miocene, Austria.

posunculensis (*Cancellaria*) Anderson & Martin, 1914:86, pl. 8, figs. 7a-c. Miocene, California, U.S.A.

potomacensis (*Cancellaria*) Clark & Martin, 1901:129, pl. 21, figs. 3, 3a. Eocene, Maryland, U.S.A.

pötzleinsdorfensis (*Cancellaria*) Sieber – see *poetzleinsdorfensis.*

pouwi (*Trigonostoma*) Janssen, 1984:24, pl. 4, figs. 5-9; pl. 6, fig. 7. Miocene, Netherlands.

praecedens (*Cancellaria*) Beyrich, 1856:571, pl. 27, figs. 2a-b; as var. of *C. cancellata* (L.). Tertiary, Germany.

praecursoria (*Admete*) Suter, 1915:3. *Nomen nudum.*

praeevulsa (*Cancellaria*) Cossmann, 1898:155; n.n. for *C. similis* Kaunhowen, 1898, *non* Sowerby, 1833. Cretaceous, Belgium.

praeevulsa (*Bonellitia*) Cossmann, 1899a:33; unnecessary n.n. for *C. similis* Kaunhowen, 1898, *non* Sowerby, 1833. (= *Cancellaria praeevulsa* Cossmann, 1898)

praeindentata (*Cancellaria*) Maury, 1925b:188, pl. 9, fig. 14. Miocene, Brazil.

praetextum (*Triton*) Bellardi, 1873:227, pl. 14, fig. 13. Miocene, Italy. [?= *Tritonoharpa*]

praetiosa (*Cancellaria*) Oppenheim, 1922:80, pl. 5, figs. 10, 10a-b; *ex* Rželiak, *in litt.* Tertiary, Czechoslovakia.

priama (*Cancellaria*) G. D. Harris, 1895a:49, pl. 1, fig. 2. Eocene, Alabama, U.S.A.

prior (*Perplicaria*) Maury, 1910:17, pl. 4, fig. 8. Miocene, Florida, U.S.A.

pristina (*Mitra*) Yokoyama, 1923:8, pl. 1, figs. 8-12. Pliocene, Japan. [Cancellariidae]

pristina (*Paladmete*) Stephenson, 1954:39, pl. 8, figs. 24-26. Cretaceous, New Jersey, U.S.A.

producta (*Admete*) Sars, 1878:217, pl. 13, fig. 2; as var. of *A. viridula* (Fabricius). Recent, Arctic Ocean.

producta (*Cancellaria*) 'Edwards MS' – Jones, 1878:236. *Nomen nudum.*

producta (*Cancellaria*) G. B. Sowerby III, 1903:220, pl. 4, fig. 5. Recent, South Africa.

producta (*Caveola*) Stephenson, 1941:364, pl. 70, figs. 11-12. Cretaceous, Texas, U.S.A.

profunda (*Babylonella*) Tabanelli, 1985:21, figs. 1-5; as subsp. of *B. nassiformis* (Seguenza). Pliocene, Italy.

profundicola (*Neadmete*) Okutani, 1964:419, pl. 3, fig. 12; pl. 7, fig. 5. Recent, Japan.

profundior (*Oamaruia*) Cotton & Godfrey, 1932:55; as subsp. of *O. pergradata* (Verco). Recent, Australia.

promensis (*Merica*) Vredenberg, 1921:140, pl. 15, figs. 12a-b. Tertiary, Burma.

propegemmata (*Cancellaria*) de Gregorio, 1890:46, pl. 3, figs. 14-15. Eocene, Alabama, U.S.A.

propevenusta (*Cancellaria*) Mansfield, 1929:pl. 16, fig. 2; 1930:47, pl. 17, fig. 2. Miocene/Pliocene, Florida, U.S.A.

prophylactica (*Cancellaria*) Icke & Martin, 1907:230, pl. 14, figs. 11, 11a. Tertiary, Indonesia.

propinqua (*Cancellaria*) Kaunhowen, 1898:105, pl. 13, figs. 4-5. Cretaceous, Belgium.

protrigonostoma (*Cancellaria*) Sacco, 1894:4, pl. 1, figs. 3a-b; see Appendix, Note 2. Miocene, Italy.

proxima (*Cancellaria*) Risso, 1826:187, pl. 6, fig. 84. Tertiary, Europe. *Nomen dubium.*

prunicola (*Cancellaria*) G. Martin, 1904:164, pl. 43, figs. 6a-b. Miocene, Maryland, U.S.A.

pseudangasi (*Tritonoharpa*) Beu & Maxwell, 1987:44, pl. 16, figs. j, m-n; pl. 19, figs. a-l; pl. 22, figs. l, o. Recent, Indo-Pacific.

pseudaustralis (*Cancellaria*) 'Tate' – Dennant, 1889:44. *Nomen nudum.*

pseudocancellata (*Cancellaria*) Noetling, 1901:330, pl. 22, figs. 10a-c. Miocene, Burma.

pseudocoronata (*Cancellaria*) Sacco, 1894:35, pl. 2, fig. 51; as var. of *C. uniangulata* Deshayes; see Appendix, Note 2. Pliocene, Italy.

pseudoevulsa (*Cancellaria*) d'Orbigny, 1852:11; n.n. for "*C. evulsa* Sowerby [*sic*]" Nyst, 1845:pl. 39, fig. 13; as *pseudo-evulsa.* Tertiary, Europe.

pseudonassoides (*Cancellaria*) Sacco, 1894:38, pl. 2, fig. 60; as var. of *C. cancellata* (L.); see Appendix, Note 2. Pliocene, Italy.

pseudotribulus (*Cancellaria*) Sacco, 1894:18, pl. 1, fig. 49; as var. of *C. dertoscalata* Sacco; see Appendix, Note 2. Miocene, Italy.

pseudotypica (*Cancellaria*) Sacco, 1894:27, pl. 2, fig. 20; as var. of *C. piscatoria* (Gmelin); see Appendix, Note 2. Pliocene, Italy.

pseudovilia (*Cancellaria*) Sacco, 1894:20, pl. 1, figs. 55a-b, 55bis; as var. of *C. trochlearis* Faujas de Saint Fond; see Appendix, Note 2. Miocene, Italy.

pseudumbilicare (*Trigonostoma*) Peyrot, 1928:240, pl. 14, figs. 27-28, 32. Tertiary, Europe.

psinifera (*Trigonostoma*) 'Grat' – Jousseaume, 1888:23. Error for *T. spinifera* (Grateloup).

ptychotropis (*Cancellaria*) Tate, 1889:156, pl. 9, fig. 5. Eocene, Australia.

pukeuriensis (*Ptychatractus*) Suter, 1917:26, pl. 12, fig. 24. Miocene, New Zealand. [*Inglisella*]

pukeuriensis (*Merica*) Finlay, 1930a:79, pl. 3, fig. 33. Miocene, New Zealand.

pulcherrima (*Cancellaria*) H. C. Lea, 1841:99, pl. 1, fig. 15. Eocene, Alabama, U.S.A.

pulcherrima (*Cancellaria*) Almera & Bofill, 1892:12; Almera, 1894:58. *Nomen nudum.*

pulcherrima (*Cancellaria*) Almera & Bofill, 1898:17, pl. 1, fig. 4. Pliocene, Spain. (= *C. bofilli* Cossmann, 1899)

pulchra (*Cancellaria*) G. B. Sowerby I, 1832a:50; 1833:fig. 37. Recent, Panamic-Pacific.

pulchra (*Cancellaria*) 'Briart & Cornet' – Dewalque, 1868:388. *Nomen nudum.*

punctulata (*Cancellaria*) 'Hinds' – Paetel, 1888:330. Error for *C. funiculata* Hinds.

punjabense (*Coptostoma*) Eames, 1952:118, pl. 5, figs. 106, 107a-b. Eocene, Pakistan.

pupa (*Cancellaria*) 'Edwards MS' – Newton, 1891:172. *Nomen nudum.*

pupa (*Coptostomella*) Finlay & Marwick, 1937:83, pl. 11, fig. 4. Paleocene, New Zealand.

purpuriformis (*Cancellaria*) Kiener, 1841:37, pl. 7, fig. 4; *ex* Valenciennes. Recent, Australia.

purnensis (*Cancellaria*) K. Martin, 1914:127, pl. 2, fig. 56. Tertiary, Indonesia.

puschi (*Cancellaria*) Semper, 1861:257; n.n. for "*C. citharella* (Brong.)" Pusch, 1837:pl. 11, fig. 16. Tertiary, Poland.

puschi (*Cancellaria*) Hoernes & Auinger, 1890:276; n.n. for "*C. michelinii* Bell." Hörnes, 1854:326, pl. 35, figs. 14-15. Miocene, Austria.

pusilla (*Cancellaria*) G. B. Sowerby I, 1832b:fig. 34. Recent, Indo-Pacific. (?= *C. contabulata* Sowerby)

pusilla (*Fasciolaria*) Philippi, 1843:59, pl. 4, fig. 11. Oligocene, Germany. [*Babylonella*]

pusilla (*Cancellaria*) H. Adams, 1869:274, pl. 19, fig. 12. Recent, Canary Islands. (?= *Brocchinia clenchi* Petit, 1986)

pycta (*Cancellaria*) Olsson, 1964:122, pl. 21, figs. 3, 3a. Miocene, Ecuador.

pygmaea (*Cancellaria*) C. B. Adams, 1852a:360; 1852b:136. Recent, Panamic-Pacific.

pygmaea (*Paladmete*) Sohl, 1964a:273, pl. 45, figs. 36-40; as subsp. of *P. gardnerae* Wade. Cretaceous, Mississippi, U.S.A.

pyramidalis (*Brocchinia*) Sacco, 1894:70, pl. 3, fig. 89; as var. of *B. mitraeformis* (Brocchi). Pliocene, Italy.

pyramidata (*Cancellaria*) Sacco, 1894:25, pl. 2, fig. 14; as var. of *C. exwestiana* Sacco; see Appendix, Note 2. Miocene, Italy.

pyramidatospira (*Cancellaria*) Sacco, 1894:25, pl. 2, figs. 18a-b; as var. of *C. mutinensis* Foresti; see Appendix, Note 2. Tertiary, Italy.

pyramidatula (*Brocchinia*) Sacco, 1894:70; n.n. for "*C. mitraeformis* (Br.)" Nyst, 1881 [*sic*; error for 1878]:pl. 38 [*sic*; error for pl. 28], fig. 9. Tertiary, Europe.

pyramidum (*Uxia*) Cuvillier, 1933:60, pl. 8, figs. 1-4, 26, 32. Eocene, Egypt.

pyrastriformis (*Muricites*) Schlotheim, 1820:142. Oligocene, Germany. [?= *Admetula evulsa* (Solander, 1766)]

pyrenaica (*Sveltia*) Peyrot, 1928:223, pl. 14, figs. 36-37. Miocene, France.

pyrgota (*Cancellaria*) Edwards in Lowry, 1866:pl. 3. Upper Eocene, England.

pyrozonias (*Buccinum*) Gmelin, 1791:3488. Recent, locality unknown. [?= *Cancellaria cancellata* (Linné, 1767)]

pyruliformis (*Turbinella*) Nyst, 1845:486, pl. 12, figs. 24a-b. Oligocene, Europe. [*Turehua*]

pyruloides (*Egerea*) Noszky, 1936:73; as var. of *E. collectiva* Gábor. Oligocene, Hungary.

pyrum (*Cancellaria*) Adams & Reeve, 1950:42, pl. 10, fig. 16. Recent, Panamic-Pacific.

