

SYSTEMATIC REVIEW AND FUNCTIONAL MORPHOLOGY OF THE
MANGROVE SNAILS *TEREBRALIA* AND *TELESCOPIUM*
(POTAMIDIDAE; PROSOBRANCHIA)

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ABSTRACT

Diagnoses of the genera *Telescopium* Montfort, 1810, and *Terebralia* Swainson, 1840, are made, based on conchological and anatomical characters. *Telescopium telescopium* (Linné, 1758) is the only living member of the genus. Three Recent *Terebralia* species are recognized: *Terebralia palustris* (Linné, 1758), *Terebralia sulcata* (Born, 1778) and *Terebralia semistriata* (Mörch, 1852). Complete synonymies and descriptions are presented for each genus-level and species-level taxon. *Cerithium crassum* Lamarck, 1822, and *Strombus semistriatus* Röding, 1798, are determined to be *nomina dubia*. Shells, radulae and anatomical features are described and compared, and intraspecific variability is noted. Both genera date from the mid-Tertiary, and most living species have fossil records extending back to the Miocene. Both genera are confined today to the Indo-West Pacific. The ecology, life history, fossil record and geographical distribution of each species are presented. Species of both genera are amphibious surface-dwellers of muddy substrates in mangrove forests, and have reduced ctenidia. Most are algal-detritivores and have a taenioglossate radula, complex stomach and long crystalline style. The radula and buccal mass of *Telescopium* are very small, but the snout is extremely long. The radula and buccal mass of *Terebralia* species are robust and large. *Terebralia palustris* is unusual in undergoing a radular transformation between juvenile and adult stages that corresponds to the trophic dimorphism between the two stages: juveniles eat detritus, whereas adults eat fallen mangrove leaves. Species of both genera are gonochoristic with aphallate males and have open pallial gonoducts. The pallial oviduct of *Telescopium* is highly complex, comprising four laminae and very large, transverse glandular ridges adjacent to the oviductal groove. The pallial oviducts of *Terebralia* species are unusual among those of cerithioideans in having medial fusions. *Terebralia* males produce elaborate, crescentic spermatophores sculptured with many transverse keels. Spawn masses of both genera are deposited with the aid of a bulbous ovipositor located on the right side of the foot and comprise long, irregular gelatinous strings filled with very small egg capsules. The ovipositor of *Terebralia* species extends deep into the foot, forming an inner glandular chamber of ectodermal origin, which is thought to secrete the outer coat of the gelatinous string during spawn deposition. Species of both genera have free-swimming larval stages. The subfamily Batillariinae is excluded from the Potamididae and raised to familial rank. The genus *Cerithidea* Swainson, 1840, is considered closely related to *Telescopium* and *Terebralia*.

Key Words: Potamididae, *Telescopium*, *Terebralia*, systematics, anatomy, reproductive biology, ecology, mangroves.

INTRODUCTION

One of the most conspicuous elements of the malacofauna of the vast mangrove swamps of the Indo-West Pacific province are the ubiquitous potamidid snails of the genera *Telescopium* Montfort, 1810, and *Terebralia* Swainson, 1840. *Terebralia* comprises three Recent species, *Terebralia palustris* (Linné, 1758), *Terebralia sulcata* (Born, 1778) and *Terebralia semistriata* (Mörch, 1852); *Tele-*

scopium telescopium (Linné, 1758) represents a now monotypic genus.

The taxonomy of Potamididae H. & A. Adams, 1854, is in disarray because earlier authors relied chiefly on shell characters in their classifications and did not set clear limits to higher taxa. They were also unaware of the significant anatomical differences between the Cerithiidae Férussac, 1819, and the Potamididae, and commonly referred many potamidid taxa to the Cerithiidae; moreover, ear-

lier workers did not understand the anatomical differences between the two subfamilies thought to comprise Potamididae (Potamidiinae H. & A. Adams, 1854, and Batillariinae Thiele, 1929). Genus-level taxa from each potamidid subfamily were frequently mixed with one another and with other cerithiid taxa in varying combinations that included nomina of extinct higher taxa. The resultant entangled higher classification is misleading and engenders frustrating searches for taxa in the older literature.

Terebralia and *Telescopium* species are large prosobranchs that occur in great numbers and frequently dominate the surface of the muddy substrates of mangrove forests. It is therefore surprising that so little is known of their anatomy, reproductive biology or life histories. Although a number of ecological studies on migratory movements and vertical distribution in the mangrove habitat have been published, there has been no attempt comprehensively to integrate these observations and other anecdotal information. So little is known about the soft anatomy and reproductive biology of these large potamidids that it has been impossible to establish a good data base for character analysis; thus, the phylogeny and systematic standing of these taxa in relation both to other potamidids and to other cerithioidean families has been unclear. It is the goal herein to rectify this situation.

MATERIALS AND METHODS

All three living species of *Terebralia* were studied in the field and in the laboratory. Populations of *Terebralia sulcata* were studied for ten days in the New Territories of Hong Kong and at the University of Hong Kong. Work on *Terebralia semistriata* and *Terebralia palustris* was conducted for five days at Magnetic Island and Townsville, Queensland, Australia. The anatomy of both *Terebralia palustris*, the type species of *Terebralia*, and of *Terebralia sulcata* is described in some detail, followed by a brief description of *Terebralia semistriata*. Observations and dissections of live *Telescopium telescopium*, the type of the genus by tautonomy, were conducted at Magnetic Island, Queensland, Australia. Living adult specimens of all of these species were removed from their shells by cracking them in a large vise. Animals were extracted from their shells, and care was taken to remove the

numerous whorls of the visceral mass without damaging the thin mantle tissue, especially around the pallial gonoducts. Extracted snails were kept alive in aquaria and finger bowls. No adult males of *Terebralia palustris* or *Telescopium telescopium* were found.

It is very difficult to remove these snails from their strong shells successfully without injuring and destroying tissues; moreover, damaged or injured snails secrete great quantities of mucus, which hinders dissection and fixation. Thus, it was not possible to prepare and examine numerous individuals in the short time spent in the field, but sufficient material was examined for comparative dissections. Animals were relaxed in 7.5% MgCl₂ solution for anatomical study and dissection under a Wild M-8 dissecting microscope. A solution of methylene blue/basic fuchsin was used to enhance anatomical features. Tissues were fixed in Bouin's solution in seawater or in 10% seawater formalin and were sectioned with a razor blade. Whole animals were too large for histological sectioning, but selected organs and tissues were embedded in paraffin, sectioned at 7 μm, and stained with Harris' hematoxylin and eosin or Mallory's triple stain for histological examination. Photomicrographs of sections were made with a Zeiss Photomicroscope III. Tissues were critical point dried and these, along with radulae and spermatophores, were examined with a Zeiss Novascan-30 scanning electron microscope. Voucher specimens have been deposited in the USNM. Preserved museum specimens of species from other geographic regions were also used for study, but most were too poorly fixed for careful dissection.

The discussion of anatomical characters of each genus and the final discussion of potamidid anatomy should be understood with reference to my paper on cerithioidean phylogeny (Houbrick, 1988).

Abbreviations: AMNH—American Museum of Natural History; AMS—The Australian Museum, Sydney; ANSP—Academy of Natural Sciences of Philadelphia; BMNH—British Museum (Natural History); CNHM—Field Museum of Natural History; DMNH—Delaware Museum of Natural History; FSM—Florida State Museum, Gainesville; MCZ—Museum of Comparative Zoology; MNHNP—Museum National d'Histoire Naturelle, Paris; USNM—United States National Museum; WAM—Western Australian Museum; ZMA—Zoologisch Museum, Amsterdam.

SYSTEMATICS

POTAMIDIDAE H. & A. ADAMS, 1854

TELESCOPIUM MONTFORT, 1810

Telescopium Montfort, 1810:438 (Type species, by od: *Telescopium indicator* Montfort, 1810 [= *Trochus telescopium* Linné, 1758, type species by tautonomy]). Tryon, 1882:250; Cossmann, 1906:124–125; Wenz, 1940:743.

Diagnosis: Shell very large, thick, conical, with numerous flat-sided whorls sculptured with spiral grooves; shell base with concentric cords and deep channel around columellar pillar. Aperture narrowly ovate, tangential (perpendicular) to shell axis with twisted, channeled columella, and outer lip curved toward centrally placed, short siphonal canal. Operculum corneous, circular and multispiral with central nucleus. Lateral tooth with broad lateral lamella. Snout very long with small buccal mass and very small taenioglossate radula. Rachidian tooth ovoid with broad central cusp. Mantle with siphonal light-sensory organ (pallial eye). Ovipositor on right side of foot in females. Pallial gonoducts completely open, highly complex. Zygoneurous nervous system. Egg capsules deposited in gelatinous strings.

Remarks: *Telescopium* was thought to date from the Late Cretaceous (Turonian) by Cossmann (1906:123), but most of the fossils attributed to this genus are campanilids. The earliest species that appears to belong to *Telescopium* as now understood is a Miocene fossil, *Telescopium pseudobeliscus* (Gratouille, 1832). Recent *Telescopium* is a monotypic genus. The genus appears never to have been species-rich, but some fossil species have been described.

Telescopium telescopium and *Campanile symbolicum* Iredale, 1917, have convergent shell morphologies and were placed in the same group in some of the older monographic literature. The shells of many extinct *Campanile* species also resemble *Telescopium*, but recent studies have shown that the campanilid group constitutes a superfamily of its own (Houbrick, 1989). *Telescopioidea* Sacco, 1895:56 (Type species, by o.d.: *Cerithium charpentieri* Basterot, 1825) and *Campanilopsis* Chavan, 1948 (Type species, by o.d.: *Cerithium ceres* Orbigny, 1847) were proposed as subgenera of *Telescopium*, but both should be excluded from it because their respective type species are members of Cam-

paniloidea. A number of Italian Tertiary fossils lacking apertures were allocated to *Telescopium* by Sacco (1895), who noted that they differed sufficiently from Recent *Telescopium* to warrant establishment of a subgenus, *Telescopioidea* Sacco, 1895, to accommodate them. Sacco (1895) noted that they more closely resembled living *Campanile symbolicum* than they did *Telescopium*; examination of these taxa confirms that they should be regarded as members of the Campanilidae. Authors such as Adams & Adams (1858:291) frequently included *Campanile symbolicum* Iredale, 1917 (cited as *Cerithium laeve* Quoy & Gaimard, 1834) in the genus *Telescopium*.

Fragmentary fossils of species of *Campanile* (Campanilidae) and the extinct potamidid, *Vicarya* Archiac & Haime, 1854, are commonly assigned to *Telescopium* by authors. Shuto (1978:116, pl. 15, fig. 4) referred *Potamides jogjacartense* (Martin, 1914) to *Telescopium*, but judging from his illustrations of the specimen, it is doubtful that it should be included in the genus.

Although many reports of fossil *Telescopium* in the literature are erroneous and based on fragments of other taxa, numerous fossils of *Telescopium* from Cenozoic deposits in East Africa, Indonesia and the Philippines are either conchologically conspecific with Recent *Telescopium telescopium*, or very closely related to it.

Allan (1950:86) included *Telescopium* in the family Telescopiidae, a name he substituted for Potamididae without giving any reasons or comment, but there is no justification for this name change, and Telescopiidae must be considered a synonym of Potamididae. In the older literature, *Telescopium* is sometimes cited as a subgenus of *Potamides* Brongniart, 1810 (see Tryon, 1882:250–251) or as a synonym of *Pyraxus* Montfort, 1810 (see Adams & Adams, 1858:291), which is a batillariid.

Telescopium telescopium (Linné)
(Figs. 1–6)

Trochus telescopium Linné, 1758:760 (Holotype: Linnaean Collection, London; Type locality herein selected: Ambon); Linné, 1767:1231; Dodge, 1958:204–205.

Cerithium telescopium Bruguière, 1792:483; Kiener, 1841:88–89, pl. 28, fig. 4; Kobelt, 1898:57, plate 12, fig. 1.

Telescopium indicator Montfort, 1810:438,

figure (in part; Type not found; Montfort's figure, a *Pyrazus* species, here selected to represent lectotype).

Telescopium fuscum Schumacher, 1817:233 (Type not found; Schumacher's figure reference to Buonanni, 1709, here selected to represent lectotype); Boettger, 1890:167.

Potamides (Telescopium) telescopium K. Martin, 1884:145, 328, 348; Martens, 1897:180–181; Koningsberger, 1915:446; Lischke, 1914:259; Oostingh, 1923:75; Benthem Jutting, 1929:86; Rensch, 1934:339.

Telescopium telescopium K. Martin, 1899:220, pl. 33, figs. 509, 509a; 1919:94, 128, 137; Regteren Altena, 1941:13–14; Wissema, 1947:46; Butot, 1954:10; Benthem Jutting, 1956:439–441, figs. 100, 108; 1959:105–106; Cernohorsky, 1972:61, pl. 13, fig. 6; Brandt, 1974:196, pl. 15, fig. 61.

Telescopium mauritsi Butot, 1974:7–12, pls. 1, figs. 3, 4; 2, figs. 2, 3 (Holotype: ZMA; Type locality: Pulo Panaitan, Sunda Strait, Indonesia); Benthem Jutting, 1959:105.

Synonymic Remarks. Specimens of this distinctive species occur in both the Linnaean Collection in London and in the "Museum Utricae" of the Uppsala Collection (Dodge, 1958:204–205). According to Dodge (1958), who presented a lengthy commentary on the types and Linnaean figure references for this species, no question has ever been raised as to the identity of *Telescopium telescopium*, and its synonymy is "unimpeachable." He believed that the specimen in the Linnaean collection in London should be accepted as Linné's probable type specimen, and I concur. Although Bruguière (1792) cited *Cerithium telescopium* without attributing authorship to Linné, he did not intend to describe it under his own authorship, for he clearly stated that he merely was transferring Linné's specimen (species) from *Trochus* to *Cerithium* (Bruguière, 1792:484). Most of Montfort's (1810) figure references for *Telescopium indicator* agree with Linné's type specimen and figure references for *Trochus telescopium*, but Montfort's (1810: figure, p. 438) own figure of *Telescopium indicator* definitely does not represent *Telescopium*, but appears to be a *Pyrazus* species; thus, his concept of *Telescopium indicator* appears to be a mixture based upon the *Telescopium* figures of other

authors and a *Pyrazus* species. The figure references for *Telescopium fuscum* Schumacher are the same as Linné's for *Trochus telescopium*. *Telescopium mauritsi* Butot, 1954, is based on a worn gerontic specimen of *Telescopium telescopium* (see discussion below).