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quadrata (*Buccinella*) Perry, 1811:pl. 27, fig. 3. Recent, locality unknown. *Nomen inquirendum.* [Cancellariidae]

quadrata (*Cancellaria*) J. Sowerby, 1822:83, pl. 360. Eocene, England.

quadrata (*Cancellaria*) Moody, 1916:56, pl. 1, fig. 6. Pliocene, California, U.S.A. (= *C. angelana* Hanna, 1924)

quadrulata (*Cancellaria*) Almera & Bofill, 1884:40, pl. C, figs. 15-16; as var. of *C. calcarata* (Brocchi). Tertiary, Spain.

quantula (*Cancellaria*) Deshayes, 1864:106, pl. 72, figs. 29-30. Middle Eocene, France.

quasilla (*Cancellaria*) Petit, 1987:154, fig. 1; n.n. for *C. cretacea* E. A. Smith, 1899, *non* Nyst, 1881. Recent, India.

quatuorcostata (*Admete*) Sacco, 1894:73, pl. 3, fig. 98; as var. of *A. nassiformis* (Seguenza). Tertiary, Europe.

quercollis (*Volutilithes*) G. D. Harris, 1896:85, pl. 8, fig. 4. Paleocene, Alabama, U.S.A. [Cancellariidae]

R

rakhiense (*Coptostoma*) Eames, 1952:118, pl. 4, fig. 100. Eocene, Pakistan.

rameum (*Coptostoma*) Palmer, 1944:323, pl. 25, fig. 3. Eocene, Texas, U.S.A.

ramonensis (*Cancellaria*) B. L. Clark, 1918:186, pl. 23, fig. 7. Oligocene, California, U.S.A.

ranelliformis (*Cancellaria*) Chenu, 1859:274, fig. 1810. ?Fossil, locality unknown. (?= *C. suturalis* Sowerby, 1822)

rapa (*Cancellaria*) Nomland, 1917:240, pl. 11, figs. 1, 1a. Pliocene, California, U.S.A.

rapella (*Cancellaria*) C. W. Johnson, 1904:143, text-fig. Pliocene, North Carolina, U.S.A.

rara (*Cancellaria*) Aoki, 1954:38, pl. 2, fig. 17. Miocene, Japan.

raricosta (*Cancellaria*) Sacco, 1894:31, pl. 2, fig. 39; as var. of *C. doderleini* Mayer; see Appendix, Note 2. Miocene, Italy.

raulini (*Cancellaria*) Mayer, 1858:81, pl. 3, fig. 7. Tertiary, France.

raulini (*Cancellaria*) 'Grateloup MS' – Peyrot, 1928:220. *Nomen nudum.*

ravni (*Narona*) Glibert, 1960b:73; n.n. for *Cancellaria angulifera* von Koenen, 1885, *non* Deshayes, 1864. Paleocene, Denmark.

recessa (*Microsveltia*) Iredale, 1925:265, pl. 43, fig. 16. Recent, Australia.

reedii (*Admete*) Bell, 1870a:213. Tertiary, England.

reevana (*Cancellaria*) 'Crosse' – Grant & Gale, 1931:613. Error for *C. reeveana* Crosse.

reeveana (*Cancellaria*) Crosse, 1861:237; unnecessary n.n. for *C. elegans* Sowerby, 1822.

regina (*Admete*) Dall, 1911:20. Recent, Bering Sea.

regularia (*Admetula*) Dockery in MacNeil & Dockery, 1984:164, pl. 58, fig. 16. Oligocene, Mississippi, U.S.A.

renovata (*Sydaphera*) Iredale, 1929a:341, pl. 38, fig. 3. Recent, Australia. (?= *Cancellaria undulata* Sowerby, 1849)

reticulata (*Voluta*) Linné, 1767:1190. Recent, Caribbean. [*Cancellaria*]

reticulata (*Cancellaria*) Binkhorst, 1861:66, pl. Va2, figs. 8a-b. Cretaceous, Belgium. (= *C. binckhorsti* Nyst, 1881)

reticulata (*Cancellaria*) 'Edwards MS' – Newton, 1891:172. *Nomen nudum.*

reticulatoides (*Cancellaria*) G. Martin, 1904:164, pl. 43, fig. 7. Miocene, Maryland, U.S.A.

revolutum (*Cymatium*) Finlay, 1924b:456, pl. 51, figs. 2a-b. Eocene, New Zealand. [*Tatara*]

rewaensis (*Hindsia*) Ladd, 1982:47, pl. 11, figs. 10-11. Pliocene, Fiji. [?= *Neadmete nausorensis* Ladd, 1982]

reyesi (*Cancellaria*) Covacevich & Frassinetti, 1986:50, pl. 2, figs. 6a-c, 7a-c, 8a-c, text-fig. 11. Miocene, Chile.

rhabdota (*Cancellaria*) Bayan, 1873:108; n.n. for *C. canaliculata* Deshayes, 1864, *non* Hörnes, 1854. Middle Eocene, France.

rhombea (*Cancellaria*) von Koenen, 1889:114, pl. 8, figs. 1a-d, 2a-d. Oligocene, Germany.

rhomboides (*Admete*) Meek, 1873:501. Cretaceous, Utah, U.S.A.

rhyssa (*Admete*) Dall, 1919:306. Recent, western Mexico.

richardpetiti (*Cancellaria*) Petuch, 1987:17, pl. 2, figs. 5-6. Recent, Florida, U.S.A.

ricinus (*Cancellaria*) Pecchioli, 1864:505, pl. 5, figs. 6-7. Pliocene, Italy.

rigida (*Cancellaria*) G. B. Sowerby I, 1832a:53; 1833:fig. 41. Recent, Panamic-Pacific. (?= *C. goniostoma* Sowerby, 1832)

ringens (*Cancellaria*) Sandberger, 1859:pl. 15, figs. 8, 8a-c; 1862:256. Tertiary, Germany.

ringiculaeformis (*Cancellaria*) 'Almera & Bofill' – Almera, 1894:110. ? Error for *Marginella ringiculaeformis* Almera & Bofill.

ripleyana (*Trigonostoma*) Sohl, 1964a:268, pl. 44, figs. 25, 27. Cretaceous, Mississippi, U.S.A. [not a cancellariid]

rissoiaeformis (*Brocchinia*) Cossmann, 1899a:20, 193, pl. 2, fig. 15. Pliocene, France.

rivalis (*Bonellitia*) Wrigley, 1935:369, pl. 33, fig. 20; pl. 35, fig. 48. Middle Eocene, England.

robustum (*Tritonium*) Geinitz, 1874a:264, pl. 59, figs. 14a-c. Cretaceous, Germany. [Cancellariidae]

rosea (*Cancellaria*) 'Beck' – G. B. Sowerby II, 1849b:453. *Nomen nudum.*

rosewateri (*Cancellaria*) Petit, 1983:250, figs. 1A-D. Recent, Gulf of Mexico.

rothi (*Cancellaria*) Semper, 1861:255; n.n. for *C. nodulifera* Beyrich, 1856, *non* Sowerby, 1825. Miocene, Austria.

rotunda (*Cancellaria*) Dall, 1892:224; as var. of *C. conradiana* Dall. Pliocene, Florida, U.S.A.

rotunda (*Cancellaria*) Anderson & Martin, 1914:87, pl. 8, figs. 4a-b. Miocene, Oregon, U.S.A. (= *C. siletzensis* Anderson, 1924)

rotundata (*Buccinella*) Perry, 1811:pl. 27, fig. 2. Recent, "South Seas". [?= *Cancellaria cancellata* (Linné, 1767)]

rotundata (*Cancellaria*) von Koenen, 1889:103, pl. 12, figs. 15a-b; as var. of *C. subangulosa* Wood. Oligocene, Germany.

rotundata (*Merica*) Friedberg, 1914:242, pl. 15, fig. 4; as var. of *M. fenestrata* (Eichwald). Miocene, Poland.

rotundulatior (*Cancellaria*) Sacco, 1894:46, pl. 3, fig. 14; as var. of *C. evulsa* (Solander); see Appendix, Note 2. Miocene, Italy.

rotundulina (*Cancellaria*) Sacco, 1894:50, pl. 3, fig. 29; as var. of *C. dertocontorta* Sacco; see Appendix, Note 2. Miocene, Italy.

rougeyroni (*Cancellaria*) Souverbie in Souverbie & Montrouzier, 1870:427, pl. 14, fig. 1. Recent, New Caledonia. (?= *C. contabulata* Sowerby, 1832)

rowelli (*Cancellaria*) Dall in Guppy & Dall, 1896:307, pl. 29, fig. 1. Miocene, Dominican Republic.

roydonensis (*Cancellaria*) 'Edwards MS' – Newton, 1891:172. *Nomen nudum.*

rudis (*Cancellaria*) 'Edwards MS' – Newton, 1891:172. *Nomen nudum.*

rudis (*Cancellaria*) Whitfield, 1892:214, pl. 33, figs. 1-2. Eocene, New Jersey, U.S.A.

rudolphi (*Cancellaria*) Covacevich & Frassinetti, 1986:51, pl. 1, figs. 6a-c, text-fig. 8. Miocene, Chile.

ruellensis (*Bonellitia*) Wrigley, 1935:367; as var. of *B. evulsa* (Sol.); *ex* de Boury MS. Upper Eocene, France.

rugosa (*Cancellaria*) Lamarck, 1822b:115. Recent, Caribbean.

rugosa (*Cancellaria*) von Koenen, 1889:120, pl. 10, figs. 8a-c; pl. 11, figs. 7a-b, 8a-c, 10a-d, 11a-c. Oligocene, Germany.

rugosior (*Cancellaria*) Sacco, 1894:58; n.n. for "*C. excellens* Beyrich" von Koenen, 1889:pl. 11, fig. 4; as var. of *C. excellens* Beyrich; see Appendix, Note 2. Oligocene, Germany.

runchaena (*Cancellaria*) Gardner, 1937:375, pl. 45, figs. 8-9. Miocene, Florida, U.S.A.

S

sabinetownensis (*Trigonostoma*) Le Blanc, 1942:142, pl. 18, figs. 1-2. Eocene, Texas, U.S.A.

saccoi (*Cancellaria*) Hoernes & Auinger, 1890:274; n.n. for "*C. bellardi* Michelotti" Hörnes, 1854:314, pl. 34, figs. 17-18. Miocene, Austria.

sacellum (*Trigonostoma*) Petit, 1976:42, pl. 2, fig. 4. Pliocene, Panama.

sadko (*Admete*) Gorbunov, 1946:310, pl. 1, figs. 5a-b. Recent, North Atlantic.

sagamiensis (*Neadmete*) Kuroda & Habe, 1971:313 (Japanese), 204 (English), pl. 109, fig. 24. Recent, Japan.

salbriacensis (*Sveltia*) Peyrot, 1928:220, pl. 13, figs. 25-26. Miocene, France.

salomacensis (*Cancellaria*) Peyrot, 1928:206, pl. 12, figs. 4-5, 8; as var. of *C. barjonae* Pereira da Costa. Miocene, France.

salomacensis (*Merica*) Peyrot, 1928:210, pl. 13, figs. 13-14. Miocene, France.

sanctaemariae (*Cancellaria*) Carson, 1926:57, pl. 3, fig. 5; as *sanctae-mariae*. Pliocene, California, U.S.A.

sandbergeri (*Cancellaria*) Tournouër, 1879:470, pl. 10, figs. 2a-b. Oligocene, France.

sandbergeri (*Rissoa*) Müller, 1851:77, pl. 6, fig. 22. Cretaceous, Germany. [?= *Voluta nitidula* Müller; ? Cancellariidae]

sanjoseensis (*Cancellaria*) 'Anderson & Martin' – Loel & Corey, 1932:172. Emendation of, or error for, *C. sanjosei* Anderson & Martin.

sanjosei (*Cancellaria*) Anderson & Martin, 1914:87, pl. 6, figs. 2a-b. Miocene, California, U.S.A.

santa (*Gerdiella*) Olsson & Bayer, 1972:877, figs. 4-6. Recent, Caribbean.

santiagensis (*Cancellaria*) Marks, 1949:462, pl. 78, fig. 6. Miocene, Ecuador.