Description

Shell: Shell (Fig. 1) very large, solid, conical-trochoid, reaching 130 mm in length, 50 mm in width, and comprising 12 to 16 flat-sided whorls with an apical angle of 30–36 degrees. Protoconch unknown. Early whorls sculptured with beaded spiral cord at suture and with two smooth spiral cords (Fig. 1H). Adult whorls sculptured with three large flat spiral cords and one narrow one, and with microscopic, colabral, axial striae (Fig. 1I,J). Spiral cords sometimes disappearing with age or erosion. Suture weakly defined. Body whorl carinate in juveniles but expanded and broad in adults. Shell base with concentric cords and deep channel around columellar pillar. Aperture small, narrow, nearly tangential (perpendicular) to shell axis, with well-rounded outer and basal margins. Outer lip thin, concave; basal lip hook-like, curved towards siphonal canal. Columella convex, having callus with thick, channeled, twisted fold extending into shell aperture and up columellar axis for length of shell (Fig. 1L). Shell color uniform dark reddish-brown to black, with whitish to light brown columellar callus.

Operculum (Fig. 1M,N) corneous, small, circular, multispiral (9–17 whorls), with central nucleus, transparent and fringed at margins.

External Anatomy: Animal black-gray with dirty-white sole. Snout large, long (Fig. 3B, sn), having pair of short broad cephalic tentacles, each with tiny black eye at peduncular base. Tentacles sharply constricted at tips. Snout dorso-ventrally compressed, lined with many deep transverse wrinkles (Fig. 2B,C), very supple, extensible for considerable distance. Snout tip (Fig. 2B) with thick, whitish, fleshy pad having vertical slit-like mouth (Fig. 2C). Foot large with whitish sole having many branching, transverse furrows (Fig. 2D). Left lateral and ventrolateral sides of foot each with deep, rounded groove (Fig. 3, llg, vg); groove strongly developed on left side. Anterior mucous gland opening a narrow, deep, slit (Fig. 2D; 3B, amg) extending halfway around sides of sole and heavily ciliated within (Fig. 2E). Groove emerging from exhalant siphon long, deep, highly ciliated in both

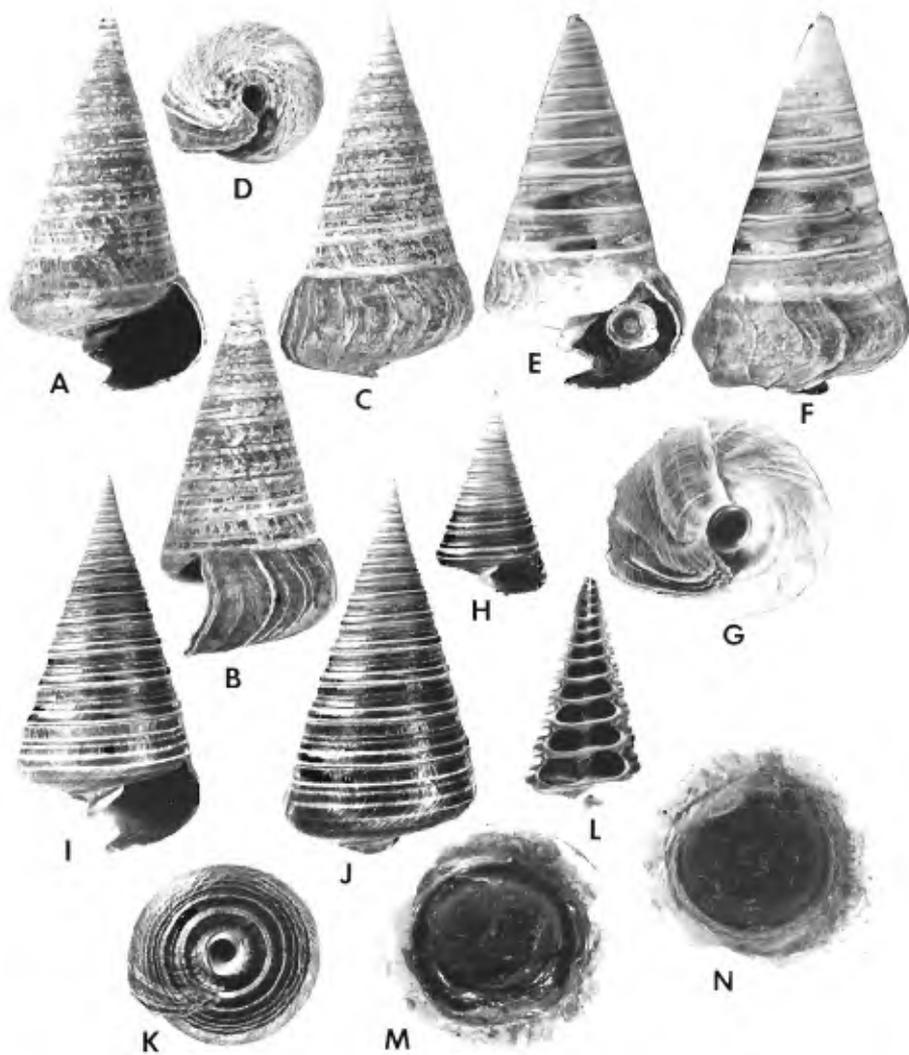


FIG. 1. *Telescopium telescopium*, shells and operculum. A–D, apertural, dorsal, side and anterior views of adult shell from Cairns, Queensland, Australia; 98.9 × 47.3 mm (USNM 795231). E–G, apertural, dorsal and anterior views of badly eroded, gerontic shell from Halmahera, Moluccas; 103 × 51 mm (USNM 837107). H, juvenile shell from Cebu, Philippines; 40.5 × 20 mm (USNM 419345). I–K, apertural, dorsal and anterior views of uneroded, cleaned shell showing sculptural details, from Batangas Bay, Luzon, Philippines; 86.5 × 37.7 mm (USNM 846507). L, shell sectioned through axis showing columellar pillar with weak interior plait. M, N, attached (M) and free (N) sides of operculum; 11.9 mm diameter.

sexes, running down right side of foot (Fig. 3A, cg) in males, ending at edge of sole; in females, ending at oval, sooty-colored, warty ovipositor (Fig. 3A, ovp) near sole margin. Ovary pale yellow; testis orange. Mantle dirty white. Dorsal half of mantle edge with small, weak, wart-like papillae (Fig. 3A, mp) and with median cleft (Fig. 3B, mc) about 5 cm deep,

separating inhalant siphon area from rest of mantle edge; ventral half of mantle edge smooth. Edge of interior of right side of mantle with thin glandular line of unknown function. Inhalant siphon thick, and interior edge with one or two orange-pigmented spots, each surrounding black, pit-like light-sensitive organ (eye) containing lens.

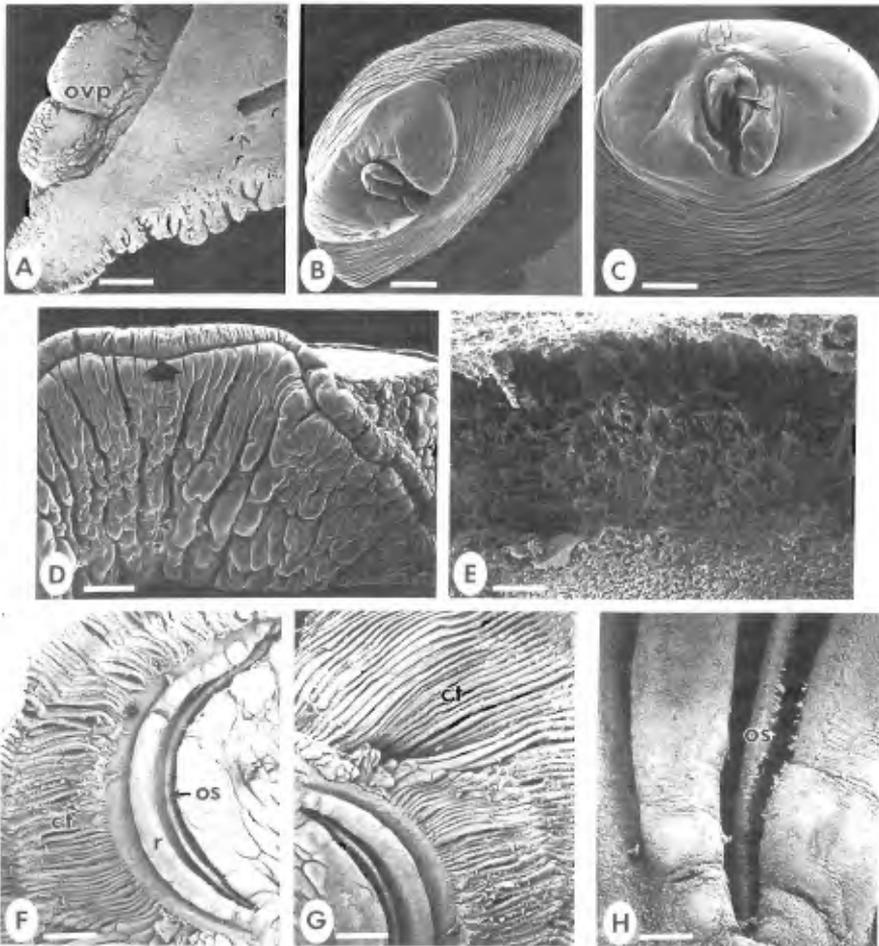


FIG. 2. *Telescopium telescopium*, SEM photographs of critical point dried tissues. A, transverse cut through right side of foot showing glandular ovipositor (ovp); bar = 0.8 mm. B, C, two views of snout tip showing pad-like tip, fleshy lips and hook-like structure at dorsal side of mouth (arrow); bar (B) = 0.9 mm, bar (C) = 0.8 mm. D, anterior edge of sole showing slit-like opening to anterior mucous gland (arrow); bar = 0.9 mm. E, dense cilia lining opening to anterior mucous gland; bar = 20 μ m. F, left side of mantle roof showing ctenidium (ct) and osphradium (os), and large ridge (r) between them; bar = 0.9 mm. G, detail of narrow posterior ctenidial filaments (ct); bar = 0.9 mm. H, detail of osphradium (os) in deep pit bordered by wide ridges; bar = 0.2 mm.

Mantle Cavity: Mantle cavity deep, spacious, occupying last two whorls. Osphradium (Fig. 2F–H, os) a short narrow ridge sunk into deep trench next to whitish, thick, crescentic ridge (Fig. 2F, r). Osphradium close to anterior part of ctenidium and about one-fourth ctenidial length. Ctenidium (Fig. 2F,G, ct) large, broad, very shallow, becoming posteriorly weaker. Ctenidium beginning about 5 mm from mantle edge, extending posteriorly for

length of mantle cavity (two whorls). Anterior part of ctenidium with narrow, equilateral triangular filaments rapidly becoming very broad and shallow on left (Fig. 3D), attaining ribbed appearance throughout much of medial and posterior parts; posterior ctenidial filaments becoming elongated, forming shallow, longitudinal ridges; raised, triangular part of each posterior filament shifts to right, adjacent to hypobranchial gland (Fig.

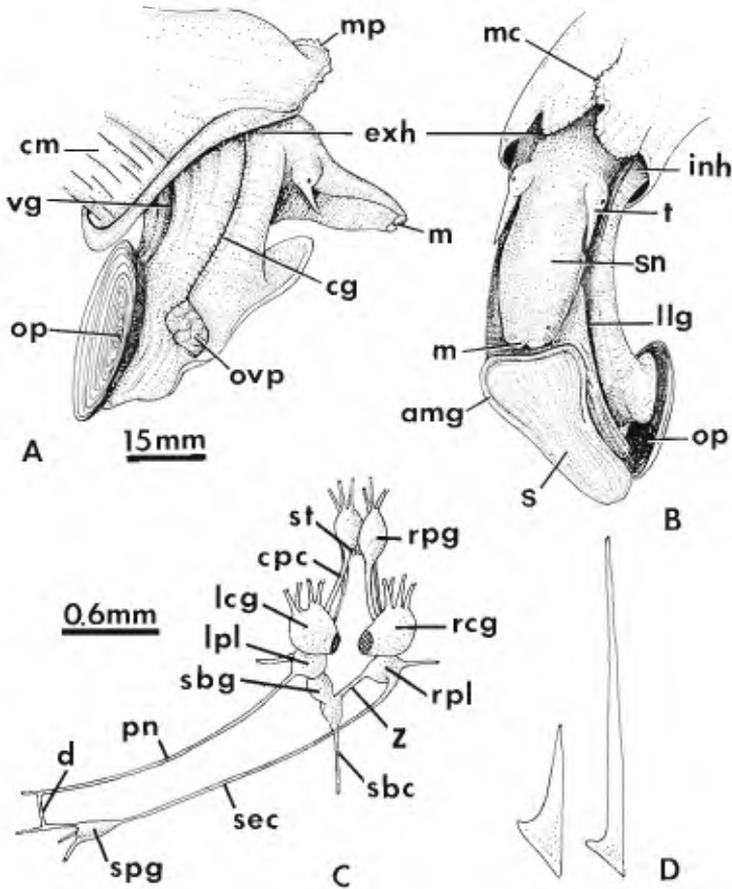


FIG. 3. *Telescopium telescopium*, anatomical features. A, right side of female showing elongate snout, large foot, ciliated groove and ovipositor on side of foot. B, anterior view of head-foot showing mantle edge, head, snout and sole; note opening of anterior mucous gland (amg) along edge of sole. C, central nervous system showing relationship of ganglia and long supraesophageal connective (sec); visceral ganglion and visceral loop not shown. D, individual ctenidial filaments from anterior (left) to posterior (right) mantle cavity. amg, opening to anterior pedal mucous gland; cg, ciliated groove; cm, columellar muscle; cpc, cerebral-pedal connective; d, dialyneury; exh, exhalant siphon; lcg, left cerebral ganglion; llg, left lateral groove; lpl, left pleural ganglion; m, mouth; mc, mantle cavity opening or inhalant siphon; mp, mantle papillae; op, operculum; ovp, ovipositor; pn, pallial nerve; rpg, right cerebral ganglion; rpl, right pleural ganglion; s, sole; sbc, subesophageal connective; sbg, subesophageal ganglion; sec, supraesophageal connective; sn, snout; spg, supraesophageal ganglion; st, statocyst; t, tentacle; vg, ventral groove; z, zygoneury.

2F, ct). Hypobranchial gland white, narrow, about one-half length of rectum, and secreting great sheets of mucus over ctenidium and rectum. Rectum very large, wide, with interior epithelium forming deep transverse ridges and complex folds, producing large surface area. Anus located well behind front of ctenidium. Pallial gonoducts open, comprising two major laminae, and parallel with rectum.