sathra (*Cancellaria*) Woodring, 1973:481; n.n. for *C. lipara* Woodring, 1970, *non* 1951; as subsp. of *C. epistomifera* Guppy. Pliocene, Panama.

scaberrima (*Bonellitia*) Chavan, 1947:140, pl. 2, figs. 14-15, text-fig. 1. Tertiary, Jordan.

scabra (*Cancellaria*) Deshayes, 1830:190. Tertiary, Europe.

scabriculus (*Murex*) Linné, 1758:751. [= *Voluta cancellata* Linné, 1767, *q.v.*]

scabriuscula (*Cancellaria*) Moroni, 1958:77, pl. 1, figs. 2, 2a-b; as subsp. of *C. doderleini* Moroni. Miocene, Italy.

scabriusculus (*Murex*) 'Linné' – Linné, 1767:1191. Error for *M. scabriculus* L.

scabroides (*Cancellaria*) Sacco, 1894:10, pl. 1, fig. 18; as var. of *C. ampullacea* (Br.); see Appendix, Note 2. Pliocene, Italy.

scala (*Murex*) Gmelin, 1791:3551. Recent, western Africa. [*Scalptia*]

scalaratula (*Cancellaria*) Sacco, 1894:33, pl. 2, fig. 43; as var. of *C. calcarata* (Br.); see Appendix, Note 2. Pliocene, Italy.

scalare (*Buccinum*) Gmelin, 1791:3495. Recent, Indo-Pacific. [*Trigonostoma*]

scalariformis (*Cancellaria*) Lamarck, 1822b:113. Recent, Indo-Pacific.

scalariformis (*Mitra*) Borson, 1825:306, pl. 19, fig. 27. Miocene, Italy. [?= *Cancellaria acutangula* Faujas de Saint Fond, 1817]

scalarina (*Cancellaria*) Lamarck, 1822b:113. Recent, Indo-Pacific.

scalarina (*Cancellaria*) G. B. Sowerby II, 1849b:452, pl. 96, figs. 87-88. Recent, Indo-Pacific. (?= *C. thomasiana* Crosse, 1861)

scalarina (*Cancellaria*) Conrad, 1863:567. *Nomen nudum.*

scalarina (*Cancellaria*) Conrad, 1866:68, pl. 4, fig. 17. Miocene, Maryland, U.S.A. (?= *C. lunata* Conrad, 1830)

scalaris (*Cancellaria*) Michelotti, 1838:396. *Nomen nudum.*

scalaris (*Cancellaria*) Bellardi, 1840:344. *Nomen nudum.*

scalaroides (*Cancellaria*) Wood, 1857:316, pl. 31, fig. 9. Tertiary, England.

scalata (*Cancellaria*) G. B. Sowerby I, 1832b:fig. 27. Recent, Mauritius.

scalatella (*Cancellaria*) Guppy, 1873:78, pl. 2, fig. 4. Pliocene, Jamaica.

scheibei (*Cancellaria*) F. M. Anderson, 1929:115, pl. 10, figs. 1-4. Miocene, Colombia.

schroeckingeri (*Cancellaria*) Hoernes & Auinger, 1890:275, pl. 33, figs. 12a-b. Miocene, Austria.

schucherti (*Cancellaria*) Olsson, 1932:162, pl. 17, figs. 3-4. Miocene, Peru.

schwartzi (*Neadmete*) Mount, 1970:3, fig. 1. Pliocene, California, U.S.A.

schythei (*Cancellaria*) Philippi, 1855:208; 1856a:164. Recent, Strait of Magellan.

scobina (*Cancellaria*) Hedley & Petterd, 1906:222, pl. 38, fig. 12. Recent, Australia.

scopalveus (*Aphera*) Finlay, 1926a:246, pl. 56, figs. 14-15. Miocene, New Zealand.

scrobiculata (*Cancellaria*) M. Hörnes, 1854:318, pl. 35, figs. 1a-b. Miocene, Austria.

sculptura (*Cancellaria*) I. Lea, 1833:140, pl. 5, fig. 137. Eocene, Alabama, U.S.A. (?= *C. alveata* Conrad, 1833)

sculpturata (*Cancellaria*) 'Lea' – Conrad, 1865a:31. Error for *C. sculptura* Lea.

secutorum (*Coptostoma*) Palmer, 1947:413, pl. 63, figs. 23-25; as var. of *C. ulmulum* (Harris). Eocene, Louisiana, U.S.A.

seftoni (*Admete*) Berry, 1956:155, figs. 2, 9. Recent, California, U.S.A.

selectum (*Trigonostoma*) Palmer, 1947:411, pl. 63, figs. 20-22. Eocene, Louisiana, U.S.A.

semiacostata (*Cancellaria*) Sacco, 1894:46, pl. 3, fig. 15; as var. of *C. evulsa* (Solander); see Appendix, Note 2. Miocene, Italy.

semiclathrata (*Cancellaria*) Morlet, 1885a:50, pl. 3, figs. 4, 4a. Middle Eocene, France.

semicostata (*Cancellaria*) Tate, 1889:157, pl. 10, fig. 3. Miocene, Australia.

semicostata (*Bonellitia*) 'Sacco' – Harmer, 1918:pl. 40, fig. 14; *et al.* Error for *B. semiacostata* (Sacco).

semidisjuncta (*Cancellaria*) G. B. Sowerby II, 1849a:137; 1849b:458, pl. 95, figs. 62-63. Recent, South Africa.

semilunaris (*Murex*) Gmelin, 1791:3549. Recent, Senegal. [?= *C. piscatoria* (Gmelin, 1791)]

semipellucida (*Cancellaria*) Adams & Reeve, 1850:42, pl. 10, figs. 3, 3a. Recent, Japan.

semiplicata (*Voluta*) Nyst, 1845:593, pl. 15, figs. 10a-b. Oligocene, Europe. [?= *Turehua subgranulata* (Schlotheim, 1820)]

semota (*Cancellaria*) Jung, 1969:541, pl. 58, figs. 4-5. Miocene, Trinidad.

semperi (*Cancellaria*) Speyer, 1867:181, pl. 16, figs. 9, 9a-c. Oligocene, Germany.

semperiana (*Cancellaria*) Crosse, 1863:65, pl. 2, fig. 7. Recent, New Caledonia.

senarium (*Trigonostoma*) Petit & Hoerle, 1976:44, pl. 2, fig. 5. Pliocene, Florida, U.S.A.

sendoi (*Cancellaria*) Hatai, 1941:110, pl. 3, figs. 5-6; as *s-endoi*. Miocene, Japan.

separata (*Cancellaria*) Deshayes, 1864:97, pl. 72, figs. 20-22. Middle Eocene, France.

septemcostata (*Cancellaria*) Odhner, 1917:55, pl. 2, fig. 57. Recent, Australia. (?= *C. bicolor* Hinds, 1843)

septemlirata (*Cancellaria*) Gabb, 1860c:94, pl. 2, fig. 10. Cretaceous, New Jersey, U.S.A. [not a cancellariid]

septentrionalis (*Inglisella*) Finlay, 1930b:240, pl. 43, fig. 14. Recent, New Zealand.

sericea (*Cancellaria*) Dall, 1892:224, pl. 14, figs. 7, 7a. Pliocene, Florida, U.S.A.

serramata (*Cancellaria*) Olsson, 1967:44; n.n. for *C. serrata* Olsson, 1964, *non* Bronn, 1831. Neogene, Ecuador.

serrata (*Anapepta*) Laws, 1935:39, pl. 6, fig. 21. Miocene, New Zealand.

serrata (*Cancellaria*) Bronn, 1831:44. Tertiary, Italy.

serrata (*Cancellaria*) Reeve, 1856:pl. 14, fig. 63. Recent, Indo-Pacific. (= *C. crossei* Semper, 1861)

serrata (*Cancellaria*) Olsson, 1964:122, pl. 28, fig. 8. Neogene, Ecuador. (= *C. serramata* Olsson, 1967)

sheppardi (*Admete*) Bell, 1919:57, fig. 1; as subsp. of *A. viridula* (Fabricius). Tertiary, England.

shilohensis (*Cancellaria*) Pilsbry & Harbison, 1933:108, pl. 3, fig. 8. Miocene, New Jersey, U.S.A.

shirleyae (*Cancellaria*) Olsson, 1967:23, pl. 3, fig. 5. Pliocene, Florida, U.S.A.

siletzensis (*Cancellaria*) Anderson in G. D. Hanna, 1924:159; n.n. for *C. rotunda* Anderson & Martin, 1914, *non* Dall, 1892. Miocene, Oregon, U.S.A.

silvaerupis (*Cancellaria*) G. D. Harris, 1897:476, pl. 20, fig. 11; as *silvaerupis* in text but *sylvaerupis*, considered to be correct, on plate caption. Eocene, Alabama, U.S.A.

silvestris (*Cancellaria*) Wrigley, 1935:379, pl. 34, fig. 38. Middle Eocene, England.

simiana (*Cancellaria*) G. D. Hanna, 1924:160; n.n. for *C. crassa* Waring, 1917, *non* Nomland, 1917. Cretaceous, California, U.S.A.

similaris (*Cancellaria*) 'Sowerby' – Reeve, 1856:pl. 3, figs. 10a-b. Error for *C. similis* Sowerby.

similis (*Cancellaria*) G. B. Sowerby I, 1833:fig. 38. Recent, western Africa.

similis (*Cancellaria*) Aradas, 1846:174, pl. 1, figs. 11a-b. Tertiary, Italy.

similis (*Cancellaria*) Giebel, 1847:823; 1853:384, pl. 6, fig. 2. Tertiary, Germany.

similis (*Cancellaria*) Kaunhowen, 1898:103, pl. 7, fig. 8. Cretaceous, Belgium. (= *C. praeevulsa* Cossmann, 1898)

simplex (*Cancellaria*) F. M. Anderson, 1905:200, pl. 15, figs. 51-52. Miocene, California, U.S.A.

simplex (*Pallidonia*) Laseron, 1955:272, figs. 13, 13a. Recent, Australia.

simplicicostata (*Cancellaria*) Sacco, 1894:44, pl. 3, fig. 8; as var. of *C. serrata* Bronn; see Appendix, Note 2. Miocene, Italy.

simplicior (*Cancellaria*) Sacco, 1894:55, pl. 3, fig. 43; as var. of *C. varicosa* (Brocchi); see Appendix, Note 2. Pliocene, Italy.

simulata (*Cancellaria*) von Koenen, 1889:107, pl. 17, figs. 9a-b. Oligocene, Germany.

sinensis (*Cancellaria*) Reeve, 1856:pl. 8, fig. 35. Recent, Japan.

sinuosa (*Cancellaria*) Cossmann, 1889:229, pl. 7, fig. 23. Lower Eocene, France.

siouxensis (*Cancellaria*) Erickson, 1974:217, pl. 20, figs. 1-5. Cretaceous, North Dakota, U.S.A.

siphonatus (*Triton*) Reeve, 1844:pl. 18, fig. 81. Recent, Panamic-Pacific. [*Tritonoharpa*]

sismondai (*Cancellaria*) D'Ancona, 1872:102, pl. 13, figs. 5a-b. Pliocene, Italy.

sismondiana (*Cancellaria*) 'Grat.' – Peyrot, 1928:225; *ex* Grateloup MS. *Nomen nudum.*

smithfieldensis (*Trigonostoma*) Oleksyshyn, 1960:101, figs. 1-2. Miocene, Virginia, U.S.A.

smithii (*Cancellaria*) Dall, 1888:70, fig. 292. Recent, Carolinas to Gulf of Mexico.

smithvillensis (*Cancellaria*) G. D. Harris, 1895a:65, pl. 6, fig. 2. Eocene, Texas, U.S.A.

smithwickensis (*Bonellitia*) Hickman, 1980:68, pl. 9, figs. 2-6. Oligocene, Oregon, U.S.A.

smocki (*Cancellaria*) Weller, 1907:793, pl. 98, figs. 2-3. Cretaceous, New Jersey, U.S.A.