Alimentary System: Snout tip with thick, fleshy, ovate pad surrounding vertical slit-like mouth. Pair of hook-like extensions (Fig. 2C) at top edge of oral tube. Pair of small jaws in sides of oral tube. Radula (Fig. 4A–D) very small, fragile, short, about 5 mm long, comprising 80 rows of teeth, and about 3.3 percent of shell length. Rachidian tooth (Fig. 4B,C) oval, taller than broad with convex anterior end and long, dagger-like basal plate;



FIG. 4. *Telescopium telescopium*, scanning electron micrographs of radula. A, mid-section of radular ribbon with marginals spread open; bar = 200 μm . B, detail of lateral and rachidian teeth; bar = 80 μm . C, half row of radula showing elongate basal plate of rachidian tooth; bar = 90 μm . D, detail of marginal teeth showing flange on outer marginal tooth; bar = 40 μm . E, half row; bar = 100 μm .

cutting edge with spoon-shaped central cusp flanked on both sides by three or four small denticles. Lateral tooth (Fig. 4B) longer than broad, having long, wide, rectangular basal plate, pointed posteriorly, and with slightly flaring outer side; cutting edge with large spatulate central cusp, two inner denticles and three outer denticles. Marginal teeth (Fig. 4C,D) with long narrow shafts and hook-like tips having long, pointed central cusps. Inner marginal tooth with four inner denticles and three outer denticles, outer marginal tooth lacking outer denticles, but with wide flange (Fig. 4D) along outer side of tooth shaft. Buc-

cal mass very small, at snout tip. Small, paired, tubular salivary glands (Fig. 5A, sgd) beginning well anterior to nerve ring, each looping and folding along sides of buccal mass, and opening into anterior dorsal oral cavity. Anterior esophagus (Fig. 5A, eso) a simple tube having dorsal food groove, twisting at nerve ring, and becoming slightly wider behind it. Mid-esophagus (Fig. 5B) long, moderately wide, with large dorsal, ventrally located food groove (Fig. 5B, df), but not developed into esophageal gland. Posterior esophagus very long, becoming narrower posteriorly, entering right lateral side of pos-

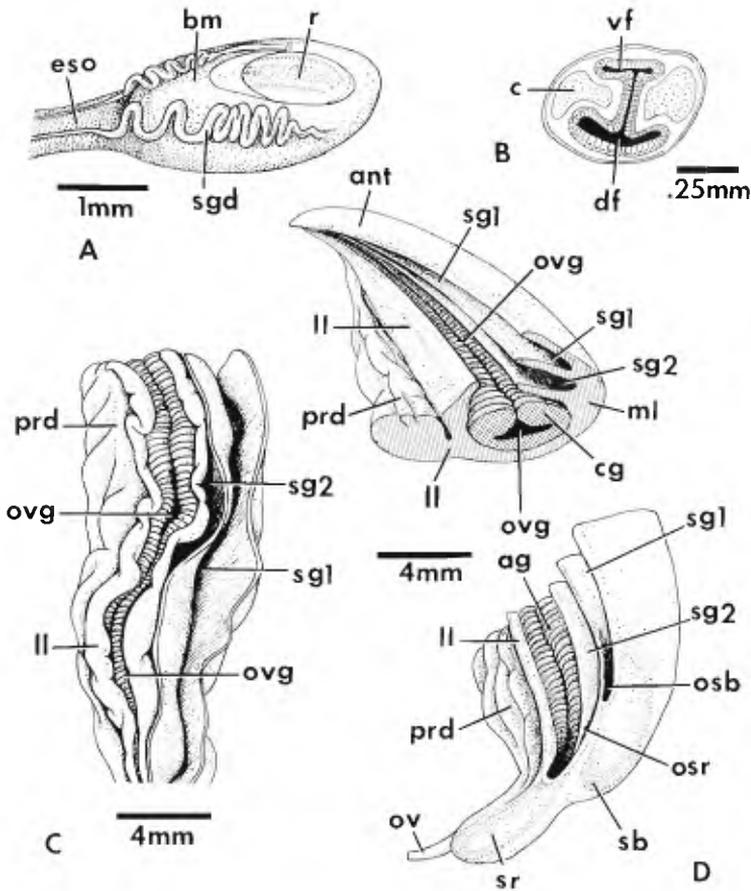


FIG. 5. *Telescopium telescopium*, anatomical features. A, representation of dorsal lateral view of buccal mass, dorsal epithelium partly opened to expose radula. B, cross-section through mid-esophagus showing dorsal food groove and cartilage-like tissue lining both sides of esophageal cavity. C, camera lucida drawing of central part of pallial oviduct. D, schematic drawing of pallial oviduct. ant, anterior part of pallial oviduct; ag, albumen gland; bm, buccal mass; c, cartilaginous tissue; cg, capsule gland; df, dorsal food channel; eso, esophagus; ll, lateral lamina; ml, medial lamina; osb, opening to spermatophore bursa; osr, opening to seminal receptacle; ov, coelomic oviduct; ovg, oviductal groove; prd, parallel ridges; r, radula; sb, spermatophore bursa; sg1, outer sperm gutter; sg2, inner sperm gutter; sgd, salivary gland; sr, seminal receptacle; vf, ventral food channel.

terior part of stomach. Stomach very large, elongate, about one and one-half whorls and comprised of three chambers: posterior sorting area with large ridge-like central pad and broad sorting area comprised of many small, transverse, epithelial folds; deep, transverse channel with centrally located cuticular gastric shield having denticulate margin; anterior portion of stomach long, tubular, consisting of very long style sac and opening to intestine. Style sac very long, adjacent to intestine, but separate from it, reaching anteriorly as far as

mantle cavity to level of pericardium. Crystalline style very long, club-shaped at gastric shield.

Reproductive System: Female pallial oviduct (Fig. 5C,D) long, comprising two complex, major laminae; lateral lamina (Fig. 5C,D, ll), fused on one side to mantle wall, and medial free lamina (Fig. 5D, ml). Medial lamina edge trifurcate, comprising three parallel minor laminae and two ciliated sperm gutters (Fig. 5C,D sg1, sg2). Inner sperm gutter (Fig.

5C,D, sg2) extending for two-thirds of lamina length, and entering duct leading to posterior seminal receptacle (Fig. 5D, sr); outer gutter (Fig. 5C,D, sg1) extending for more than two-thirds of length of medial lamina, entering into spermatophore bursa (Fig. 5D, sb) in posterior third of lamina. Lateral lamina (Fig. 5C,D, ll) bifurcate at free edge, with one lamina adjacent to oviductal groove and other lamina comprising broad, twisted parallel ridges (Fig. 5D, prd) with which trifurcate edges of medial lamina interdigitate. Glandular parts of bases of both laminae formed of paired row of numerous thick, transverse ridges, bordering deep oviductal groove (Fig. 5C,D, ovg). Albumen gland (Fig. 5D, ag) in posterior portion of oviduct. Capsule gland (Fig. 5D, cg) in thickened base of anterior third of oviductal groove. Male pallial oviduct unknown. Euspermatozoa classified in structural group 2 (Healy, 1983:65,73). Paraspermatozoa with head region and tail tuft; assigned to structural group 1 (Healy, 1986:187).

Nervous System: Central nervous system (Fig. 3C) epiathroid. Cerebral ganglia (lcg, rcg) with short commissure and with pleural ganglia (rpl, lpl) closely joined. Short connectives (cpc) between cerebral and pedal ganglia; pedal-pleural connectives thin, adjacent to pedal-cerebral connectives. Pedal ganglia (rpg) each with three nerves and with statocyst (st). Zygoneury (z) between subesophageal (sbg) and right pleural ganglia (rpl). Very long connective (sec) between right pleural and supraesophageal ganglia (spg). Dialyneury (d) between supraesophageal nerve and left pallial nerve (pn). Labial nerves very long, matching snout length. Long visceral loop extending back to visceral ganglion at posterior end of mantle floor.

Remarks

It is remarkable that no contemporary studies have been made on the anatomy and life history of this large, common prosobranch. Aside from a few notes by Prashad (1925) on the mantle cavity and ctenidium, the only published anatomical account of substance is an early paper by Berkeley & Hoffman (1834) describing the gross anatomy, but with several major errors. The nervous system was well described and figured by Bouvier (1887:145–146, pl. 8, fig. 32).

Shell: The shell of *Telescopium telescopium* is one of the most distinctive of all living prosobranchs, and is not likely to be confused

with that of any other species except *Campañile symbolicum* Iredale, 1917, with which it is convergent. The adult shell is normally 90–100 mm long, but Brandt (1974:196) has recorded a very large specimen reaching 130 mm in length. *Telescopium telescopium* is one of the few gastropods with an aperture tangential (perpendicular) to the shell axis. The anterior canal is nearly centrally located and weakly reflected dorsally (Fig. 1D,G,H). Sculptural elements occur on younger individuals (Fig. 1H–J), but are usually eroded in older shells (Fig. 1A–C). The columellar plait is strong at the aperture but becomes weaker internally (Fig. 1L).

Telescopium mauritsi Butot, 1954, described from the Sunda Straits, Indonesia, as a new Recent species with smoother sculpture, was later shown by Brandt (1974:196) to be merely a gerontic, fully adult form of *Telescopium telescopium*, with its spiral sculpture partly eroded, and covered with something that Brandt (1974:196) called “a secondary layer of unknown substance.” Budiman (1988:240) also demonstrated that the two taxa are indeed synonymous and joined by a complete series of intermediate forms. He further showed that the secondary coating of the smooth form is not part of the shell, but a deposit of an organo-metallic complex (Fe, Mn), which is a common feature of epifaunal mollusks in this habitat.

Anatomy: The ventral and lateral grooves (Fig. 3A,B, vg, llg) of the foot are unusual and not seen in other potamidids. The slit-like opening to the anterior mucous gland is unusual in extending from the edge of the propodium along both sides of the sole, for half its distance (Figs. 2D, 3B, amg). Both sexes have a ciliated groove (Fig. 3A, cg) leading from the exhalant siphon down the right side of the foot to the edge of the sole, whereas in other potamidids and cerithioideans, the groove is seen only in females. Budiman (1988:244) suggested that males use this groove to transport and introduce sperm into the female aperture. However, if spermatophores are present, as they are in all other known cerithioideans, this function is difficult to visualize. The groove in males might merely remove mucus and debris from the mantle cavity, transporting it in a mucous string to the foot margin. The ovipositor (Fig. 3A, ovp) is near the edge of the foot and, in section, is seen to comprise a glandular pad (Fig. 2A, ovp) that does not mark the entrance

to an internal chamber, as in *Terebralia* species.

The pallial light-sensitive organ appears to have a lens, but is poorly organized. It is undoubtedly homologous with similar organs in *Terebralia* species and with the well-developed pallial eyes of *Cerithidea* species (Houbrick, 1984:10–11).

The osphradium (Fig. 2F,H, os), which is quite short in relation to the large ctenidium (Fig. 2F,G, ct), is reduced to an anterior, extremely narrow ridge and is unique among potamidids in that it lies in an elongate pit (Fig. 2G,H) next to the efferent ctenidial sinus. To the right of the osphradium, the epithelium is folded into thick ridges, while to the left, lying between the osphradium and the efferent sinus, is a wide, ridge-like structure (Fig. 2F, r) of unknown function. Prashad (1925:141) noted "a large elongate gland next to the osphradium which secreted a green sticky substance when the animal was disturbed"; this is probably the ridge-like structure I observed although I did not see any secretions. The ctenidium, poorly depicted by Berkeley & Hoffman (1834:pl. 20, figs. 3,5), has been accurately described and figured by Prashad (1925:140, fig. 3a). The change in the ctenidium from anterior, triangular leaflets (Fig. 2F) to posterior elongate, parallel ridges or corrugations on the posterior pallial roof (Fig. 2G) is unusual, but a similar ctenidial modification also occurs in some *Cerithidea* species (Houbrick, 1984). As Prashad (1925:140–141) noted, the afferent ctenidial vein is absent in *Telescopium*, and hemolymph from the abdominal sinus is taken up directly by the ctenidial ridges from numerous sinuses into which the abdominal sinus divides after entering the mantle. Similar blood sinuses and vessels are known to occur in the mantle roof of *Cerithidea* species such as *Cerithidea obtusa* (Lamarck, 1822) in which the ctenidia are very much reduced (Houbrick, 1984:11).

I have interpreted the long, narrow, white area of the mantle roof between the ctenidium and rectum, which secretes great sheets of mucus that coat the ctenidium, as a hypobranchial gland. Prashad (1925:141) on the other hand, wrote that the hypobranchial gland had entirely disappeared, its place being occupied by prolongations of the ctenidial filaments, but the ctenidium does not occupy the entire area of this part of the mantle roof.

The supple, extensible snout (Fig. 3B, sn) is almost proboscis-like in function, and perhaps the longest among neotaenioglossans

(mesogastropods) of the suborder Discopoda Fischer, 1884; it was well illustrated by Berkeley & Hoffman (1834:pl. 20, fig. 1). The radula has never been well illustrated, but Das et al. (1988, pl. 3) recently depicted the cutting edges of the rachidian, lateral and some marginal teeth in an SEM photomicrograph. The rachidian tooth is unique among those of potamidids in being ovoid-triangular, and in having an elongate, very narrow basal plate (Fig. 4B,C). The contrast between the very large snout and the very small buccal mass and radula is notable. Indeed, the small radula, jaws and buccal mass also contrast with the large size of the animal, and reflect the fine particulate food eaten by it.

My observations on the arrangement of the salivary glands differ from those of Berkeley & Hoffman (1834:433, pl. 21, fig. 14), who described each duct as running back from the anterior buccal mass, tightly coiling and then joining the other duct just below the apex of the radula. I noted a pair of salivary glands, each originating in front of the nerve ring, coiling anteriorly, and exiting at the anterior end of the buccal mass (Fig. 5A, sgd), but did not find a connection between the two glands as depicted by Berkeley & Hoffman.

The large, complex stomach of *Telescopium* is typical of members of the Potamidinae, and is highly adapted to deal with the fine particulate matter ingested. The gastric shield, well illustrated by Berkeley & Hoffman (1834, pl. 20, fig. 6), is unusual in having a denticulate margin. The exceptionally long crystalline style (about 50 mm long in adults), is held completely separate from the intestine in the heavily ciliated style sac (Alexander & Rae, 1974:56). The dilated, club-like posterior end of the style was noted by Seshaiya (1932:171). The style follows and parallels the intestine as far forward as the level of the mid-region of the mantle cavity. Alexander & Rae (1974) made a detailed study of the structure and formation of the crystalline style of *Telescopium*, and noted that the style persists even when the animal is starved for considerable periods. They showed that the style does not vary in size during the tidal cycle, unlike those in many style-bearing pelecypods in which the style might break down and reform, and that the style is present even in the smallest specimens of *Telescopium telescopium*. Enzymatic activity of the style of *Telescopium telescopium* has been studied by Alexander et al. (1979).