sobrantensis (*Cancellaria*) B. L. Clark, 1918:187, pl. 23, fig. 6. Oligocene, California, U.S.A.

solat (*Solatia*) Jousseaume, 1887b:222, fig. 3; *ex* Adanson. Recent, western Africa. (?= *S. piscatoria* (Gmelin, 1791)).

solida (*Cancellaria*) G. B. Sowerby I, 1832a:50; 1832b:fig. 6. Recent, Panamic-Pacific.

soriensis (*Cancellaria*) Eames, 1952:116, pl. 5, figs. 104-105. Eocene, Pakistan.

sotoensis (*Cancellaria*) Aldrich, 1908:74, pl. 5, fig. 3. Eocene, Mississippi, U.S.A.

souverbiei (*Cancellaria*) Crosse, 1868:272, pl. 9, fig. 5. Recent, ? Indo-Pacific.

sowerbyi (*Cancellaria*) Bellardi, 1841:9; as *sowerby* [*sic*]; unnecessary n.n. for *C. mitraeformis* [*sic*] Sowerby, *non* Brocchi.

sowerbyi (*Cancellaria*) Crosse, 1861:242; unnecessary n.n. for *C. mitraeformis* [*sic*] Sowerby, *non* Brocchi.

spatiosa (*Cancellaria*) Nelson, 1870:191. Miocene, Peru.

speciosa (*Cancellaria*) Deshayes, 1864:100, pl. 73, figs. 1-3. Lower Eocene, France.

speciosa (*Caveola*) Sohl, 1964a:270, pl. 44, figs. 9-14; as subsp. of *C. acuta* (Wade). Cretaceous, Mississippi, U.S.A.

speciosum (*Trigonostoma*) Vredenburg, 1921:141, pl. 15, figs. 13a-c. Tertiary, Burma.

speciosum (*Triton*) Bellardi, 1873:226, pl. 14, fig. 12. Miocene, Italy. [*Tritonoharpa*]

spectabilis (*Cancellaria*) Deshayes, 1864:102, pl. 72, figs. 23-25. Middle Eocene, France.

specularis (*Cancellaria*) Watson, 1882a:325; 1886:274, pl. 11, fig. 11a-c. Recent, Kerguelen Islands.

spellenbergi (*Cancellaria*) Riedel, 1932:118, pl. 23, figs. 13, 13a, 14, 14a, text-fig. 32. Cretaceous, Cameroon.

spengleriana (*Cancellaria*) Deshayes, 1830:185. Recent, Japan.

spengleriana (*Cancellaria*) 'Kiener' – Sherborn, 1930:6055. Error for *C. spengleriana* Deshayes.

sphaericula (*Cancellaria*) Cossmann, 1889:230, pl. 7, fig. 30. Middle Eocene, France.

sphaeroidea (*Admete*) Luković, 1924:57, pl. 3, figs. 11, 11a. Eocene, Asia.

sphaeroidea (*Admete*) 'Dukooizen, 1925' – Zoological Record for 1925. Error for Luković, 1924.

sphenoidostoma (*Cancellaria*) Gardner, 1937:376, pl. 45, figs. 11-12. Miocene, Florida, U.S.A.

spherotopleura (*Cancellaria*) Gardner, 1937:370, pl. 44, figs. 14-15. Miocene, Florida, U.S.A.

spinifera (*Cancellaria*) Grateloup, 1832:342; 1847:pl. 25, fig. 15. Tertiary, France.

spinosa (*Admete*) Sangiorgi, 1926:104, pl. 7, fig. 22; as var. of *A. nassiformis* (Seguenza). Tertiary, Italy.

spinosa (*Cancellaria*) Grateloup, 1827:21. Tertiary, France.

spinosella (*Cancellaria*) Sacco, 1894:5; n.n. for "*C. umbilicaris* (Br.)" Nyst, 1878:pl. 28, fig. 8; as var. of *C. umbilicaris* (Brocchi); see Appendix, Note 2. Tertiary, Belgium.

spinosissima (*Cancellaria*) Sacco, 1894:33, pl. 2, fig. 44; as var. of *C. calcarata* (Brocchi); see Appendix, Note 2. Pliocene, Italy.

spinosula (*Cancellaria*) 'Br.' – Borson, 1820:213. Error for *C. spinulosa* (Brocchi).

spinulatior (*Cancellaria*) Sacco, 1894:57, pl. 3, fig. 51; as var. of *C. dertovaricosa* Sacco; see Appendix, Note 2. Miocene, Italy.

spinulosa (*Voluta*) Brocchi, 1814:309, pl. 3, fig. 15. Pliocene, Italy. [*Sveltia*]

spirata (*Cancellaria*) Lamarck, 1822b:115. Recent, Australia.

spirata (*Cancellaria*) 'Edwards MS' – Newton, 1891:172. *Nomen nudum.*

spiratior (*Cancellaria*) Sacco, 1894:30; n.n. for *C. barjonae* Pereira da Costa, 1867:pl. 25, fig. 11 (only); as var. of *C. barjonae* Pereira da Costa; see Appendix, Note 2. Miocene, Portugal.

spiratior (*Cancellaria*) Sacco, 1894:8, pl. 1, fig. 12; as var. of *C. cassidea* (Brocchi); see Appendix, Note 2. Pliocene, Italy.

spirifer (*Cancellaria*) 'von Koenen' – Nyst, 1881:8. Error for *C. spinifera* Grateloup.

spirulata (*Cancellaria*) 'Doderlein MS' – Davoli, 1982:36. *Nomen nudum.*

springvaleensis (*Cancellaria*) Mansfield, 1925:31, pl. 2, fig. 12. Miocene, Trinidad.

squarrosa (*Cancellaria*) Davoli, 1980:228, pl. 1, figs. 1a-c, 12a-c; *ex* Doderlein MS; as teratological form of *C. serrata* Bronn. Tertiary, Italy.

stantoni (*Cancellaria*) Dickerson, 1913:282, pl. 12, figs. 2a-b. Eocene, California, U.S.A.

staringi (*Cancellaria*) 'Bosquet' – Staring, 1860:372. *Nomen nudum.*

stemerdinki (*Babylonella*) Janse & Janssen, 1983:134, pl. 3, figs. 9a-b, text-figs. 6a-b. Miocene, Netherlands.

stenomphala (*Trigonaphera*) Habe, 1961b:432, pl. 24, fig. 12. Recent, Japan.

stibara (*Cancellaria*) Gardner, 1937:368, pl. 44, figs. 9-10. Miocene, Florida, U.S.A.

stimpsonii (*Cancellaria*) Calkins, 1878:250, pl. 8, figs. 4-5. Recent, Florida, U.S.A. (?= *Trigonostoma tenerum* (Philippi, 1848))

striatula (*Cancellaria*) 'Deshayes' – Deshayes, 1835:expl. to pl. 79; error for *C. striatulata* Deshayes; corrected on errata page 814.

striatulata (*Cancellaria*) Deshayes, 1835:503, pl. 79, figs. 29-30. Middle Eocene, France.

stricta (*Admete*) Hedley, 1907:295, pl. 54, fig. 10. Recent, Australia.

strictoturrita (*Cancellaria*) Sacco, 1894:51, pl. 3, fig. 31; as var. of *C. altavillae* Libassi; see Appendix, Note 2. Pliocene, Italy.

strombecki (*Cancellaria*) Speyer, 1864:267, pl. 40, figs. 2, 2a-b. Oligocene, Germany.

stromboides (*Cancellaria*) Grateloup, 1832:343. Tertiary, France.

strongi (*Cancellaria*) Shasky, 1961:19, pl. 4, fig. 4. Recent, western Mexico.

strozzii (*Cancellaria*) Pecchioli, 1864:503, pl. 5, figs. 3-5. Pliocene, Italy.

stuardoi (*Cancellaria*) McLean & Andrade, 1982:16, fig. 53. Recent, Chile.

subacuminata (*Cancellaria*) d'Orbigny, 1852:56; n.n. for *C. acuminata* Bellardi, 1841, *non* Sowerby, 1832. Tertiary, Italy.

subalta (*Cancellaria*) Conrad, 1869:100, pl. 9, fig. 22. Upper Cretaceous, New Jersey, U.S.A.

subangulata (*Cancellaria*) 'Scacchi' – Dall, 1889a:131. ? Error for *C. coronata* Scacchi.

subangulosa (*Cancellaria*) Wood, 1842:538. *Nomen nudum.*.

subangulosa (*Cancellaria*) Wood, 1848:66, pl. 7, figs. 20a-bb. Eocene, England.

subangulosa (*Cancellaria*) 'Weinkauff' – Paetel, 1888:331. Error for *C. subangulosa* Wood.

subanodosa (*Brocchinia*) Sacco, 1894:69, pl. 3, fig. 83; as var. of *B. mitraeformis* (Brocchi). Pliocene, Italy.

subantarctica (*Zeadmete*) Powell, 1933:236, pl. 20, fig. 7. Recent, Antarctic.

subareticulata (*Aphera*) Sacco, 1894:67, pl. 3, fig. 78; as var. of *A. bronni* (Bellardi). Miocene, Italy.

subaspinosa (*Cancellaria*) Peyrot, 1928:206, pl. 12, fig. 6; as var. of *C. barjonae* Pereira da Costa. Miocene, France.

subasuturata (*Brocchinia*) Sacco, 1894:69, pl. 3, fig. 87; as var. of *B. mitraeformis* (Brocchi). Pliocene, Italy.

subasuturata (*Cancellaria*) Sacco, 1894:57, pl. 3, fig. 52; as var. of *C. dertovaricosa* Sacco; see Appendix, Note 2. Miocene, Italy.

subauriculata (*Cancellaria*) Sacco, 1894:7, pl. 1, fig. 10; as var. of *C. taurocrassum* Sacco; see Appendix, Note 2. Miocene, Italy.

subbiplicata (*Cancellaria*) Sacco, 1894:40, pl. 2, fig. 65; as var. of *C. dertonensis* Bellardi; see Appendix, Note 2. Miocene, Italy.

subcanaliculata (*Cancellaria*) Grateloup, 1832:343; as *sub-canaliculata*; as var. of *C. umbilicaris* (Brocchi). *Nomen nudum.*

subcanaliculata (*Cancellaria*) Grateloup, 1847:pl. 25, fig. 14; as var. of *C. umbilicaris* (Brocchi). Tertiary, France.

subcancellata (*Cancellaria*) d'Orbigny, 1852:54; n.n. for "*C. cancellata* (L.)" Grateloup, 1847:pl. 25, figs. 7, 10. Tertiary, France.

subcarinata (*Cancellaria*) Bronn, 1831:44. Tertiary, Italy.

subcylindrica (*Cancellaria*) von Koenen, 1889:138, pl. 12, figs. 8a-c. Oligocene, Germany.

subevulsa (*Cancellaria*) d'Orbigny, 1850b:315. Eocene, Europe.

subevulsopsis (*Cancellaria*) de Gregorio, 1890:49, pl. 3, fig. 28; as var. of *C. tortiplica* Conrad. Eocene, Alabama, U.S.A.

subfusiformis (*Admete*) Meek, 1873:502. Cretaceous, Utah, U.S.A.

subgranulatus (*Muricites*) Schlotheim, 1820:140. Oligocene, Europe. [*Turehua*]

subhirta (*Cancellaria*) d'Orbigny, 1852:55; n.n. for "*C. hirta* (Br.)" Grateloup, 1847:pl. 25, fig. 25. Tertiary, France.

sublaevis (*Cancellaria*) Bellardi, 1840:344. *Nomen nudum.*

submitroides (*Admete*) Cossmann & Pissarro, 1905:40, pl. 16, figs. 17-18. Middle Eocene, France.

suboblitecostata (*Cancellaria*) Sacco, 1894:30, pl. 2, fig. 30; as var. of *C. hirta* (Brocchi); see Appendix, Note 2. Pliocene, Italy.

subobtusa (*Cancellaria*) Crosse, 1863:pl. 2, fig. 9; as var. of *C. cumingiana* Petit de la Saussaye. Recent, Panamic-Pacific.

subovula (*Uxia*) Pchelintsev, 1953:272, pl. 41, figs. 12a-f, text-fig. 44. Cretaceous, U.S.S.R.

subsinensis (*Cancellaria*) Löbbecke, 1881:12, pl. 2, fig. 3; as var. of *C. reeveana* Crosse. Recent, Indo-Pacific.

subspinulosa (*Cancellaria*) Wood, 1872:49, pl. 6, fig. 10; as var. of *C. spinulosa* (Brocchi). Tertiary, England.

subsuturalis (*Cancellaria*) d'Orbigny, 1852:10; n.n. for *C. suturalis* Grateloup, 1832, *non* Sowerby, 1822. Tertiary, France.

subtaurinensis (*Tritonidea*) Vergneau, 1965:79, figs. 7a-b. Oligocene, France. [*Loxotaphrus*]

subteres (*Mataxa*) Stephenson, 1941:366, pl. 70, figs. 4-5. Cretaceous, Texas, U.S.A.

subthomasiae (*Cancellaria*) Dall, 1890:44, pl. 11, fig. 3. Oligocene, Florida, U.S.A.

subtiarophora (*Cancellaria*) Gardner, 1937:366, pl. 44, figs. 3-4. Miocene, Florida, U.S.A.

subtilicancellata (*Cancellaria*) Maury, 1925b:190, pl. 9, fig. 5. Miocene, Brazil.

subumbilicata (*Cancellaria*) Grateloup, 1832:340; as *sub-umbilicata*; as var. of *C. varicosa* (Brocchi). *Nomen nudum.*

subumbilicata (*Cancellaria*) Grateloup, 1847:pl. 25, fig. 8; as var. of *C. varicosa* (Brocchi); see Appendix, Note 1. Tertiary, France. (= *C. subvaricosa* d'Orbigny, 1852)

suburbana (*Sveltella*) Wrigley, 1935:363, pl. 32, fig. 9. Lower Eocene, England.

subvaricosa (*Cancellaria*) d'Orbigny, 1852:54; n.n. for "*C. varicosa* (Br.)" Grateloup, 1847:pl. 25, fig. 8. Tertiary, France. (= *C. subumbilicata* Grateloup, 1847, *q.v.*)

succineiformis (*Cancellaria*) Boettger, 1906:51. Miocene, Romania.

suessi (*Cancellaria*) R. Hoernes, 1875:355, pl. 11, figs. 22a-b, 23a-b. Tertiary, Europe.

sulcata (*Cancellaria*) Bellardi, 1840:344. *Nomen nudum.*

sulcata (*Cancellaria*) Bellardi, 1841:29, pl. 3, figs. 1-2. Miocene, Italy.

supercretacea (*Cancellaria*) Favre, 1869:91, pl. 10, fig. 17. Cretaceous, Europe.

superstes (*Bonellitia*) Finlay, 1930b:240, pl. 43, fig. 16. Recent, New Zealand.

suppar (*Cancellaria*) Ryckholt, 1862:pl. 36, fig. 25. Cretaceous, Belgium.

supracosticillata (*Cancellaria*) Sacco, 1894:70, pl. 3, fig. 93; as var. of *C. parvula* Beyrich; see Appendix, Note 2. Miocene, Italy.

supracostulata (*Cancellaria*) Sacco, 1894:11, pl. 1, fig. 25bis; as var. of *C. fenestrata* Eichwald; see Appendix, Note 2. Miocene, Italy.

suprafasciata (*Cancellaria*) Sacco, 1894:38, pl. 2, fig. 57; as var. of *C. cancellata* (L.); see Appendix, Note 2. Pliocene, Italy.

suprafasciolata (*Cancellaria*) Sacco, 1894:18; as var. of *C. dertoscalata* Sacco; see Appendix, Note 2. Miocene, Italy.

surpacifica (*Cancellaria*) Olsson, 1967:44; n.n. for *C. pacifica* Pilsbry & Olsson, 1941, *non* Anderson, 1905. Pliocene, Ecuador.

sursalta (*Cancellaria*) Marks, 1949:461, pl. 78, fig. 4. Miocene, Ecuador.

suteri (*Admete*) Marshall & Murdoch, 1920:132, pl. 6, figs. 5, 5a. Miocene, New Zealand.

sutherlandi (*Neadmete*) Kanakoff & McLean, 1966:4, figs. 1-2. Pliocene, California, U.S.A.

suturalis (*Cancellaria*) G. B. Sowerby I, 1822:fig. 4; in text as *C. suturalis*; on plate as *C. biplex*. Eocene, France.

suturalis (*Cancellaria*) Grateloup, 1832:343. Tertiary, France. (= *C. subsuturalis* d'Orbigny, 1852)

sylvaerupis (*Cancellaria*) G. D. Harris, 1897:476, pl. 20, fig. 11; as *silvaerupis* in text and *sylvaerupis* on plate caption; we consider *sylvaerupis* to be the intended spelling. Eocene, Alabama, U.S.A.

synchrona (*Cancellaria*) Ryckholt, 1862:pl. 33, fig. 2. Cretaceous, Belgium.

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tabatai (*Cancellaria*) Yokoyama, 1926a:265, pl. 32, fig. 12. Pliocene, Japan.

tabulata (*Admete*) G. B. Sowerby II, 1875:128, pl. 24, fig. 3. Recent, Arctic Ocean.

tabulata (*Admete*) 'Friele' – Bell, 1919:58. ? Error for *A. contabulata* Friele.

tabulata (*Cancellaria*) Gardner & Aldrich, 1919:23, pl. 1, fig. 9. Pliocene, Virginia, U.S.A.

taeniata (*Cancellaria*) G. B. Sowerby II, 1849a:137; 1849b:445, pl. 95, figs. 75-76. Recent, unknown locality. (?= *C. coronata* Scacchi, 1835)

taiwanensis (*Cancellaria*) Nomura, 1935:132, pl. 6, figs. 61a-b [not 60a-b]. Pliocene, Taiwan.

tampaensis (*Trigonostoma*) Petit, 1967:218; n.n. for *C. depressa* Dall, 1915, *non* Tuomey & Holmes, 1856. Oligocene, Florida, U.S.A.

tapeina (*Cancellaria*) Woodring, 1970:335, pl. 51, figs. 8-9. Pliocene, Panama.

tasmanica (*Cancellaria*) Tenison-Woods, 1876:150. Recent, Tasmania.

tatei (*Aneurystoma*) Cossmann, 1899a:24; n.n. for *C. gradata* Tate, 1889, *non* Hörnes, 1854. Miocene, Australia.

tauracuta (*Cancellaria*) Sacco, 1894:12, pl. 1, fig. 26; as var. of *C. fenestrata* Eichwald; see Appendix, Note 2. Miocene, Italy.

taurangulifera (*Cancellaria*) Sacco, 1894:24, pl. 2, figs. 12a-b; see Appendix, Note 2. Miocene, Italy.

taurangolosa (*Cancellaria*) Sacco, 1894:pl. 3, fig. 64; plate caption error for *C. taurangulosa* Sacco.

taurangulosa (*Cancellaria*) Sacco, 1894:62, pl. 3, figs. 64, 64bis; as var. of *C. lyrata* (Brocchi); misspelled as *taurangolosa* on plate caption; see Appendix, Note 2. Miocene, Italy.

taurapertum (*Cancellaria*) Sacco, 1894:11; error for *C. taurocrassum*, corrected in errata on p. 73.

taurelegens (*Cancellaria*) Sacco, 1894:46, pl. 3, fig. 13; as var. of *C. evulsa* (Solander); misspelled as *tauroelegans* on plate caption; see Appendix, Note 2. Miocene, Italy.

taurinensis (*Pollia*) Bellardi, 1873:175, pl. 12, fig. 13. Miocene, Italy. [*Loxotaphrus*]

taurinia (*Cancellaria*) Bellardi, 1840:343, 344.[1]

taurinia (*Cancellaria*) Bellardi, 1841:11, pl. 1, fig. 16; as var. of *C. varricosa* (Brocchi).[1] Tertiary, Italy.

taurinia (*Cancellaria*) Bellardi, 1841:14; as var. of *C. lyrata* (Brocchi).[1] Tertiary, Italy.

taurinia (*Cancellaria*) Bellardi, 1841:17, pl. 2, figs. 15-16; as var. of *C. uniangulata* Deshayes.[1] Tertiary, Italy.

taurinia (*Cancellaria*) Bellardi, 1841:20, pl. 2, figs. 3-4; as var. of *C. nodulosa* Lamarck.[1] Tertiary, Italy.

taurinia (*Cancellaria*) Bellardi, 1841:24, pl. 3, figs. 15-16; as var. of *C. bonelli* Bellardi.[1] Tertiary, Italy.

taurinia (*Cancellaria*) Bellardi, 1841:25, pl. 2, figs. 17-18; as var. of *C. evulsa* Sow. [*sic*].[1] Tertiary, Italy.

taurinia (*Cancellaria*) Bellardi, 1841:27, pl. 3, figs. 19-20; as var. of *C. cancellata* Lam. [*sic*].[1] Tertiary, Italy.

taurinia (*Cancellaria*) Bellardi, 1841:pl. 3, figs. 9-10; as var. of *C. contorta* Basterot.[1] Tertiary, Italy.

taurinia (*Cancellaria*) Bellardi, 1841:35, pl. 4, figs. 13-14; as var. of *C. ampullacea* (Br.).[1] Tertiary, Italy.

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[1] In 1840 Bellardi used *taurinia* as a specific name for a *Cancellaria* and also as a varietal name for nine other species. All of these 1840 usages are *nomina nuda*. In 1841 he used *taurinia* as a varietal name for nine different species of *Cancellaria*. Sacco (1894:58) elevated one of these, the "var." of *C. varicosa* (Brocchi), to species level.

tauroacosticillata (*Cancellaria*) Sacco, 1894:41, pl. 2, fig. 69; as var. of *C. dertonensis* Bellardi; see Appendix, Note 2. Miocene, Italy.

tauroaspina (*Cancellaria*) Sacco, 1894:56, pl. 3, fig. 48; as var. of *C. varicosa* (Br.); see Appendix, Note 2. Miocene, Italy.

tauroaspinosa (*Cancellaria*) Sacco, 1894:31, pl. 2, fig. 35; as var. of *C. barjonae* Pereira da Costa; see Appendix, Note 2. Miocene, Italy.

tauroaspira (*Cancellaria*) Sacco, 1894:21, pl. 1, figs. 60a-b; as var. of *C. bernardii* Mayer; see Appendix, Note 2. Miocene, Italy.

taurobispinosa (*Cancellaria*) Sacco, 1894:62, pl. 3, fig. 65; as var. of *C. lyrata* (Br.); see Appendix, Note 2. Miocene, Italy.

taurobliquata (*Cancellaria*) Sacco, 1894:40, pl. 2, fig. 66; as var. of *C. dertonensis* Bellardi; see Appendix, Note 2. Miocene, Italy.

taurocaudata (*Cancellaria*) Sacco, 1894:21, pl. 1, figs. 59a-b; as var. of *C. bernardii* Mayer; see Appendix, Note 2. Miocene, Italy.

taurocompressa (*Cancellaria*) Sacco, 1894:41, pl. 2, fig. 70; as var. of *C. dertonensis* Bellardi; see Appendix, Note 2. Miocene, Italy.

tauroconnectens (*Cancellaria*) Sacco, 1894:34, pl. 2, fig. 48; as var. of *C. calcarata* (Br.); see Appendix, Note 2. Miocene, Italy.

tauroconnectens (*Cancellaria*) Sacco, 1894:11, pl. 1, fig. 22; as var. of *C. gradata* Hörnes; see Appendix, Note 2. Miocene, Italy.