The rectum is characterized by being very

wide and by having its interior walls folded into complex ridges and pockets, thus increasing its surface area and perhaps functioning as a compactor of the ovoid fecal pellets.

The large, complex, pallial oviduct (Fig. 5C,D) is basically an open, slit tube, comprising two laminae, the lateral (right) one attached to the mantle roof (ll), and the medial (left) one (ml) free—a typical cerithioidean plan. However, it departs from this layout in its complexity, having the two major laminae subdivided to form five minor parallel laminae, and in having two sperm gutters (sg1, sg2) in the major lamina. The tripartite condition of the pallial oviduct mentioned by Berkeley & Hoffman (1834:435), who throughout their text, refer to the oviduct as “the matrix,” is probably a misinterpretation, for there are really three well-defined minor laminae on the medial lamina and two minor laminae on the lateral lamina, the fifth one being broad. Berkeley & Hoffman (1834) noted that the oviduct consisted of “. . . three strong folds which fit over a thick longitudinal wrinkled rib [the fifth, broad lamina] so closely that it appears like a simple sac and requires a minute inspection to ascertain the real structure.” This description is fairly accurate, but incomplete inasmuch as it mentions neither the bursa or seminal receptacle nor the parallel ridges (prd) of the fifth, broad lamina next to the lateral lamina. I found it very difficult to interpret the arrangement of the pallial oviduct in preserved specimens of *Telescopium telescopium*, but dissections of several live specimens have clarified the complex details of the ducts and chambers within the laminae comprising the pallial oviduct; nevertheless, much remains unknown regarding the function of these parts. A diagram of the pallial oviduct is shown in Figure 5D. The medial lamina has undergone extensive modification in that it has become longitudinally trilobed, having two sperm gutters. The oviductal groove (ovg) lies between the inner lobe of the medial lamina and the attached lateral lamina, and it is here that the eggs presumably are fertilized, surrounded by albumen in the albumen gland (ag), encapsulated in the capsule gland (cg), and moved anteriorly to the ciliated groove on the foot and thence to the ovipositor. The edge of the lateral lamina (ll) is bifurcate, and one ridge forms small parallel longitudinal folds (prd) with which the inner lobe of the medial lamina interdigitates. Thus, although the pallial oviduct is anatomically open, it is functionally

closed except anteriorly, owing to the close juxtaposition of the laminae. The pair of transverse glandular ridges lying along the length of the base of the oviductal groove undoubtedly comprises the albumen (ag) and capsule glands. This area was thought by Berkeley & Hoffman (1834:435) to function as “many little bags for the reception of eggs”; although it is a transport area for eggs, the area should not be construed as a pallial brood pouch. These paired transverse ridges on each side of the oviductal groove also occur in members of the Turritellidae (Fretter & Graham, 1962:366; Carrick, 1980).

The nervous system (Fig. 3C), well described by Bouvier (1887), is similar to those of *Terebralia* species, but differs from them in the greater length of the connective (sec) between the supraesophageal and right pleural ganglia (see Bouvier, 1887, pl. 8, fig. 32). Both zygoneury and dialyneury are well established in *Telescopium*.

Ecology: Several good papers exist on aspects of the ecology of *Telescopium telescopium*. These include the studies of Lasiak & Dye (1986) in Queensland, Australia, the work of Wells (1986) in Western Australia, and studies made at Indonesian sites in Java, the Moluccas, and Irian Jaya (Western New Guinea) by Budiman (1988). Other, less comprehensive accounts include some ecological notes of Butot (1954) on Prinsen Island in the Straits of Sunda, Indonesia, the observations of Benthem Jutting (1956) in Java, and those of Brandt (1974) in Thailand. The information from these studies and my own is summarized below.

Telescopium telescopium lives intertidally on soft, nearly liquid, muddy substrates associated with mangrove forests in which it is frequently found in shady places in the more exposed parts of the mangrove and around the runoff gulleys common in these habitats. A good depiction of an individual plowing through muddy substrate in its natural habitat is given by Coleman (1981:36, fig. 81). The animals are shy to any movement and quickly retreat into their shells whenever approached. This shyness was also recorded by Berkeley & Hoffman (1834:431), who reported great difficulty in making drawings of the living animal. I observed *Telescopium telescopium* living in a mangrove habitat at Magnetic Island, Queensland, Australia, in which it coexists with large populations of *Terebralia palustris*. In this population, many individuals ranging

from adults to young snails (less than 5 mm long) occurred together, although the smallest appeared to prefer the higher ground around the bases of mangrove roots. Lasiak & Dye (1986:174) and Budiman (1988:240) observed the same phenomenon at Northern Australian and Indonesian sites, respectively, the latter author pointing out that both adults and juveniles are deposit feeders, having the same radular morphology. This is unlike the radular dimorphism seen between adults and juveniles of *Terebralia palustris*, and suggests that the segregation of adults and juveniles is not due to trophic factors. Budiman (1988) and Shokita et al. (1984) noted that *Telescopium telescopium* had a restricted distribution mostly at the middle and landward edge of the mangrove intertidal zone.

According to Lasiak & Dye (1986:174) and Budiman (1988:242), *Telescopium telescopium* is active only when exposed by low tide, withdrawing into its shell whenever covered with water. Lasiak & Dye (1986:178) demonstrated that movement in *Telescopium telescopium* was related to the tidal regime and was not due to endogenous factors. The animal becomes active shortly before the ebbing tide uncovers the substrate, when it emerges from its partly burrowed position and begins creeping on the exposed mud. All activity ceases during hours of high tide, when the animals burrow into the muddy substrate, taking a semi-vertical position just below the surface (Budiman, 1988:244). Benthem Jutting (1956:440) noted that the tip of the spire projected when the shell was partly buried in the mud. During one tidal cycle *Telescopium telescopium* might be under water for as long as three or four hours (Alexander et al., 1979:88).

Telescopium telescopium is a deposit feeder, using its long, extensible snout to engulf fine mud and detritus from the surface of mudflats during low tide. Lasiak & Dye (1986:174) maintained that *Telescopium telescopium* can feed only at low tide; this observation has been confirmed by Alexander et al. (1979:88), who have shown that there are reduced enzyme levels in the crystalline style at high tide, in contrast to increased levels during low tide, indicating a fasting mode whenever snails are covered by water. Nevertheless, Budiman (1988:244) opined that *Telescopium telescopium* can maintain its feeding activity from its burrow by using its long, extensible snout, even when covered by high tide. This possibility led Budiman (1988:244) to suggest

that exposed activity periods were more vital for sexual activity than for feeding.

Telescopium telescopium is able to tolerate a wide range of salinities, from 15 ppt to full-strength sea water (Alexander & Rae, 1974:56), and can withstand a considerable degree of desiccation. During dry, inactive periods, individuals frequently cluster together in shady refuge microhabitats beneath the mangroves, for extreme temperatures can result in high mortality. Although high temperatures might cause mortality, this species can endure astonishing periods of desiccation: Benson (1834) recorded that animals collected in India endured a trip to England lasting more than six months, with only occasional immersions in sea water, and lived.

Predation has not been observed, and it is doubtful that large, thick-shelled adults can be attacked successfully and eaten by any predators with the exceptions of the large, powerful mud crab, *Scylla serrata* (Forskål), and man, who is known to use *Telescopium* for food in Southeast Asia, Indonesia, Borneo and the Philippines (Tryon, 1882:259; Benthem Jutting, 1956:441; Brandt, 1974:196). Juveniles are more likely to fall victim to the predatory activities of mangrove crabs, birds and mammals. On the southeastern coast of India, this species is seldom eaten by man, but is exploited in the lime industry. Kasinathan & Shanmugam (1988) have documented the overexploitation of *Telescopium* in this region: in a period of six months, nearly 22 large bags (500–900 kg/day) of *Telescopium*, each weighing 70–80 kg, were collected every week from the Pithavaram mangroves and Vellar Estuary, and sent to the lime industry.

Reproductive Biology: Budiman (1988:244) noted that sexual pairing occurred at all times during periods of activity at low tide, when many paired individuals were seen. According to his observations, the male holds the female's shell with his foot, manoeuvring her so as to position her shell aperture against his shell aperture. When this position is attained, the male puts his head and foot into the female's shell aperture. Budiman (1988) suggested that sperm might be transferred by means of the groove on the right side of the male's foot, but in light of the fact that other potamidids produce spermatophores (Houbrick, 1984:7; this study), sperm transfer probably is effected by production and transfer of spermatophores either along the male groove or by pallial currents, as has been ob-

served in other cerithioideans (Houbrick, 1973).

Spawn masses of *Telescopium telescopium* were not observed in the field nor were any preserved spawn examined. A good description of the spawn and spawning behavior of *Telescopium telescopium* was published by Ramamoorthi & Natarajan (1973), who studied this species at Porto Novo, India. They recorded that in its natural habitat on the mudflats of the Vellar estuary, this animal spawned at the low water mark from April to July, but always just below the water mark. During this period snails were frequently seen associated in pairs. Animals kept in finger bowls and in experimental ponds on the mud flats attached their egg masses to the sides of bowls and to cement slabs and stones, under water.

Because Ramamoorthi & Natarajan (1973) did not mention its use during egg laying, the exact function of the ovipositor during this process remains unknown. The ciliated groove on the right side of the female's foot begins just below the aperture of the pallial oviduct and terminates at the ovipositor, passing behind and under it (Fig. 3A, cg). The glandular composition of this large, padlike structure (Fig. 2A, ovp) suggests that it contributes to the secretion of the gelatinous coat surrounding both the strings of egg capsules and perhaps also to the outer coat of the gelatinous strings. Spawn is deposited in a continuous, compact ribbon, folded closely upon itself such that the spawn mass is long and sheet-like upon completion (Ramamoorthi & Natarajan, 1973:159, figs. 1, 2). These authors noted that the egg mass is covered by a transparent, gelatinous matrix and that the eggs are light blue. Egg masses are very large, varying from 24–49 cm long and from 1.5–2 cm wide ($n=20$), and each egg mass contains an average of 50,000 eggs. Individual eggs are about 125 μm in diameter, and are surrounded by a fluid, presumably albumen, and a thin, transparent capsule of 200 μm (Ramamoorthi & Natarajan, 1973:158). At Porto Novo, free-swimming veliger larvae with smooth, transparent shells and a blue tint hatched from the egg masses 96 hours after spawning. To my knowledge, no other observations have been made on spawning or larvae, and nothing is known of the duration of the free-swimming veliger stage prior to settlement, or of growth and longevity of adults. Because even the protoconchs of tiny juveniles are very eroded, it is impossible to infer

the length of planktonic life by observing the size and sculpture of protoconch-2, but the small diameter of the egg capsules and their great numbers in a spawn mass suggest a long planktotrophic larval stage.

Fossil Record: Fossils of *Telescopium telescopium* occur in Upper Miocene through Holocene strata. This species has been found in many localities throughout the Indonesian archipelago, in which it has been recorded from the Upper Miocene of Java (K. Martin, 1884: 145–146; 1889:220, pl. 33, fig. 509; Wissema, 1947:46) and E. Borneo (Wissema, 1947:48); from the Miocene of Java and Timor (Tesch, 1920:58–59, pl. 132, fig. 191); from the Quaternary of Nias (Wissema, 1947:47); the Pliocene of Nias (Tesch, 1920:59), Timor and Java (Wissema, 1947:46–47); from the Pleistocene of E. Java and Timor (Wissema, 1947); and from the Holocene of E. Sumatra and S.W. Celebes (for more detailed locality data, see Regteren Altena, 1941:13–14, and Wissema, 1947:46–47). In the Philippines, *Telescopium telescopium* has been recorded from the Miocene Vigo Formation (Popenoe & Kleinpell, 1978: pl. 2, fig. 13) and from the Upper Miocene of the Tartaro Formation of Luzon (Kanno et al., 1982:95, pl. 17, fig. 7). K. Martin (1889) described two fossil *Telescopium* species from the Pliocene of Java, *Telescopium jogjacartensis* and *Telescopium titan*, which are morphologically very similar to Recent *Telescopium telescopium*, and possibly conspecific with it. Oostingh (1935:52) has recorded several localities for *Telescopium titan* on Java.

Distribution: This species occurs in suitable habitats in the western Pacific from the Ryukyus south through Taiwan (Tapparone Canefri, 1883:58), the Philippines, New Guinea and throughout tropical Australia (Fig. 6). It is found throughout the Indonesian archipelago and the coasts of Southeast Asia. In the Indian Ocean it occurs in the Mergui archipelago, the Andamans, and along the coasts of India and Ceylon west to Karachi. It has been cited from Reunion (Deshayes, 1863:95) and Madagascar (Rajagopal & Mookherjee, 1982:31), but the latter record is probably incorrect, because this region has been well collected and there are no other records. Although cited from both the Gulf of Oman (Bosch & Bosch, 1982:47), and the Persian Gulf (Smythe, 1979:65), these records were based on dead or subfossil specimens. A single museum record from the

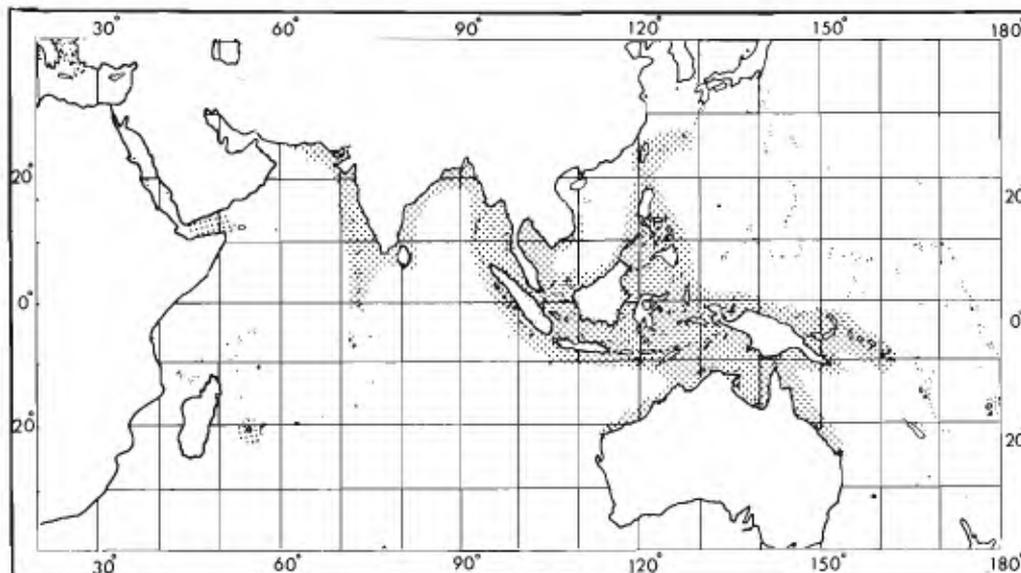


FIG. 6. Geographical distribution of *Telescopium telescopium*.

Gulf of Aden (ANSP 191200) needs confirmation.

Material Examined: ARABIA: Gulf of Aden, near Aden (ANSP 191200). PAKISTAN: Majia Id, Karachi (MCZ 255730); Baba Id, Karachi (CNHM 69795); Patiani Creek, Karachi (USNM 633063); near Karachi (USNM 693979; AMNH 109797). INDIA: Calcutta (CNHM 5070; USNM 18585; MCZ 135602; AMNH 32128); Vengurla, N of Goa (USNM 443203); Colaba, Bombay (USNM 443317); Bandara, N of Bombay (USNM 443623); Bombay (ANSP 231872; AMNH 135320); Mulund, Bombay (AMNH 104797); Juhu, Var-sava (USNM 598139, 611579); Matapalem Creek, Godavary Estuary, Andhra, Pradesh (MCZ 260876); Cochin Harbor, Kerala (ANSP 303822); Canning, Bengal (USNM 638074). BANGLADESH: Burigoalni Sundarbans (MCZ 256420). CEYLON: Trincomallee (MCZ 101297). THAILAND: Pattani (MCZ 238425); Lem Ngob, Trad (USNM 384178, 776705); Narativat (USNM 776707); Lem Sing, Chant-aburi Prov. (USNM 419159; MCZ 238375); Goh Phi Phi (Pipidon) (USNM 661487); Chantabun (USNM 529520); Grabi (USNM 776706); Laam Yamu, E. Phuket Id (ANSP 285908, 286210). MALAYA: Singapore (ANSP 18003); Kuala Selangor, Selangor, Malaysia (ANSP 320715). VIET NAM: Nha Trang Harbor (AMNH 156581). INDONE-

SIA: Tjiperwagaran, Bantam, Java (USNM 260571); Pasir Putih, Jailolo District, Halma-hera, Moluccas (USNM 837107); Papajato River, Celebes (USNM 244076). BORNEO: road to new port, Port Swettenham, Selangor, Malaysia (CNHM 140958); NE corner Palau Lumut, Port Swettenham, Selangor, Malaysia (USNM 661019); Po Bui Id, Sandakan, N. Borneo (USNM 244066; AMNH 150838); Sempora, N. Borneo (USNM 658194); Tan-jong Aru, Jesselton, N. Borneo (USNM 658594); W Marudu Bay, N. Borneo (USNM 632215; ANSP 255776); Jesselton, N. Bor-neo (ANSP 275078). NEW GUINEA: Daugo Id, Papua (CNHM 140290); Bosnek, Sorida, Papua (AMNH 99187); E Kaipori Village, Koeroedoi Id, Geelvink Bay, W Irian (ANSP 206509). AUSTRALIA: Bowen, Queensland (ANSP 234264); Cooktown, Queensland (ANSP 195583); Cairns, Queensland (USNM 603491, 795231; ANSP 204885); Cockle Bay, Magnetic Id, Queensland (USNM 828833, 828804, 842987); Broome, Northern Territory (ANSP 232006; MCZ 265997). PHILIPPINES: E of Nagsulu, Batangas Prov, Luzon (ANSP 229709); Batangas Bay, Luzon (USNM 846507); Camp Wallace, La Union, Luzon (USNM 233100); Bacoor Bay, Luzon (USNM 244060); Mariveles, Luzon (USNM 283258); Borogan Village, E side Samar (ANSP 223068); Mangarin, Mindoro (USNM 542677); Iloilo, Panay (USNM 385080,

383986); Banio Luloc, Panay (USNM 419549); mouth of Jardau River, Gimaras (USNM 243882); Tiglaugan Pt, Cadiz, Negros (USNM 313027); Balolan, Negros (USNM 313233); Marongas, Jolo (USNM 233238); Port Dupon, Leyte (USNM 232964); Enrique Villanova, Siquijor (USNM 617818); Cebu, Cebu (USNM 244071); Palawan (USNM 303929); Nakoda Bay, Palawan (USNM 240238); Tilig, Lubang (USNM 243981); Panabuban Bay, Mindanao (USNM 244075); Dos Amigos Bay, Tawi Tawi Gp (USNM 214067); Port Tataan, Tataan, Tawi Tawi (USNM 244002, 244067). RYUKYUS: Miyako (CNHM 68787).

TEREBRALIA SWAINSON, 1840

Terebralia Swainson, 1840:315 (Type species, by subsequent designation (Sacco, 1895:51), *Strombus palustris* Linné, 1758.

Diagnosis: Shell moderately large, solid, brown, with numerous flat-sided whorls, and sculptured with spiral cords and axial ribs; aperture ovate, outer lip sweeping in arc to join moderately-developed anterior canal, frequently forming complete peristome. Columella with paired internal plaits; internal palatal teeth opposite varices. Operculum corneous, round, multispiral with central nucleus. Mantle edge at inhalant siphon with pit-like light-sensory organ. Snout broad, muscular, with large buccal mass. Anterior pedal mucous gland opening slit-like, extending halfway down sides of sole. Radula taenioglossate; rachidian tooth rectangular with large central cusp; outer marginal tooth with wide lateral lamella. Stomach elongate, with gastric shield, and long style sac. Right side of foot in females with large, complex ovipositor. Pallial oviducts with medial fusion. Nervous system epiathroid, zygoneurous. Spermatozoophores crescentic, having transverse ridges. Eggs deposited in coiled gelatinous ribbons.

Remarks: The genus *Terebralia*, *sensu stricto*, can be traced with relative certainty to the Early Miocene. *Terebralia bidentata* (DeFrance in Grateloup, 1832), from that epoch, differs little in shell morphology from Recent *Terebralia* species. Cossmann (1906:126) cited the genus from the Late Cretaceous (Maastrichtian), but the fossils from that period are at best equivocal, and it is unlikely

that they belong to *Terebralia* as now understood. The genus was common in the Tethys Sea, from which it spread into the tropical Atlantic and Indo-Pacific Oceans. According to Woodring (1959:178), *Terebralia* species were widely distributed in Tertiary seas until about the end of the Miocene, but are today restricted to the tropical Indo-West-Pacific Oceans. There are several well-authenticated American Miocene species from the Caribbean region, such as *Terebralia dentilabris* (Gabb, 1873) (see Hoerle, 1972:20–21, pl. 1, figs. 9–11). Although many fossil species have been correctly attributed to *Terebralia*, numerous others must be removed from this genus. For example, K. Martin (1916) described seven species from the Upper Miocene of Java, none of which should be allocated to this genus, inasmuch as they are more like cerithiids or batillariids. A large number of fossils that appear to be true *Terebralia* species were described from the Late Miocene of Piemont, Italy, by Sacco (1895), and numerous typical *Terebralia* taxa have been described from Neogene formations of Southeast Asia. The numerous described Tertiary species have not been critically reviewed. Of the three living species, *Terebralia palustris* and *Terebralia sulcata* have fossil records going back to the Miocene (see species accounts in this paper for details).

In the older literature, *Terebralia* species are sometimes assigned to the genus *Potamides* Brongniart, 1810, or *Pyrazus* Montfort, 1810. *Terebralia* was placed in synonymy with *Pyrazus* by Adams & Adams (1858:291). Tryon also (1882:250) considered *Terebralia* to be a synonym of *Pyrazus*, which he regarded as a subgenus of *Potamides*. The genus *Potamides* was proposed to accommodate some Paris Basin fossils, but the shell of the type species of *Potamides*, *Potamides lamarckii* (Brongniart, 1831), does not in the least resemble those of living *Terebralia* species, and although related, is probably not congeneric with them. It is, however, very probably a member of the family Potamididae. The type species of the genus *Pyrazus*, *P. baudini* Montfort, 1810 (now known as *P. ebininus* [Bruguère, 1792]), is herein considered a member of the subfamily Batillariinae, based on its anatomy (Houbrick, pers. obs.), and not closely related to *Terebralia*.

The anatomical information on *Terebralia* species presented herein is based primarily upon detailed dissection and study of *Terebralia sulcata*. The other two species, *Tere-*

bralia palustris (the type species) and *Terebralia semistriata*, are not known in such great detail. The order of presentation below begins with brief morphological descriptions of *Terebralia palustris* and *Terebralia semistriata*; this is followed by a more detailed description of *Terebralia sulcata*.

Terebralia palustris (Linné, 1767)
(Figs. 7–9)

Strombus palustris Linné, 1758:213 (Seba figure [1765, pl. 50, figs. 13, 14] here selected to represent lectotype; Type locality: here restricted to Singapore); Dodge, 1956:291.

Trochus trisulcatus Forskål, 1775:126 (Lectotype: Zoological Museum of the University of California, Berkeley, 114 × 50 mm; Type locality: Lohaia, Red Sea). Yaron et al., 1986.

Strombus agnatus Gmelin, 1791:3521 (Seba figure [1765, pl. 50, fig. 19] here selected to represent lectotype; Type locality: not given).

Cerithium palustre Bruguière, 1792:486 (Seba figure [1765, pl. 50, figs. 13, 14] here selected to represent lectotype; Type locality: East Indies); Kiener, 1841: 81–82, pl. 1.

Cerithium carnicum Perry, 1811: pl. 35, fig. 3 (Perry figure [pl. 35, fig. 3] here selected to represent lectotype).

? *Cerithium crassum* Lamarck, 1822:294 (*nomen dubium*).

Cerithium sulcatum Bruguière [*sic*]. Kiener, 1841: pl. 27, figs. 1, 2, 2a (in part: is mixture of three species; only fig. 2a is *Terebralia palustris*).

Pyrazus palustris (Linné). H. & A. Adams, 1854:291, pl. 30, figs. 8, 8a, 8b; Taparone Canefri, 1874:41.

Cerithium (Potamides) palustre (Linné). Sowerby, 1855:883, pl. 185, fig. 261.

Potamides (Pyrazus) palustris (Linné). Martens, 1880:281; Tryon, 1887:160, pl. 32, figs. 41, 42.

Potamides (Terebralia) palustris Bruguière. Fischer, 1884:681, fig. 447; K. Martin, 1907:217; Oostingh, 1925:46–50.

Potamides (Tympantonus) palustris (Linné). Tryon, 1887:160, pl. 32, figs. 41, 42.

Cerithium palustre (Linné). Kobelt, 1898:35, pl. 8, figs. 1, 2; pl. 9, figs. 1, 2.

Clava caledonica Jousseaume, 1884:191, pl. 4, fig. 12 (Syntypes: MNHNP; Type locality: New Caledonia).

Potamides Caledonicus (Jousseaume). Tryon, 1887:160, pl. 23, figs. 43, 44.

Cerithium (Pyrazus) palustre (Linné). Kobelt, 1890:35–37, pl. 8, figs. 1, 2; pl. 9, figs. 1, 2.

Potamides (palustre var. ?) tryoni Kobelt, 1895:169, pl. 32, fig. 1 (no type; refers to *C. caledonicum* Tryon, 1887, pl. 32, fig. 43).

Cerithium (Pyrazus) caledonicum (Jousseaume). Kobelt, 1895:169, pl. 32, fig. 8.

Potamides palustris (Linné). Martens, 1897: 176; Tomlin, 1932:317.

Terebralia palustris (Linné). Cox, 1927:84, pl. 18, fig. 4; Regteren Altena, 1941:15–16; Rensch, 1934:338; Benthem Jutting, 1959:106; Brandt, 1974:194–195, pl. 14, figs. 57, 58.

Synonymic Remarks: This species is the type species of *Terebralia*, by subsequent designation of Sacco (1895). A lengthy history of the synonymy of *Strombus palustris* has been published by Dodge (1956). Although it is not in the Linnaean Collection in London and was not described in the "Museum Ulricae", Dodge (1956:291–292) pointed out that the identification of this species by the immediate followers of Linné must have been based on the recognizable figures of the *palustris* of authors in its synonymy. The figure references of Linné (1758) all show *Strombus palustris* with sufficient accuracy to define it, and Seba's (1765) pl. 50, figs. 13, 14 are here selected to represent the lectotype. The type locality, "In Indiae paludibus," is here restricted to Singapore. Yaron et al. (1986:187–188, fig. 30) have found and figured the type of *Trochus trisulcatus* Forskål, identifying it as a junior synonym of *Terebralia palustris*. Although the types of *Strombus agnatus* Gmelin and *Cerithium palustre* Bruguière are missing, they both share the same figure references with *Strombus palustris* Linné, and are obviously conspecific with it. The figure of *Cerithium carnicum* Perry is sufficiently characteristic to identify it unequivocally with *Terebralia palustris*. Lamarck (1822) did not supply his description of *Cerithium crassum* with figure references, but noted that: "It is related to the *cerithium [sic] palustre* but differs from it by its aperture which is very narrow, the right margin being much inverted." His description is unclear and because there are no figures or types, the name should be regarded as a *nomen dubium*. Although *C. crassum* appears in virtu-