tauroconvexula (*Cancellaria*) Sacco, 1894:47, pl. 3, figs. 22a-b; see Appendix, Note 2. Miocene, Italy.

taurocostatior (*Cancellaria*) Sacco, 1894:20, pl. 1, fig. 57; as var. of *C. obsoleta* Hörnes; see Appendix, Note 2. Miocene, Italy.

taurocosticillata (*Cancellaria*) Sacco, 1894:7, pl. 1, fig. 8; as var. of *C. scabra* Deshayes; see Appendix, Note 2. Miocene, Italy.

taurocrassum (*Cancellaria*) Sacco, 1894:7, pl. 1, figs. 9a-b; see Appendix, Note 2. Miocene, Italy.

tauroelegans (*Cancellaria*) Sacco, 1894:pl. 3, fig. 13; plate caption error for *taurelegans* Sacco.

tauroelongata (*Cancellaria*) Sacco, 1894:39, pl. 2, fig. 61; as var. of *C. cancellata* (L.); see Appendix, Note 2. Miocene, Italy.

tauroelongata (*Cancellaria*) Sacco, 1894:11, pl. 1, fig. 24; as var. of *C. fenestrata* Eichwald; see Appendix, Note 2. Miocene, Italy.

taurofasciata (*Cancellaria*) Sacco, 1894:23, pl. 2, fig. 8; as var. of *C. geslini* Basterot; see Appendix, Note 2. Miocene, Italy.

taurofaveolata (*Cancellaria*) Sacco, 1894:18, pl. 1, figs. 51a-c. Probably an error for *taurofoveolata*, as in the text reference is made to *faveolata* [*sic*] Sowerby; see *taurofoveolata*; see Appendix, Note 2. Miocene, Italy.

taurofoveolata (*Cancellaria*) Sacco, 1894:pl.1, figs. 51a-c; plate caption only; in text and index as *taurofaveolata*, *q.v.*; see Appendix, Note 2 Miocene, Italy.

taurolaevigatum (*Cancellaria*) Sacco, 1894:12, pl. 1, figs. 28a-c; see Appendix, Note 2. Miocene, Italy.

taurolaevior (*Cancellaria*) Sacco, 1894:53, pl. 3, fig. 36; as var. of *C. callosa* Partsch; see Appendix, Note 2. Miocene, Italy.

taurolatior (*Cancellaria*) Sacco, 1894:20, pl. 1, figs. 56a-b; as var. of *C. obsoleta* Hörnes; see Appendix, Note 2. Miocene, Italy.

tauroparva (*Brocchinia*) Sacco, 1894:68, pl. 3, fig. 82; as var. of *B. mitraeformis* (Br.). Miocene, Italy.

tauroparvula (*Cancellaria*) Sacco, 1894:24, pl. 2, figs. 13a-b; as var. of *C. westiana* Grateloup; see Appendix, Note 2. Miocene, Italy.

tauroparvula (*Cancellaria*) Sacco, 1894:10, pl. 1, fig. 19; as var. of *C. ampullacea* (Br.); see Appendix, Note 2. Miocene, Italy.

tauropercostata (*Cancellaria*) Sacco, 1894:10, pl. 1, fig. 20; as var. of *C. ampullacea* (Br.); see Appendix, Note 2. Miocene, Italy.

tauropercostata (*Cancellaria*) Sacco, 1894:52, pl.3, fig. 33; as var. of *C. deshayesiana* Desm. [*sic*]; see Appendix, Note 2. Miocene, Italy.

taurospinulosa (*Cancellaria*) Sacco, 1894:65, pl. 3, fig. 75; see Appendix, Note 2. Miocene, Italy.

taurotransiens (*Cancellaria*) Sacco, 1894:23, pl. 2, fig. 9; as var. of *C. geslini* Basterot; see Appendix, Note 2. Miocene, Italy.

tauroturris (*Cancellaria*) Sacco, 1894:41, pl. 2, fig. 68; as var. of *C. dertonensis* Bellardi; see Appendix, Note 2. Miocene, Italy.

tauroturrita (*Cancellaria*) Sacco, 1894:53, pl. 3, fig. 37; as var. of *C. callosa* Partsch [*sic*]; see Appendix, Note 2. Miocene, Italy.

tauroturritula (*Cancellaria*) Sacco, 1894:49, pl. 3, fig. 26; as var. of *C. contorta* Basterot; see Appendix, Note 2. Miocene, Italy.

tegalense (*Trigonostoma*) Oostingh, 1938:108, pl. 6, figs. 116a-c. Pliocene, Indonesia.

telemba (*Cancellaria*) Olsson, 1964:121, pl. 21, fig. 4. Miocene, Ecuador.

tenera (*Cancellaria*) Philippi, 1848:24. Recent, Caribbean.

tenuilineata (*Uxia*) Wrigley, 1935:375, pl. 34, fig. 30. Upper Eocene, England.

tenuiplica (*Cancellaria*) 'Edwards MS' – Newton, 1891:173. *Nomen nudum.*

tenuiplicata (*Sveltia*) Wrigley, 1935:360, pl. 32, fig. 5. Lower Eocene, England.

tenuis (*Cancellaria*) A. Adams, 1855:123. Recent, "China Seas". (?= *C. scalata* Sowerby, 1832)

tenuis (*Cancellaria*) Reeve, 1856:pl. 16, figs. 75a-b; *ex* Adams MS. Recent, ? Indo-Pacific.

tenuispiralis (*Turehua*) Beu & Maxwell, 1987:22, Pl. I, figs. i, o-p. Oligocene, New Zealand.

tenuistriata (*Cancellaria*) von Koenen, 1865:471, pl. 15, fig. 1. Oligocene, Germany.

tera (*Cancellaria*) de Gregorio, 1890:46, pl. 3, figs. 12-13. Eocene, Alabama, U.S.A. (?= *C. babylonica* Lea, 1833)

teramachii (*Trigonaphera*) Habe, 1961a:73, Appendix p. 27, pl. 36, fig. 4; 1961b:436, pl. 24, fig. 8. Recent, Japan.

terebralis (*Cancellaria*) von Koenen, 1889:137, pl. 8, figs. 4a-c. Oligocene, Germany.

teres (*Zeadmete*) Laws, 1940:54, pl. 6, fig. 21. Pleistocene, New Zealand.

terrareginensis (*Cancellaria*) Etheridge, 1907:327, pl. 60, fig. 11. Lower Cretaceous, Australia.

terryi (*Cancellaria*) Olsson, 1942:62, pl. 8, fig. 1. Neogene, Panama.

teschi (*Cancellaria*) Koperberg, 1931:67. Tertiary, Indonesia.

tessella (*Trigonostoma*) Garrard, 1975:30, pl. 3, fig. 18. Recent, Australia.

tessellata (*Cancellaria*) G. B. Sowerby I, 1832a:51; 1832b:figs. 20, 20*. Recent, Panamic-Pacific.

tessellata (*Cancellaria*) I. Lea, 1833:140, pl. 5, fig. 138. Eocene, southeastern U.S.A. (= *C. leai* Crosse, 1861; ?= *C. alveata* Conrad, 1833)

testaventricosa (*Cancellaria*) Grateloup, 1847:pl. 25, fig. 16; see Appendix, Note 1. Tertiary, France.

textilis (*Cancellaria*) Kiener, 1841:10, pl. 7, fig. 1. Recent, Indo-Pacific.

thiemeana (*Cancellaria*) Geinitz, 1874b:175, pl. 31, figs. 11a-b. Cretaceous, Germany.

thisbe (*Trigonostoma*) Olsson, 1964:126, pl. 22, fig. 6. Pliocene, Ecuador.

tholoensis (*Cancellaria*) Ladd, 1934:230, pl. 41, fig. 2. Miocene, Fiji.

thomasiae (*Cancellaria*) 'Crosse' – Dall, 1890:44. Error for *C. thomasiana* Crosse.

thomasiana (*Cancellaria*) Crosse, 1861:231; n.n. for "*C. scalarina* Lam." Reeve, 1856:pl. 6, fig. 25. Recent, Indo-Pacific.

thuringiae (*Cancellaria*) Giebel, 1853:384. Tertiary, Germany.

thysthlon (*Trigonostoma*) Petit & Harasewych, 1987:79, figs. 5, 8-13. Recent, Philippines.

timorensis (*Cancellaria*) Koperberg, 1931:68; as subsp. of *C. nassoides* Schepman. Tertiary, Indonesia.

tjibaliungensis (*Cancellaria*) K. Martin, 1895:50, pl. 7, figs. 116a-c. Tertiary, Indonesia.

toroensis (*Cancellaria*) Olsson, 1922:84, pl. 6, fig. 4. Miocene, Panama.

torquayensis (*Cancellaria*) Chapman, 1922:16, pl. 3, fig. 25. Oligocene, Australia.

torquilla (*Cancellaria*) Zekeli, 1852:81, pl. 14, fig. 11. Cretaceous, Europe. [not a cancellariid]

tortiplica (*Cancellaria*) Conrad, 1865a:32. *Nomen nudum.*

tortiplica (*Cancellaria*) Conrad, 1865b:145. Eocene, Texas, U.S.A.

tortoniana (*Cancellaria*) Sacco, 1894:46; n.n. for "*C. bellardii* Michelotti" Hörnes, 1854:pl. 34, fig. 18 only. See *C. saccoi* Hoernes & Auinger, 1890; see Appendix, Note 2. Miocene, Austria.

torula (*Cancellaria*) Weisbord, 1962:398, pl. 40, figs. 9-11. Tertiary, Venezuela.

tosaensis (*Fusiaphera*) Habe, 1961a:72, Appendix p. 28, pl. 35, fig. 21. Recent, Japan.

tosaensis (*Trigonaphera*) Habe, 1961a:72, Appendix p. 26, pl. 35, fig. 17. Recent, Japan.

tournoueri (*Sveltia*) Peyrot, 1928:224, pl. 13, figs. 11, 12; *ex* Benoist list. Miocene, France.

trachyostraca (*Cancellaria*) Brown & Pilsbry, 1911:345, pl. 23, figs. 1-2; as var. of *C. dariena* Toula. Miocene, Panama.

trailii (*Cancellaria*) 'Hutton' – Garrard, 1975: 44. Error for *C. trailli* Hutton.

trailli (*Cancellaria*) Hutton, 1873:26. Recent, New Zealand.

tranhirta (*Cancellaria*) Sacco, 1894:pl. 2, fig. 22; plate caption error for *transhirta* Sacco.

transennus (*Ficus*) Suter, 1917:13, pl. 3, fig. 9. Miocene, New Zealand. [*Tatara*]

transhirta (*Cancellaria*) Sacco, 1894:27, pl. 2, fig. 22; as var. of *C. piscatoria* (L.) [*sic*]; see Appendix, Note 2. Pliocene, Italy.

trapezium (*Cancellaria*) Borson, 1820:214. Pliocene, Italy.

traverseensis (*Tromina*) Clarke, 1961:365, pl. 2, fig. 8. Recent, South Atlantic. [*Iphinopsis*]

traversensis (*Tromina*) 'Clark, 1959' – Bouchet & Warén, 1985:261. Error for *T. traverseensis* Clarke, 1961.

trema (*Cancellaria*) Olsson, 1932:162, pl. 15, figs. 11-12. Miocene, Peru.

triangularis (*Cancellaria*) Nelson, 1870:191, pl. 6, fig. 10. Miocene, Peru.

tribulis (*Cancellaria*) Nomland, 1917:238, pl. 12, figs. 1, 1a; as var. of *C. fernandoensis* Arnold. Pliocene, California, U.S.A.

tribulus (*Voluta*) Brocchi, 1814:310, pl. 3, fig. 14. Pliocene, Italy. [*Sveltia*]

tribulus (*Cancellaria*) 'Nomland' – G. D. Hanna, 1924:160. Error for *C. tribulis* Nomland.