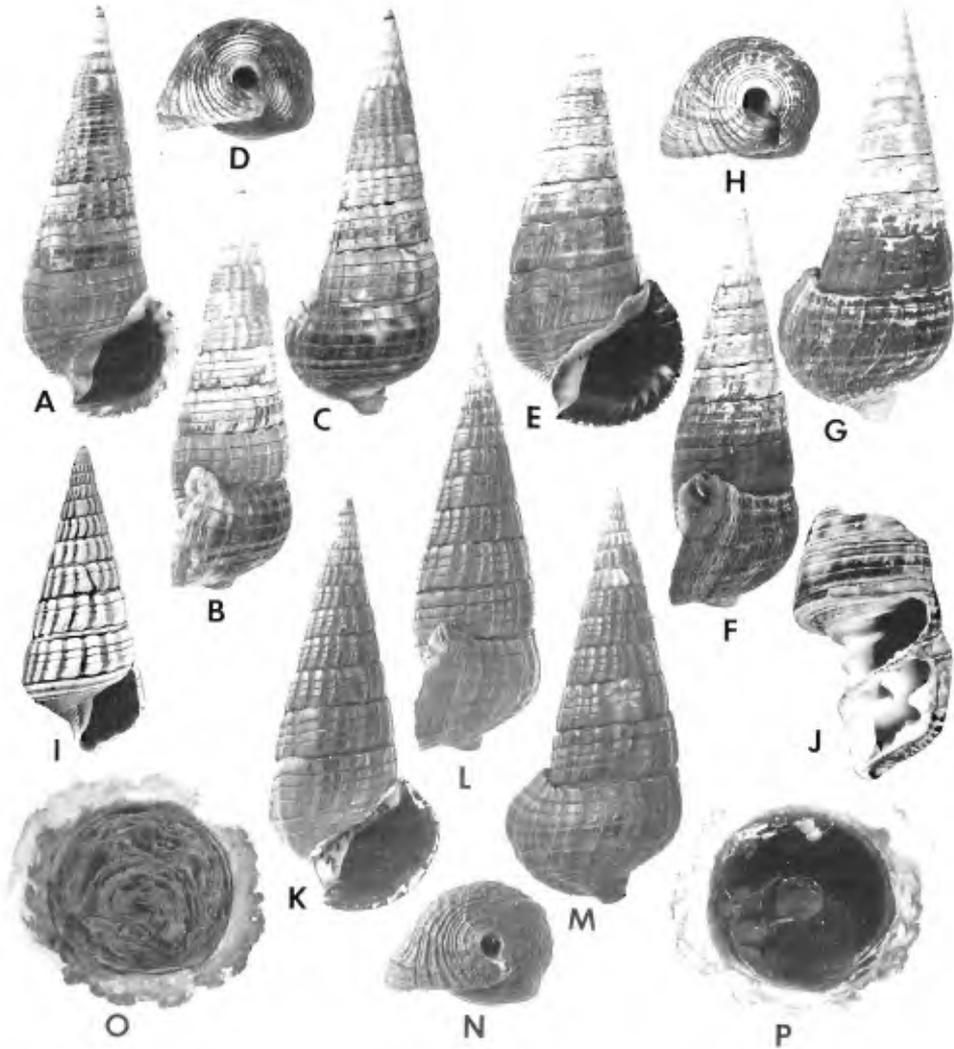


FIG. 7. *Terebralia palustris*, shell and operculum. A–D, adult shell from Zanzibar, Zanzibar; 103.1 × 36.9 mm (USNM 604453). E–H, adult shell from Pulau Panjo, Sumatra, Indonesia; 121.9 × 49.7 mm (USNM 661891). I, juvenile shell from Magnetic Island, Queensland, Australia; shell whitened with ammonium chloride to enhance sculptural details (USNM 828805). J, shell fragment with aperture removed to show columellar and palatal folds; 58.7 mm long (USNM 808336). K–N, adult shell from Anse Vata, New Caledonia; 61.9 × 23.3 mm (USNM 835665). O, P, free and attached sides of operculum; 15.7 mm diameter.

ally every synonymy of *Terebralia palustris* (see Dodge, 1956:291), it is cited in the above synonymy with a query. *Clava caledonica*, described from New Caledonia, is merely a dwarfed form of *Terebralia palustris* (see below). Kobelt's (1895) description of *Cerithium tryoni* was based upon one of the figures of *Clava caledonica* presented by Tryon (1887).

Description

Shell: Shell (Fig. 7) elongate, thick, solid and turreted, comprising as many as 20 flat-sided whorls and reaching a length of 190 mm. Protoconch unknown. Early whorls (Fig. 7I) sculptured with strong, colabral axial ribs; spiral incised lines appearing on ninth or tenth whorl, gradually increasing to three in num-

ber. Adult whorls sculptured with four equal-sized, flattened spiral cords, three deep spiral grooves, and overlain by broad axial ribs, producing weak, square nodules. Varices broad, prominent and randomly distributed. Suture deeply impressed. Body whorl large, wide, with large varix opposite outer lip of aperture. Shell base moderately constricted, sculptured with many small spiral cords and numerous, very small, weak axial striae. Aperture ovate, grooved within; columella concave with thick callus and weak plait at anal canal; outer lip sinuous and flaring at anal canal (Fig. 7B, F, L), sweeping in broad arc to anterior canal, although not joining it. Anterior siphonal canal (Fig. 7D, H, N) short, tubular and nearly closed at junction of outer lip. Columellar pillar with two internal folds (Fig. 7J). Palatal tooth opposite each external varix. Shell brown to bluish-black, occasionally with wide lighter bands; aperture glossy brown, columella light tan. Operculum (Fig. 7O, P) corneous, circular, multispiral with central nucleus, transparent and tattered at edge.

External Anatomy: Head-foot dark brown; snout and tips of cephalic tentacles black. Head with muscular, broad, transversely-lined snout, and with broad cephalic tentacles, each bearing large eye at peduncular base. Foot large, having white sole and large anterior mucous gland extending around anterior half of sole periphery. Dorsal surface of foot (mesopodium) deeply grooved, conforming to heavy columellar plaits of shell. Ciliated groove on right side of foot in females, emerging from anterior pallial oviduct and leading to very large, bulbous, white ovipositor near base of foot; ciliated groove at posterior end of ovipositor opening into large, cylindrical, jelly-producing chamber in inner right part of foot, beneath ovipositor. Inner ovipositor chamber filled with plug of tissue arising from posterior wall of chamber; chamber extending posteriorly, terminating under operculum. Mantle green; mantle edge bifurcate with scalloped outer fringe and inner row of 15–20 papillae. Inhalant siphon marked by indentation. Papillae at inhalant siphon white-tipped. Inhalant siphon thick, muscular, with black undersurface at edge; inner surface of inhalant siphon with black-pigmented area surrounded by yellowish ring and with white, deep, semicircular light-sensitive pit, bordered with transverse ridge. Light-sensitive pit with white, villous epithelium comprising many small indentations and tiny pits, under-

lain by large vacuolated cells over layer of darkly pigmented cells, and forming pigment cup. Sensory area of inhalant siphon innervated by extension of left mantle nerve. Exhalant siphon black, bulging beyond mantle edge.

Mantle Cavity: Mantle cavity very deep, occupying last two whorls. Osphradium comprising extremely thin, straight ridge about 0.5 mm wide, with microscopic, transverse indentations along edge, extending two-thirds of ctenidial length. Osphradium separated from ctenidium by broad epithelial membrane. Ctenidium very broad, shallow, comprising boomerang-shaped filaments, each about 6.5 mm long. Leading (left) edge of each filament with thin, vitreous rod-like structure and with many small transverse muscle fibers; right side of filament gradually becoming long and shallow; tip of leading edge with small indentation. Hypobranchial gland thick, broad, white, transversely ridged, secreting copious mucus. Intestine large, broad. Pallial gonoducts open, comprising two parallel laminae attached to mantle roof.

Alimentary System: Large buccal mass; radula dark brown anteriorly, having long alary processes. Pair of large jaws (1.7 mm long) with scale-like cutting surfaces, nearly fused where upper lateral edges meet in oral aperture.

Radula (Fig. 8) dimorphic owing to ontogenetic change between juveniles and adults. Adult radular ribbon (Fig. 8C, D) robust, broad, brown at anterior end, about one-fourth of shell length. Rachidian tooth (Fig. 8D) rectangular, having nearly smooth cutting edge with weak central, dull point; rachidian tooth much broader than high with very narrow basal plate; rachidian tooth asymmetrically orientated at 45-degree angle to other teeth. Lateral tooth (Fig. 8C, D) large, broadly massive, having angulate, concave anterior, and broad basal plate with long, medial, ventral extensions and thin lateral extension; cutting edge smooth, sinuous, with very large inward-pointing cusp. Marginal teeth (Fig. 8C) small, with narrow stick-like shafts and spatulate tips; inner marginal tooth with one weak outer denticle on each side of tip and with narrow inner flange; outer marginal tooth with broad, outer flange on tooth shaft and lacking outer denticle.

Juvenile radula (Fig. 8A, B) with oval, rectangular rachidian tooth (Fig. 8B) having large central cusp flanked by three smaller denti-

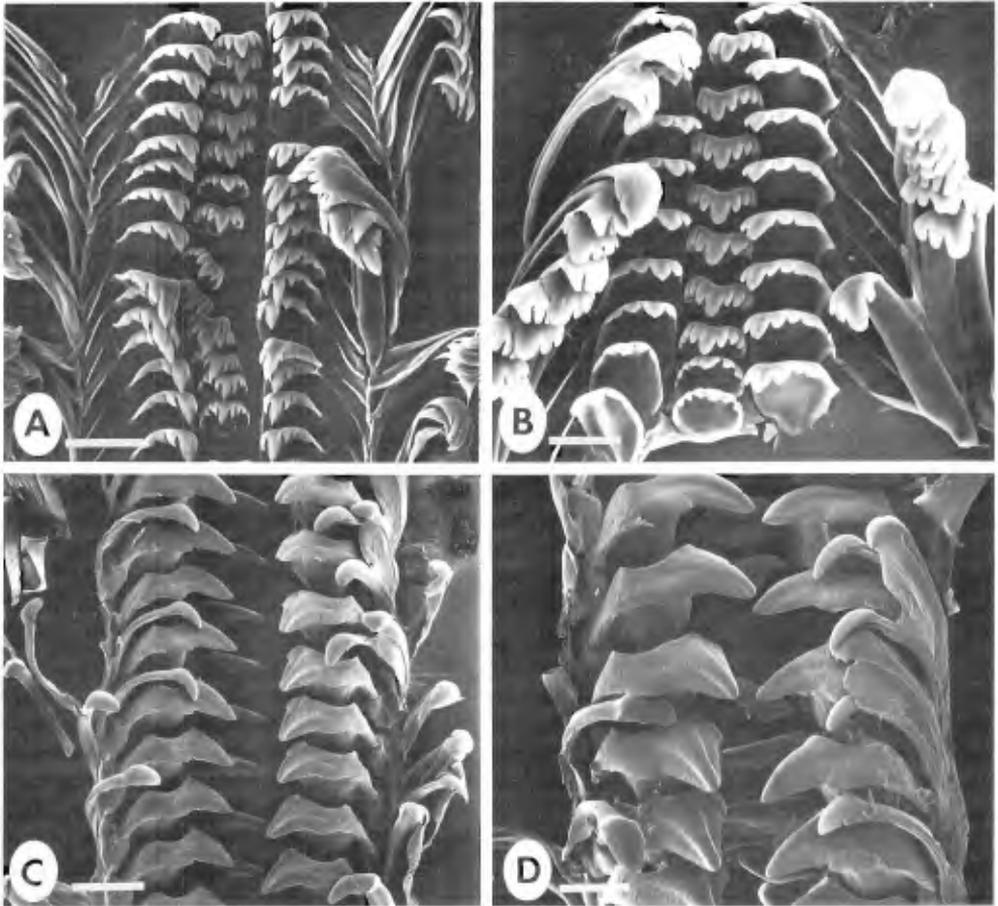


FIG. 8. *Terebralia palustris*, scanning electron micrographs of juvenile (A, B) and adult (C, D) radulae showing ontogenetic change in morphology. A, juvenile radula with marginal teeth spread open; bar = 40 μm . B, detail of juvenile radula; bar = 30 μm . C, adult radula showing small narrow marginal teeth spread open; bar = 0.4 mm. D, adult radula, details of massive lateral and narrow rachidian teeth; bar = 0.3 mm.

cles on each side. Lateral tooth (Fig. 8B) with broad basal plate having long lateral extension and serrated with one large cusp, one inner denticle and two or three outer denticles. Marginal teeth (Fig. 8B) large, elongate, having hook-like tips serrated with three inner denticles, long central cusp and one outer denticle; outer marginal tooth without outer denticles.

Reproductive System: Female pallial oviduct as in *Terebralia sulcata*, but with very narrow medial fusion along free edges of laminae comprising oviduct.

Nervous System: Cerebral ganglia ovoid with short, thick commissure. Pleural ganglia closely connected to cerebrals, having long

connectives to parietal ganglia; pedal ganglia having short connectives to cerebrals and with three well-developed pedal nerves. Zygoneury between subesophageal and right pleural ganglia, and dialyneury between left pallial nerve and left pleural nerve. Long visceral loop; visceral ganglion beneath floor of posterior mantle cavity.

Remarks

Shell: *Terebralia palustris* is by far the largest prosobranch found in the mangroves, and, for a potamidid, it can attain a truly remarkable shell size: Benthem Jutting (1956) cited a shell 160 mm long from Java, but an even greater giant of 190 mm in length has been

recorded from Arnhem Land, Australia (Loch, 1987:4). Loch (1987:4) hypothesized that gigantic specimens were the result of parasitic castration, suggesting that in animals with destroyed gonads, the energy normally directed to reproduction is diverted to growth. *Terebralia palustris* has a shell three to four times the size of *Terebralia sulcata*, and about twice the size of large *Terebralia semistriata*. The only other mangrove snail that approaches it in size is *Telescopium telescopium*.

Aside from its large size, there is nothing unusual about the shell except that in longitudinal section there are two columellar plaits, a strong central one and a weaker parietal one. Opposite these, on the inner shell wall, there are palatal folds wherever an external varix has been formed (Fig. 7J). An excellent depiction of these folds in cut shells of *Terebralia palustris* and *Terebralia sulcata* has been presented by Martens (1897, pl. 9, figs. 24, 27). According to Tryon (1882:250), this character was discovered by Brot, and does not occur in other potamidids. Juvenile shells are quickly eroded and partly dissolved in the very acidic environment of the mangroves; shells with extant protoconchs were not found during this study.

Clava caledonica, described by Jousseaume (1884) from New Caledonia, is a dwarfed form of *Terebralia palustris*. Examination of eight syntypes (MNHN) and of many dwarfed specimens from New Caledonia (USNM 724043, 724536) did not reveal significant differences from larger, more typical specimens. Jousseaume (1884:192) distinguished this taxon by its elongate shell, its reddish color, and the "form of its aperture." Populations of dwarfed and elongate, narrow individuals occur throughout the range of *Terebralia palustris*, precluding subspecific recognition of the New Caledonian populations of dwarfs. Normal-sized individuals also occur in New Caledonia and the reddish coloration of New Caledonian specimens is probably due to the presence of nickel in the mud.

Brandt (1974:195) recorded the existence of two forms of *Terebralia palustris* throughout its range, which differed from each other in radular morphology, the one having a cusped rachidian tooth, the other one having a smooth rachidian, and he doubted whether the two forms were conspecific. These two "forms" are merely the juveniles and adults of *Terebralia palustris*, and it is obvious that Brandt was unaware of the ontogenetic differences in radular morphology that exist in this species.

Anatomy: An excellent illustration of a crawling snail showing the head-foot and color of the living animal is in Kiener (1841, pl. 1). The gross anatomy of *Terebralia palustris* was briefly described by Starmühlner (1983:200–203), and is basically the same as that of *Terebralia sulcata*, which is a much smaller snail. The large, muscular, darkly pigmented snout contains a massive buccal mass, dark-brown, robust radula, and a pair of large jaws, which allows adults effectively to consume fallen mangrove leaves.

The pallial light-sensitive pit in the inhalant siphon was noted previously by Pflugfelder (1977:248–249), who referred to it as a sensory area. It probably functions as a pallial eye and is undoubtedly homologous with the similar organ in *Telescopium telescopium* and with the pallial eye of *Cerithidea* and *Tympanotonus* species (Houbrick, 1984:10–11).

The reproductive system of this species is very similar to that of *Terebralia sulcata*, but differs from that of *Terebralia semistriata* in having a more narrow medial closure of the laminae forming the open pallial oviduct. The ovipositor of *Terebralia palustris* is more posterior and closer to the operculum than in *Terebralia sulcata* (Fig. 15A, ovp).

The nervous system has been well illustrated by Starmühlner (1983: fig. 38), and both zygoneury and dialyneury are well established. The subesophageal ganglion comprises two lobes, the configuration characteristic of cerithiid and potamidid taxa (Bouvier, 1887:131).

The radula of *Terebralia palustris* differs considerably from those of its congeners. The small stick-like marginal teeth and massive lateral teeth are distinctive.

One of the remarkable aspects of the ontogeny of *Terebralia palustris* is the trophic dimorphism between juveniles and adults and the correlative change in radular morphology between the two. Young snails are segregated spatially from adults and are deposit feeders, while adults eat only dead, decomposing mangrove leaves. Juveniles have a radula (Figure 8A,B) similar to those described for some adult species of *Cerithidea* Swainson, 1840, subgenus *Cerithideposilla* Thiele, 1929 (see Houbrick, 1984). Sewell (1924:544) noted that adults of *Cerithidea obtusa* have radulae similar to those in the youngest stages of *Terebralia palustris*. The rachidian and lateral teeth have pointed cusps on their cutting edges (Fig. 8A,B), and the lateral teeth have long shafts and are

spatulate and cusped at their tips. In adults, the buccal mass is very large, as are the jaws, and a large alary process anchors the radular ribbon to the odontophore. During radular transformation, the rachidian tooth becomes diminutive, compressed dorsoventrally, and asymmetrically placed at a 45-degree angle to the other teeth. The lateral tooth becomes dominant, massive and strongly pointed at its inner edge, and both the rachidian and lateral teeth lose their cusps. The marginal teeth remain small, narrow and stick-like, and their curved tips lose some cusps. In short, the lateral teeth are the dominant instruments for dealing with mangrove leaves, while the rachidian and marginal teeth become small and vestigial (Fig. 8C,D). This transformation in radular morphology was first noted by Sewell (1924) and was studied further by Annandale (1924), who gave a more detailed account of the process, and presented a figure depicting the progression of changes in the radula from six snails of different ages (Annandale, 1924:550, fig. 11). Ontogenetic radular change appears to be limited to *Terebralia palustris*, for no such change has been observed in *Terebralia sulcata*, and Sewell (1924:544) did not detect radular differences in individuals of different ages of *Telescopium* or *Cerithidea* species.

Reproductive Biology: Sewell (1924:542) noted that males appeared to be smaller than females of the same age in a population from the Nicobar Islands. Although spermatophores were not found in the female gonoduct during the course of this study, it is assumed that they occur, and that they are similar to those described for *Terebralia sulcata*. The only account of spawning is that of Shokita et al. (1984:51–52), who studied this species in Thailand, where spawning occurs during the dry season, from December to January. They depicted spawning snails (p. 50, fig. 9) in vertical position, leaning against the mangrove prop roots. Egg capsules are deposited within gelatinous egg-strings that are attached to the roots of mangroves in the inner part of the mangroves. The use of the ovipositor in forming and depositing spawn masses was not discussed. Shokita et al. (1984) remarked that the same spawning habit has been observed in Okinawa, where the reproductive season lasts from May to October. Although the spawn masses of *Terebralia palustris* were not described in detail, photographs published by Shokita et al. (1984: fig. 9) show

that they are nearly identical to the spawn of *Terebralia sulcata*, illustrated herein (Fig. 21D–F). A free-swimming larval stage in the development of *Terebralia palustris* was reported by Rao (1938), but details of the size and duration of the veliger stage and its settlement are unknown.

Ecology: This large, conspicuous species occurs in great numbers in brackish water on coastal mudflats in mangrove regions, where it appears to prefer fine mud substrates (Wells, 1980:1–2). Ecological studies have been conducted in the Nicobar Islands (Sewell, 1924), the Andaman Islands (Rao, 1938), Java (Soemodihardjo & Kastoro, 1977), Okinawa (Nishihira, 1983), Thailand (Shokita et al., 1984), and in northwestern Australia (Wells, 1980, 1986). I observed a large population of *Terebralia palustris* in the mangroves of Magnetic Island, Queensland, Australia, where it is sympatric with *Terebralia semistriata* and *Telescopium telescopium*. The adult population was restricted to the higher, seaward portion of the mangrove forest on a substrate of fine silty sand adjacent to a sandbar, and although very few individuals were found on open flats, they were abundant in tidal channels, where they appeared to have been washed out. Few young snails occurred in the open flats, but were common around mangrove roots. Segregation of juveniles, which inhabit intertidal channels and pools, from adults, which migrate into upper intertidal mangroves, was noted in New Caledonian populations by Plaziat (1984:122). In some areas, adult densities as high as 150/m² have been recorded (Plaziat, 1984:136).

The change from juvenile to adult radula is undoubtedly a reflection of their change of diet. The apparent correlation between radular morphology and diet is a trait I have noted in *Rhinochlamys* and *Clavocerithium* (Houbrick, 1986). This is in contrast to the situation in predatory thaidid gastropods (Thaidinae), in which Kool (1987) found that diet did not have a strong selective effect in the evolution of radular morphology. To date, the most comprehensive work on trophic dimorphism and feeding in *Terebralia* is by Nishihira (1983). Trophic dimorphism has also been observed in populations from New Caledonia (Plaziat, 1977), and is probably characteristic of the species throughout its range. *Terebralia palustris* adults appear to be important in the *in situ* degradation of mangrove litter. Stom-

achs of dissected adults from Queensland, Australia, and Palawan, Philippines, were filled with small pieces of mangrove leaves. Plaziat (1977:37, fig. 32), Shokita et al. (1984: 51, fig. 10) and Nishihira (1983:52, 54–55, figs. 5, 6a, 6b) have depicted the grazed mangrove leaves eaten by adults. Nishihira (1983) showed that snails larger than 30 mm commonly form feeding aggregations and graze directly on mangrove litter, including leaf, stipule, calyx, fruit and propagule. Large snails, including juveniles more than 30 mm long, can use both detritus and mangrove litter, while juveniles less than 30 mm in shell length eat detritus and do not graze on leaves. These observations correlate with the study of Rao (1938), who pointed out that juveniles preferred a muddy habitat to a rocky or sandy one. The oldest adults appear to occur on coarser-grained substrates than do subadults and juveniles (Shokita et al., 1984:42), which seem to prefer silt and mud. Budiman (1988: 240) pointed out that migratory behavior between open mudflats and mangrove forests was related to change in diet, which, in turn, seems to be correlated with the morphological change of the radular teeth.

The first worker to attempt to study growth in *Terebralia palustris* was Sewell (1924), who traced the growth of a population over a period of four years, in which shells attained an average length of 120 mm. Rao (1938) was unable to present a complete life history of a population he studied in the Andaman Islands, which consisted of mostly sexually immature individuals belonging to the growth stages of first- and second-year classes. Nevertheless, he showed that a free-swimming larval stage was present, for a large number of very young shells appeared in May, indicating a breeding season and release of larvae elsewhere in March to April. Shells were 5 mm long in the first year of growth, 18–20 mm long in the second year, and 40 mm in the third year. Growth under laboratory conditions was equally rapid. In Java, Soemodihardjo & Kastoro (1977) recorded that young individuals gained an average additive length of 10 mm during a four-month period. Because no one has followed a population through to death, the lifespan of this species remains unknown. It appears that growth is determinate, because maturity is indicated by a thickening of the margins of the aperture, including the outer lip. Individuals more than 57 mm long had thickened lips in a Western Australian population examined by Wells (1980:2), but

this feature probably varies throughout the geographic range, for populations of dwarfed adult individuals, less than 45 mm long, occur in New Caledonia (USNM 724043, 724536). Shokita et al. (1984) showed that two types of adult shells occurred in a population, a long type and a short type. This phenomenon does not indicate sexual dimorphism, but can be explained by physical factors: older shells are shorter owing to erosion of their upper whorls by the acidic environment of the mangrove forest floor.

Terebralia palustris can tolerate considerable environmental stresses. Rao (1938:203) showed that it can live without food for a considerable period (as long as four months), and Soemodihardjo & Kastoro (1977) found that it can live out of water and without food for as long as three months.

As is the case with large adults of *Telescopium telescopium*, it is unlikely that many predators can successfully attack and eat adult individuals of *Terebralia palustris*, although the mud crab, *Scylla serrata* (Forskål, 1775), common in Indo-Pacific mangrove forests, is large and strong enough to crush the largest potamidids. Crushed *Terebralia* shells were observed around the mouths of burrows of these crabs in northern Australia (David Reid, pers. comm.). I did not see any empty shells with peeled apertures indicative of crab predation in Magnetic Island, Queensland, Australia. It is assumed that mortality due to predation occurs mainly in juveniles, but this has not been observed. Another predator of *Terebralia palustris* is man. Tryon (1882:250) remarked that "... in the Eastern Archipelago this species is assiduously collected by the natives, who roast them and suck the contents of the shell through an aperture made by breaking off the tip of the spire." This species is also eaten by Australian aborigines in Arnhem Land (Loch, 1987).

Shells of *Terebralia palustris* often are encrusted with oysters and/or barnacles in some areas, and the species frequently is corroded in the very acidic mangrove soils, which are rich in humic and fulvic acids. Scratches on the periostracum and borings by endolithic blue-green algae lead to increasing chemical dissolution of the shell, especially the apex. *Terebralia palustris* reacts by abandoning damaged apical whorls and building successive menisciform septa. Plaziat (1984:132) noted that shell corrosion occurred in New Caledonia even at neutral pH values, indicating the primary role of boring

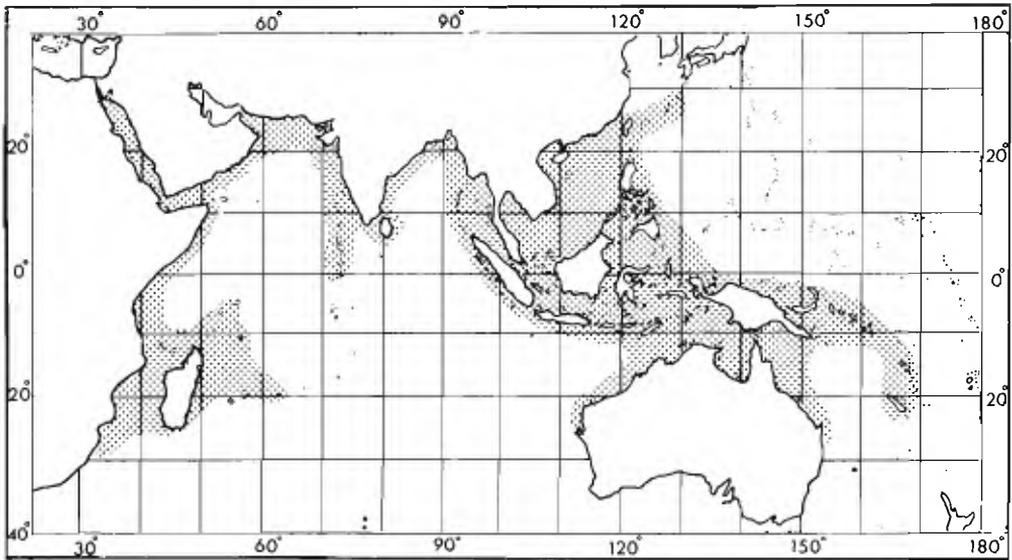


FIG. 9. Geographic distribution of *Terebralia palustris*.

algae in shell dissolution. Dissolution of the shell in older adults can result in the formation of dissolution bevels on the ventral shell surface, and an upper dissolution bevel can be formed by boring algae (see Plaziat, 1984: 135, fig. 22, for illustrations of this phenomenon). Post-mortem dissolution can reduce shells to their columellae.

Fossil Record: Numerous fossils with wide geographic distributions occur in formations ranging in age from Early Miocene through Holocene. Sacco (1895:51, pl. 3, fig. 26) recorded *Terebralia palustris* var. *lineata* Borsari from the Late Miocene of Piemonte, Italy. His engraved figure of this fossil and the photograph of the specimen later published by Mortara et al. (1985:199, pl. 36, fig. 7a,b) show that this fossil is indistinguishable from Recent specimens of *Terebralia palustris*.

In East Africa, *Terebralia palustris* is listed from the Quaternary of Somalia (Regteren Altena, 1941:16; Wissema, 1947:48), Saudi Arabia (on raised beaches along the Red Sea, Regteren Altena, 1941:16; Smythe, 1982:46), Zanzibar (Cox, 1927:84, pl. 18, fig. 4), and Kenya (Regteren Altena, 1941:16). Crame (1986:191) found Late Pleistocene fossils in Kenya. *Terebralia palustris* also occurs in Pleistocene formations in Djibouti

(Abrard, 1942:62, pl. 4, fig. 32; Wissema, 1947:48). This species is common as a fossil in Indonesia: K. Martin (1899:210–211, pl. 32, fig. 478) recorded it from the Miocene of Java, and Tesch (1920:57, pl. 131, figs. 183–184) recorded it from the Pliocene of Timor and also listed it from the Quaternary of the Celebes, the Pliocene of Nias and Java, and the Miocene of Java. Oostingh (1925:49–50) and Regteren Altena (1941:15–16) presented numerous fossil distributions, including the Pliocene of Timor and Java and the Pleistocene of New Guinea, Nias and the Celebes. This species has been recorded from the Philippines by Tesch (1920:57), Oostingh (1925:50), Regteren Altena (1941:16) and Wissema (1947:48). Fossil shells of *Terebralia palustris* are morphologically indistinguishable from Recent ones, indicating that this species has been in morphological stasis, with a fossil record going back to the Early Miocene.