tributus (*Cancellaria*) 'Br.' – Cossmann, 1899a:13. Error for *C. tribulus* (Brocchi).

tricarinata (*Narona*) Traub, 1979:114, pl. 17, figs. 5a-b, 6a-b. Paleocene, Austria.

tricincta (*Cancellaria*) von Koenen, 1885:10, pl. 1, figs. 5a-b. Paleocene, Denmark.

tricostata (*Cancellaria*) Sacco, 1894:17, pl. 1, figs. 46a-b; as var. of *C. dertoscalata* Sacco; see Appendix, Note 2. Miocene, Italy.

trigonostoma (*Delphinula*) Lamarck, 1822a:231. Recent, Indo-Pacific. [?= *Trigonostoma scalare* (Gmelin, 1791)]

trilineata (*Cancellaria*) Handmann, 1882:263. Miocene, Austria.

trinodosa (*Cancellaria*) Chenu, 1859:274, fig. 1812. ?Recent, locality unknown. (?= *C. tuberculosa* Sowerby, 1832)

triplicata (*Admete*) Namias, 1898:39. Pliocene, Italy.

triplicatus (*Cantharus*) Röding, 1798:133. Recent, locality unknown. [= *Buccinum pyrozonias* Gmelin, 1791; ?= *Cancellaria cancellata* (Linne, 1767)]

tritonidea (*Cancellaria*) Gabb, 1866:11, pl. 2, fig. 18. Pliocene, California, U.S.A.

tritonis (*Cancellaria*) G. B. Sowerby I, 1832b:fig. 15. Recent, Indo-Pacific. (?= *C. spengleriana* Deshayes, 1830)

triumpha (*Trigonostoma*) Olsson, 1964:126, pl. 22, figs. 7, 7a. Pliocene, Ecuador.

trochilia (*Cancellaria*) Olsson, 1964:125, pl. 22, figs. 5, 5a-b. Pliocene, Ecuador.

trochlearis (*Cancellaria*) Faujas de Saint Fond, 1817:197, pl. 10, figs. 2a-b. Tertiary, France.

trochlearis (*Cancellaria*) Lamarck, 1822b:116. Tertiary, France. (?= *C. trochlearis* Faujas de Saint Fond, 1817)

truncata (*Cancellaria*) G. B. Sowerby II, 1849a:137; as var. of *C. undulata* Sowerby. Recent, ? Philippines.

tuberculata (*Cancellaria*) 'Sowerby' – G. B. Sowerby II, 1849b:457; *et al.* Error for *C. tuberculosa* G. B. Sowerby I.

tuberculata (*Fasciolaria*) Giebel, 1861:40. Oligocene, Germany. [*Turehua*]

tuberculifera (*Anapepta*) Laws, 1935:38, pl. 6, fig. 19. Miocene, New Zealand.

tuberculosa (*Cancellaria*) G. B. Sowerby I, 1832a:51; 1833:fig. 36. Recent, Panamic-Pacific.

tuberculosa (*Cancellaria*) Sacco, 1894:24; n.n. for "*C. westiana* Grat." Almera & Bofill, 1884:pl. B, figs. 1-3; as var. of *C. exwestiana* Sacco; see Appendix, Note 2. Tertiary, Spain.

tumescens (*Cancellaria*) von Koenen, 1889:123, pl. 10, figs. 5a-c, 6a-c, 7a-c. Oligocene, Germany.

tumida (*Cancellaria*) von Koenen, 1889:125, pl. 9, figs. 9a-b. Oligocene, Germany.

tumida (*Bonellitia*) Hickman, 1980:71, pl. 8, figs. 20-23. Oligocene, Oregon, U.S.A.

tumida (*Nothoadmete*) Oliver, 1982:16, figs. 1-5. Recent, Antarctic.

turbiformis (*Paladmete*) Stephenson, 1953:191, pl. 43, figs. 30-31. Cretaceous, Texas, U.S.A.

turbiniformis (*Paladmete*) 'Stephenson' – Sohl, 1964a:271. Error for *P. turbiformis* Stephenson.

turgidula (*Cancellaria*) Cocconi, 1873:166, pl. 3, figs. 32-33; as var. of *C. bonellii* Bellardi. Tertiary, Italy.

turgidula (*Cancellaria*) 'Guidotti MS' – Cocconi, 1873:168. *Nomen nudum.*

turneri (*Cancellaria*) White, 1889:25, pl. 3, figs. 6-7. Cretaceous, California, U.S.A.

turricula (*Cancellaria*) Lamarck, 1822b:116. Tertiary, Italy. (?= *C. lyrata* (Brocchi,1814))

turriculata (*Cancellaria*) Tate, 1889:156, pl. 10, fig. 14. Eocene, Australia.

turriculata (*Hilda*) Newton, 1922:29, pl. 4, figs. 24-25. Eocene, Nigeria. [*Varicohilda*]

turriculatum (*Triton*) Deshayes, 1835:608, pl. 80, figs. 7-12. Eocene, France. [*non Triton turriculatum* Deshayes, 1833; = *Plesiotriton deshayesianus* Beu & Maxwell, 1987]

turris (*Cancellaria*) 'Edwards MS' – Newton, 1891:173. *Nomen nudum.*

turrita (*Cancellaria*) 'Bell.' – Michelotti, 1838:396; Bellardi, 1840:344. *Nomen nudum.*

turrita (*Cancellaria*) Bellardi, 1841:20, pl. 2, figs. 11-12; as var. of *C. nodulosa* Lamarck. Tertiary, Italy.

turrita (*Cancellaria*) G. B. Sowerby II, 1874:721, pl. 59, fig. 12. Recent, unknown locality.

turritella (*Cancellaria*) Hoeninghaus, 1831:145. *Nomen nudum.*

turritior (*Cancellaria*) Sacco, 1894:9, pl. 1, fig. 17; as var. of *C. ampullacea* (Br.); see Appendix, Note 2. Pliocene, Italy.

turritissima (*Cancellaria*) Meyer, 1886:73, pl. 1, fig. 15. Eocene, Alabama, U.S.A.

turritovula (*Cancellaria*) Sacco, 1894:45; n.n. for "*C. evulsa* (Sol.)" Speyer, 1867:pl. 11 [*sic*; error for pl. 16], fig. 1; as var. of *C. evulsa* (Solander); see Appendix, Note 2. Tertiary, Germany.

turritula (*Cancellaria*) Sacco, 1894:32, pl. 2, fig. 40; as var. of *C. doderleini* Mayer; see Appendix, Note 2. Miocene, Italy.

turrituloides (*Cancellaria*) Sacco, 1894:53, pl. 3, fig. 39; as var. of *C. deperdita* Michelotti; see Appendix, Note 2. Oligocene, Italy.

tyosenensis (*Cancellaria*) Hatai & Nisiyama, 1940:128, pl. 5, fig. 3. Miocene, Japan.

typica (*Cancellaria*) 'Krause' – Paetel, 1888:332. *Nomen nudum.*

U

uaquala (*Cancellaria*) Mansfield, 1935:27, pl. 2, figs. 7-8; as subsp. of *C. agria* Mansfield. Miocene, Florida, U.S.A.

ulmula (*Cancellaria*) G. D. Harris, 1895a:66, pl. 6, fig. 6. Eocene, Texas, U.S.A.

umbilicaris (*Voluta*) Brocchi, 1814:312, pl. 3, figs. 10-11. Pliocene, Italy. [*Ventrilia*]

umbilicata (*Cancellaria*) Lesson, 1842:203. Recent, western Mexico. *Nomen dubium.*

umbilicata (*Admete*) Hickman, 1980:77, pl. 9, fig. 13. Oligocene, Washington, U.S.A.

umbilicatior (*Admete*) Sacco, 1894:71; n.n. for "*C. subangulosa* Wood" von Koenen, 1889:pl. 12, fig. 14; as var. of *A. minuta* (Braun); see Appendix, Note 2. Tertiary, Germany.

umbilicina (*Cancellaria*) Sacco, 1894:20, pl. 1, fig. 58; as var. of *C. doliolaris* Basterot; see Appendix, Note 2. Miocene, Italy.

unalaschkensis (*Admete*) 'Dall' – Kobelt, 1887b:103. Error for *A. unalashkensis* (Dall).

unalashkensis (*Cancellaria*) Dall, 1873:58, pl. 2, fig. 1. Recent, Aleutian Islands, Alaska, U.S.A.

undata (*Admete*) Leche, 1878:47; n.n. for "*C. viridula* (Fab.)" Middendorff, 1849:pl. 10, figs. 3-4; as var. of *A. viridula* (Fabricius). Recent, North Atlantic. (?= *Admete viridula* (Fabricius, 1780))

undatocostata (*Admete*) Verkrüzen, 1875:237; as *undato-costata.* Recent, North Atlantic. (?= *A. viridula* (Fabricius, 1780))

undulata (*Cancellaria*) G. B. Sowerby II, 1849a:136; 1849b:443, pl. 92, fig. 12; pl. 95, fig. 79. Recent, Tasmania.

uniangulata (*Cancellaria*) Deshayes, 1830:181. Pliocene, Italy.

unicosticillata (*Cancellaria*) Sacco, 1894:43, pl. 3, fig. 2; as var. of *C. bonelli* Bellardi; see Appendix, Note 2. Miocene, Italy.

unidentata (*Cancellaria*) 'Sowerby' – H. & A. Adams, 1854:276. ? Error for *C. indentata* Sowerby.

unifasciata (*Cancellaria*) 'Orbigny' – Dall, 1909b:281. *Nomen nudum.*

uniplicata (*Cancellaria*) G. B. Sowerby I, 1832b:fig. 13. Recent, western Mexico. (?= *C. mitriformis* Sowerby, 1832)

urceolata (*Cancellaria*) Hinds, 1843:47; 1844b:41, pl. 12, figs. 7-8. Recent, Panamic-Pacific.

urcianensis (*Cancellaria*) d'Ancona, 1872:117, pl. 12, figs. 4a-c. Pliocene, Italy.

urumacoensis (*Cancellaria*) H. K. Hodson in Hodson & Hodson, 1931:45, pl. 18, figs. 2-3. Miocene, Venezuela.

V

valida (*Mataxa*) Stephenson, 1941:365, pl. 70, figs. 1-3. Cretaceous, Texas, U.S.A. (?= *M. elegans* Wade, 1916)

varicifera (*Cancellaria*) Tenison-Woods, 1879:231, pl. 21, fig. 12. Miocene, Australia.

variciferus (*Phos*) Tate, 1888:169, pl. 11, fig. 3. Miocene, Australia. [*Loxotaphrus*]

varicosa (*Cancellaria*) 'Brocchi' – error for, or emendation of, *Voluta varricosa* Brocchi, 1814. Spelled as *varicosa* by almost all authors after Brocchi.

varicosa (*Cancellaria*) Bellardi, 1840:344; as var. of "*C. bonellii* Bellardi". *Nomen nudum.*

varicosa (*Merica*) Shuto, 1969:172, pl. 11, figs. 4-5, 15-16; as subsp. of *M. asperella* (Lamarck). Neogene, Philippines.

varicosissima (*Cancellaria*) Handmann, 1882:264. Miocene, Austria.

varicosus (*Cantharus*) Tate, 1888:166, pl. 8, fig. 10. Eocene, Australia. [*Semitriton*]

variculosa (*Merica*) Peyrot, 1928:212, pl. 12, figs. 42-43. Miocene, France.

variecosticillata (*Cancellaria*) Sacco, 1894:38; as "anom." of *C. cancellata pluricosticillata* Sacco; see Appendix, Note 2. Tertiary, Italy.

varricosa (*Voluta*) Brocchi, 1814:311, pl. 3, fig. 8. Pliocene, Italy. [*Sveltia*]

vectensis (*Uxia*) Wrigley, 1935:378, pl. 34, fig. 37; pl. 35, fig. 53; as var. of *U. elongata* (Nyst). Eocene, England.

venatrix (*Cancellaria*) 'Edwards MS' – Newton, 1891:173. *Nomen nudum.*

venatrix (*Bonellitia*) Wrigley, 1935:370, pl. 33, fig. 23. Middle Eocene, England.

veneranda (*Admete*) Beets, 1946:93, pl. 4, figs. 32-36; pl. 6, fig. 1. Pliocene-Pleistocene, Netherlands.

venezuelana (*Cancellaria*) H. K. Hodson in Hodson & Hodson, 1931:45, pl. 23, figs. 1, 4. Miocene, Venezuela.

ventricosa (*Cancellaria*) Hinds, 1843:47; 1844b:41, pl. 12, figs. 11-12. Recent, Panamic-Pacific.

ventricosa (*Cancellaria*) Grateloup, 1847:2, pl. 1, fig. 16; as var. of *C. geslini* Basterot. Tertiary, France.

ventricosa (*Admete*) Friele, 1879:275; as var. of *A. viridula* (Fabricius). Recent, North Sea.

ventrilia (*Ventrilia*) Jousseaume, 1887a:164, text-fig. 2. Recent, Caribbean. (?= *Trigonostoma tenerum* (Philippi, 1848))

venusta (*Cancellaria*) Tuomey & Holmes, 1856:144, pl. 28, fig. 18. Pliocene, South Carolina, U.S.A.

vera (*Cancellaria*) Beyrich, 1856:557; as var. of *C. evulsa* (Solander). Tertiary, Germany.

verauxii (*Cancellaria*) 'Kiener' – H. Adams & A. Adams, 1854:276. Error for *C. verreauxii* Kiener.

verbeeki (*Cancellaria*) K. Martin, 1895:49, pl. 7, figs. 115, 115a. Pliocene, Indonesia.

verrauxii (*Cancellaria*) 'Kiener' – G. B. Sowerby II, 1849b:450. Error for *C. verreauxii* Kiener.

verreauxii (*Cancellaria*) Kiener, 1841:17, pl. 8, fig. 3. Recent, Indo-Pacific.

vespertina (*Cancellaria*) F. M. Anderson, 1905:200, pl. 16, figs. 77-78. Tertiary, California, U.S.A.

vetusta (*Cancellaria*) Gabb, 1866:12, pl. 2, fig. 19. Tertiary, California, U.S.A.

vexillata (*Tritonoharpa*) Dall, 1908:320, pl. 8, fig. 7. Recent, Panamic-Pacific.

vicarii (*Cancellaria*) d'Archiac, 1850:291. *Nomen nudum.* [described as *Buccinum vicaryi* d'Archiac & Haime, 1854; not a cancellariid]

vidali (*Cancellaria*) Philippi, 1887:64, pl. 7, fig. 5. Miocene, Chile.

vigneauxi (*Daguinia*) Magne, 1966:127, fig. 1. Miocene, France.

vincenti (*Uxia*) Glibert, 1938:120, pl. 4, fig. 10;, text-fig. 35. Oligocene, Belgium.

vindobonensis (*Cancellaria*) Sacco, 1894:62; n.n. for "*C. lyrata* (Br.)" Hörnes, 1854:pl. 34, fig. 5; see Appendix, Note 2. Miocene, Austria.

vinnulum (*Trigonostoma*) Iredale, 1925:263, pl. 42, fig. 18. Recent, Australia.

viridula (*Tritonium*) Fabricius, 1780:402. Recent, North Atlantic. [*Admete*]

vivus (*Plesiotriton*) Habe & Okutani, 1981:194, figs. 2-3. Recent, Philippines.

vokesae (*Colubraria*) Allen, 1970:71, pl. 2, figs. 10-11. Eocene, Louisiana, U.S.A. [*Plesiotriton*]

vokesae (*Olssonella*) Petit, 1970:84, pl. 1, figs. 1a-b. Oligocene, North Carolina, U.S.A..

volutanus (*Murex*) Risso, 1826:198. Tertiary, Europe. [?= *Cancellaria spinulosa* (Brocchi, 1814)]

volutella (*Cancellaria*) Lamarck, 1803:63. Eocene, France.

volvutella (*Cancellaria*) 'Lamarck' – Sohl, 1960:128. Error for *C. volutella* Lamarck.

vossi (*Admetula*) Petit, 1976:39, pl. 1, fig. 5. Recent, Caribbean.

W

waikaiaensis (*Trigonostoma*) Finlay, 1924b:466, pl. 49, figs. 4a-b. Oligocene, New Zealand.

waltonensis (*Mitra*) Aldrich, 1910:121, pl. 11, fig. 1. Miocene, Florida, U.S.A. [*Aphera*]

waltoniana (*Cancellaria*) Gardner, 1937:366, pl. 44, figs. 5-6. Miocene, Florida, U.S.A.

wannonensis (*Cancellaria*) Tate, 1889:156, pl. 8, fig. 11. Miocene, Australia.

washingtonensis (*Cancellaria*) Weaver, 1916:51, pl. 5, figs. 77-78. Oligocene, Washington, U.S.A.

watanabei (*Admete*) Shikama, 1962:47, pl. 2, figs. 12a-b. Recent, Japan.

watsoni (*Zeadmete*) Petit, 1970:86; n.n. for *Cancellaria carinata* Watson, 1882, *non* Briart & Cornet, 1877. Recent, Kerguelen Islands.

wattebledi (*Trigonostoma*) Peyrot, 1928:255, pl. 14, figs. 15-17; *ex* Benoist MS. Neogene, France.

waynensis (*Cancellaria*) Mansfield, 1940:207, pl. 27, fig. 19. Oligocene, Mississippi, U.S.A.

weaveri (*Cancellaria*) Etherington, 1931:108, pl. 14, figs. 1, 3, 17. Miocene, Washington, U.S.A.

werenfelsi (*Cancellaria*) Jung, 1965:552, pl. 75, figs. 9-11. Miocene, Venezuela.

westi (*Cancellaria*) 'Bast.' – Mayer, 1872:505. *Nomen nudum.*

westiana (*Cancellaria*) 'Grateloup' – M. Hörnes, 1854:325; Crosse, 1861:248; *et al.* Error for, or emendation of, *C. westziana* Grateloup.

westralia [*Tritonoharpa*] Beu & Maxwell, 1987:47, pl. 14, figs. a-g, l. Recent, Australia.

westralis (*Cancellaria*) Garrard, 1975:5, pl. 1, figs. 2-3; as subsp. of *C. melanostoma* Sowerby. Recent, Australia.

westziana (*Cancellaria*) Grateloup, 1847:pl. 1, figs. 18, 21. Tertiary, France.

wigginsi (*Cancellaria*) Emerson & Hertlein, 1964:362, figs. 5d-e. Pleistocene, Mexico.

wildi (*Cancellaria*) Mayer, 1872:505. *Nomen nudum.*

williamsi (*Olssonella*) Petit, 1976:36, pl. 2, figs. 2a-b. Pliocene, Virginia, U.S.A.

wilmeri (*Cancellaria*) G. B. Sowerby II, 1881:637, pl. 56, fig. 2. Recent, Andaman Islands, India.

withrowi (*Trigonaphera*) Petit, 1976:39, pl. 2, fig. 3. Recent, Senegal. (?= *Scalptia scala* (Gmelin, 1791))

woodii (*Admete*) Sacco, 1894:72; n.n. for "*C. costellifera* Sow." Wood, 1848:pl. 7, fig. 21; as var. of *A. costellifera* (Sowerby); see Appendix, Note 2. Tertiary, England.

woodringi (*Trigonostoma*) Jung, 1965:557, pl. 76, figs. 1-2. Miocene, Venezuela.

woodworthi (*Admete*) Dall, 1905:123. Recent, California, U.S.A.

wouweri (*Admete*) Harmer, 1918:410, pl. 39, fig. 50. Pliocene, Netherlands.

wynoocheensis (*Cancellaria*) 'Weaver' – Etherington, 1931:107. Error for *C. wynoochensis* Weaver, 1916.

wynoochensis (*Cancellaria*) Weaver, 1916:50, pl. 4, figs. 51-54; as *wynootchensis* in text and *wynoochensis* on plate explanation; we consider *wynoochensis* to be the intended spelling. Miocene, Washington, U.S.A.

wynootchensis (*Cancellaria*) Weaver – Error for *wynoochensis, q.v.*

X

xavieri (*Colubraria*) Campbell, 1961:141, pl. 10, figs. 7-8. Recent, Panamic-Pacific. [?= *Tritonoharpa vexillata* Dall, 1908]

xenia (*Cancellaria*) Olsson, 1964:119, pl. 21, fig. 9. Miocene, Ecuador.

Y

yokoyamai (*Admete*) Oyama in Taki & Oyama, 1954:24, pl. 3, fig. 5; n.n. for "*Admete viridula* Fabricius" Yokoyama, 1920:45, pl. 2, fig. 5. Pliocene, Japan. (= *Lora cancellata* Otuka, 1937, *q.v.*)

yolandia (*Cancellaria*) Pilsbry & Olsson, 1941:21, pl. 4, fig. 3. Pliocene, Ecuador.

yonabaruensis (*Cancellaria*) MacNeil, 1960:98, pl. 5, fig. 4. Miocene, Okinawa.

ytenensis (*Cancellaria*) 'Edwards MS' – Newton, 1891:173. *Nomen nudum.*

ytenensis (*Bonellitia*) Wrigley, 1935:369, pl. 33, fig. 18; pl. 35, fig. 47. Middle Eocene, England.

Z

zahni (*Cancellaria*) Böse, 1910:239, pl. 13, fig. 16. Tertiary, Tehuantepec, Mexico.

zapoteca (*Cancellaria*) Böse, 1910:240, pl. 13, fig. 17. Tertiary, Tehuantepec, Mexico.

zetes (*Trigonostoma*) Kautsky, 1925:141, pl. 10, figs. 10-11. Miocene, Germany.

ziervogeliana (*Cancellaria*) Lamarck, 1822b:115. [= *Voluta ziervogelii* Gmelin, 1791; Mitridae]

zitteli (*Cancellaria*) Wanner, 1902:139, pl. 19, figs. 12-13. Cretaceous, northern Africa.

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[1] Moriz Hörnes and Rudolph Hoernes, although father and son, used different orthography for their surname. This difference is consistent in all their published work which we have seen.

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APPENDIX

Note 1. **Grateloup.** In his *Atlas* of 1847, Grateloup listed varieties for a number of species of *Cancellaria*. Most of the varietal names appear in polynominal form. The index to the *Atlas*, valid in its own right, lists varieties only in binary form. Many of Grateloup's varietal names were utilized by later authors although the validity of dating some of them from Grateloup is questionable. The *Atlas*, although dated 1840, was not published earlier than 1847. The plates are numbered consecutively within each of the families represented, with one to five plates for each family or major group of families, as though each set of plates was to be accompanied by a monograph. The plate captions for most plates have a second number given in parentheses which indicates the position of the plate in the *Atlas*. The index uses these numbers. In some citations, the *Cancellaria* plate is cited as "Plate 1", while in other citations it is shown as "Plate 25", the number given in the index.

Note 2. **Sacco.** In his monograph of 1894 Sacco utilized five genera in Cancellariidae and included 14 subgenera within the genus *Cancellaria*. In his text, nomina are treated as if the subgenera are actually genera. As an example, page 4 of his work is headed "Gen. *Cancellaria*" with a subheading showing *Trigonostoma* as a subgenus. The species he includes in the subgenus *Trigonostoma* are listed in such a manner that the genus would appear to be *Trigonostoma* (*e.g.*, *Trigonostoma oligolongum* instead of *Cancellaria* (*Trigonostoma*) *oligolonga*). This same format is utilized for all other subgenera. Taxa are also listed in this manner in the index, although the text is clear as to the relative positions of the genus-group taxa. In this compilation, new taxa are listed under the genus in which they were originally proposed. We note that monographers and cataloguers of other families have treated Sacco's taxa similarly.

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