Distribution: This species has the widest range of any *Terebralia* species (Fig. 9). In the tropical Western Pacific, it occurs from the Ryukyus south through the Philippines, Borneo and New Guinea and throughout tropical Australia. It extends eastward to Palau and southeast to the New Hebrides (*vide* Oostingh, 1925) and to New Caledonia. Old

records citing the Gambier Islands in Polynesia (Oostingh, 1925:49) probably refer to *Pseudovertagus clava* (Gmelin, 1791), which resembles *Terebralia palustris* in size and superficially in sculpture. *Terebralia palustris* occurs in mangrove habitats throughout the Indonesian archipelago and in the estuaries of Southeast Asia, west to India and Ceylon. In the Indian Ocean, it is found in Nicobar and Andaman Islands, the Maldives, Mauritius, the Seychelles, the Amirantes and Madagascar (Oostingh, 1925:49). Populations in eastern Africa occur from South Africa northward to the Red Sea.

Material Examined: RED SEA: Berenice, Egypt (ANSP 189208). ARABIA: Muscat, Oman (USNM 657262). EAST AFRICA: Djibouti, Djibouti (ANSP 194510); Mogadiscio, Somalia (USNM 673801); Malindi, Kenya (MCZ 106082); Mombassa, Kenya (USNM 707019); Kunduchi, Tanzania (USNM 703932; MCZ 271943); Bagamoyo, Tanzania (MCZ 261684); Kendawa Id, 4 m ESE of Dar es Salaam, Tanzania (MCZ 261683); Dar es Salaam, Tanzania (ANSP 156229; MCZ 109942); Mboa Maji, Tanzania (USNM 604600); Kijangiwani, S of Zanzibar, Zanzibar (USNM 604453; MCZ 280403); 1 mi N of Chukwani, W Zanzibar (MCZ 219010); Cape Inhambane, Mozambique (MCZ 234816); Inhaca Id, near Lourenço Marques, Mozambique (MCZ 201716); Bazaruto Id, Basaruto Bay, Mozambique (MCZ 234810); Durban Bay, South Africa (USNM 846524). INDIAN OCEAN ISLANDS: Ile Glorieuse (USNM 126217); Nosse Bé, Madagascar (USNM 719443); Ambatozavavy, E Nossi Bé, Madagascar (USNM 633349); Tulear (MCZ 261644); Grande Terre, Aldabra Atoll, Seychelles (USNM 836591); Seychelles (USNM 633323); Port Glaud, W Mahé, Seychelles (ANSP 311378); Curieuse Id, Seychelles (ANSP 298037); Mauritius (MCZ 1314); S half Kendikoln Id, Miladummadulu Atoll, Maldives (ANSP 305513); Port Blair, Andaman Ids (USNM 609734); Ara Pt, Nilaveli, Ceylon (USNM 542240); Ceylon (USNM 90880, 18588; MCZ, unnumbered lot). THAILAND: Lem Sing (USNM 419160); Lem Ngob (USNM 384177); Welu River, near Ban Long Mai, Khlung, Chantaburi Prov. (MCZ 289125); Welu River, Trad Prov. (USNM 776701, 776703, 776702; MCZ 267508); Chantaburi River, Tachalaeb (USNM 776686); Klung Harbor, Chantaburi (USNM

776704). INDONESIA: Menscheneter Id, Java (ANSP 225485); Tjiperwagaran, Bantam, Java (USNM 260572); Kampong, Taberfane, mouth Maikoor River, Aru, Moluccas (USNM 755620, 755615); Pruput, Java (USNM 260578); Pulau Siburu, N of Sipora, SW Sumatra (USNM 654762); Pulau Penju, SW Sumatra (USNM 661891); Mega, Mentawai Ids, SW Sumatra (USNM 655078). BORNEO: W Marudu Bay, N Borneo (USNM 632189); Tanjong Aru, Jesselton, N Borneo (USNM 658481). NEW GUINEA: Milne Bay, Papua (USNM 543036). AUSTRALIA: Cockle Bay, Magnetic Id, Queensland (USNM 828832, 828805, 842986, 828801); East Arm, Darwin, Northern Territory (USNM 828803); Nightcliff Pt, Darwin, Northern Territory (USNM 602168); Mangrove Pt, Carnarvon, Western Australia (USNM 828811); Shark Pt, Barrow Id, Western Australia (USNM 691930); North West Pt, Bay of Rest, Western Australia (USNM 847078, 801600); Dampier Creek, Broome, Western Australia (USNM 828802). CAROLINE ISLANDS: Peleliu, Palau Ids (CMNH 25069). SOLOMON ISLANDS: Pavuvu Id, Russell Gp (USNM 488321); Segi Pt, New Georgia (USNM 617791). NEW CALEDONIA: Tomo, Baie de St Vincent (USNM 725137); 3 mi N of Touho (USNM 631858); 3 mi E of Noumea (USNM 724043); St Marie, E side Noumea (USNM 724205); Pointe aux Long Cous, Noumea (USNM 724215); 2 km S of Conception (USNM 724536); near Port Laguerre (USNM 724778); E side Baie Boulare (USNM 664676); Dumbea River, Dumbea (USNM 724767, 724122, 724113); S of Ansi Vata (USNM 835665); San Gabriel (USNM 801591). PHILIPPINES: Pasacao, Luzon (USNM 240418); Sablayan, Mindoro (USNM 244073); E coast of Pollilo (USNM 311205); Catbalogau, Samar (USNM 243734); Tilig, Lubang Id (USNM 243681); Busuanga (USNM 244061); Jolo Id (USNM 243964); Port Busin, Burias (USNM 232927); Tara Id, Tapul Gp, Palawan (USNM 244069); Iwahig, 17 km W of Puerto Princesa, Palawan (FSM KA487); Mantagain Beach, Palawan (USNM 244068); Cape Melville, Balabac Id, Palawan (FSM KA438); 1 km SSE of Tapul, Polloc, Mindanao (USNM 244078); mouth of Mataling River, Malabang, Mindanao (USNM 243978); N of Mindanao River, Cobabato, Mindanao (USNM 244079); Zamboanga, Mindanao (USNM 243995); Port Tataan, Tataan, Tawi Tawi (USNM 243697). RYUKYUS: Okinawa (USNM 622035).

Terebralia semistriata (Mörch, 1852)
(Figs. 10–13)

Strombus semistriatus Röding, 1798:97
(Type not found, no figure reference,
nomen nudum).

Cerithium semistriatum Mörch, 1852:57.

Cerithium semitrisulcatum Sowerby, 1855:
884, pl. 185, fig. 263 (Type: not located,
Sowerby's fig. 263 selected to represent
lectotype; Type locality: Port Essington,
Queensland, Australia); Dautzenberg &
Fischer, 1905:129.

Pyrasmus semitrisulcatum (Sowerby) Sowerby,
1865: pl. 1, fig. 4.

Potamides (*Terebralia*) *semitrisulcatus*
Mörch. Tryon, 1887:160, pl. 32, fig. 45;
Odhner, 1917:10.

Pyrasmus semisulcatus (Bolten). Dautzenberg
& Fischer, 1905 (error for *semitrisulcatus*
Sowerby, 1865).

Synonymic Remarks: *Strombus semistriatus* Röding was introduced as distinct from *Strombus mangos* Röding (= *Terebralia sulcata* [Born, 1778]), and is probably the entity now known as *Terebralia semistriata* (Mörch, 1852), a larger, smoother species than *Terebralia sulcata*. Röding (1798) cited no figure reference for *Strombus semistriatus*, but did refer to Gmelin's *Murex moluccanus*, which is a synonym of *Terebralia sulcata*. Because there is no extant type and no figure reference, *Strombus semistriatus* Röding must be regarded as a *nomen nudum*. The figure cited for *Cerithium semistriatum* Mörch, 1852, clearly represents the larger, smoother species and Mörch's name is available, because Röding introduced the same name under *Strombus*. Sowerby (1855:899) listed *Cerithium semistriatum* Röding in his index, noting that it was "unidentified," but did not include it in the monograph. Next in the index he listed *Cerithium semitrisulcatum* Sowerby, presenting a full description and an excellent illustration that is unequivocally conspecific with *Cerithium semistriatum* Mörch. Thus, Sowerby's *semitrisulcatum* is a junior synonym of the larger, smoother species named *semistriatum* by Mörch (1852).

Dautzenberg & Fischer (1905:130), after examination of many specimens, remarked that although Kiener, Tryon and Sowerby maintained the separation of *Terebralia semistriata* (cited as *semitrisulcata*) from *Terebralia sulcata*, they were unable to find the line separating the two forms, and considered the

former name to be a synonym. This study has shown that there is good conchological, radular and anatomical evidence to accord specific status to *Terebralia semistriata*.

Description

Shell: Shell large, solid, turreted, comprising 10 to 12 flat-sided to weakly-inflated whorls and reaching 57 mm in length (Fig. 10A–C,G,H). Protoconch unknown. Early whorls (Fig. 10H) sculptured with dominant axial ribs, but later developing spiral cords and becoming more cancellate. Adult shells (Fig. 10A–C) sculptured with broad, subsutural, flattened spiral cord and four or five smaller spiral cords diminishing in size abapically, and with weak axial ribs and incised lines, stronger in early whorls, becoming progressively weaker and narrower abapically, presenting overall smooth, tessellate appearance. Several varices randomly distributed. Suture distinct, slightly inset into each successive anterior whorl. Body whorl very large with strong varix opposite circular, flaring outer lip. Shell base (Fig. 10D) weakly constricted, sculptured with numerous spiral cords and weak, colabral, axial striae. Aperture large, circular-ovate, with concave columella having weak callus. Outer lip of aperture thick, smooth, circular, fusing with anterior canal to form complete peristome. Anterior canal centrally located, tubular, projecting through shell base. Anal canal weakly defined. Shell color dark- to light-brown. Aperture tan with shiny brown and whitish patches on columella and outer lip. Operculum (Fig. 10E,F) corneous, circular, multispiral with central nucleus and ragged, transparent edge.

Anatomy: Animal essentially same as other *Terebralia* species. Head-foot blackish, snout mostly black with some cream-colored blotches, upper foot gray, sole white. Tentacular peduncles thick and long; tentacle tips narrow, short. Inhalant siphon thick, fringed at edge; internally, with close-set papillae and with crescentic, lightly pigmented, slit-like, sunken sensory pit bordered with black pigment. Ridge-like osphradium very narrow, long. Ctenidium long, very wide, comprised of extremely shallow leaflets. Mantle tissue supporting ctenidium very thin. Rectum large, wide. Style sac extremely long, extending from stomach anteriorly to pericardium. Kidney bright green. Female pallial oviduct with wide medial fusion. Male pallial gonoduct comprising two simple laminae.

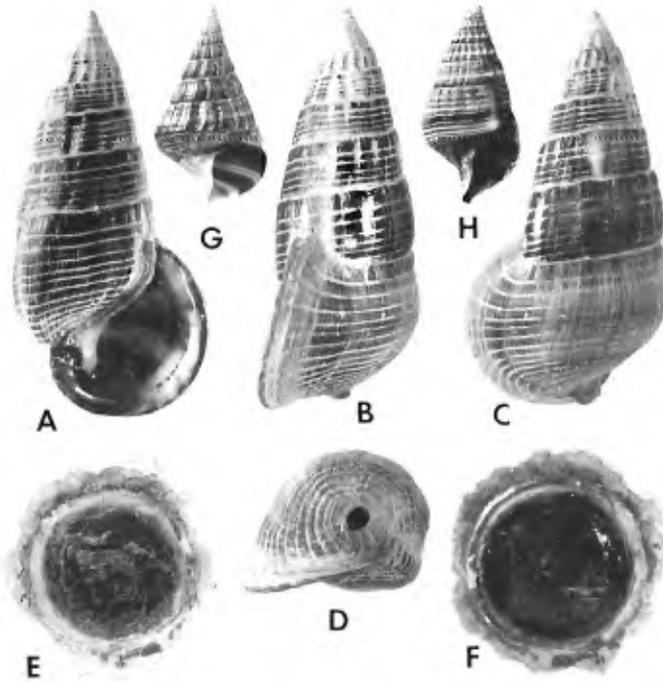


FIG. 10. *Terebralia semistriata*, shell and operculum. A–D, adult shell from Darwin, Northern Territory, Australia; 56.7 × 25.8 mm (USNM 828831). E, F, operculum, showing free (E) and attached (F) sides; 11.1 mm diameter. G, early juvenile shell from Cockle Bay, Magnetic Island, Queensland, Australia, showing distinctive axial sculpture; 19.1 × 9.3 mm (USNM 828806). H, half-grown shell from Cape Bowling Green, Queensland, Australia, without varix on outer lip; 36.3 × 16.8 mm (USNM 622920).

Alimentary System: Buccal mass relatively large. Pair of large jaws about 1 mm in length, comprised of scale-like plates attached to each other at anterior tips. Radula (Fig. 11A–D) moderately long, robust, brown anteriorly and with long alary processes. Radula with nine rows of teeth per mm. Rachidian tooth (Fig. 11C,D) rectangular-pentagonal with straight anterior end and broad basal plate with weak, ventrally located, central projection; cutting edge with large, spade-shaped central cusp flanked on each side with one or two, rarely three, very small denticles. Lateral tooth (Fig. 11D) higher than wide, rectangular with basal plate having broad central pillar and pointed base; cutting edge with large, pointed, central cusp, one rounded inner denticle, and two small outer denticles. Marginal teeth (Fig. 11A,B) with long narrow shafts, flared, T-shaped tips. Inner marginal with long central cusp, two or three inner denticles, two outer denticles and narrow outer flange; outer marginal tooth same, but lacking outer denticles and with broad outer flange (Fig. 11B) on

outer tooth shaft. Pair of tiny, tightly coiled, pinkish salivary glands anterior to nerve ring, not passing through it.

Remarks

Shell: The shell (Fig. 10A–D,G,H) of *Terebralia semistriata* closely resembles that of *Terebralia sulcata*, but is much larger and heavier, has weaker sutures, is weakly sculptured with flattened spiral cords and, except in juveniles, lacks axial ribs. The peristome is complete in adults. This species lacks the sculptural variability seen in the other two *Terebralia* species.

Anatomy: The anatomy of this species (Fig. 12) was not studied in great detail, but the few dissections made show that it is nearly identical to *Terebralia sulcata*, although twice the size of the latter. A distinguishing character is the wide medial fusion in the center of the open female pallial oviduct (me), which contrasts sharply with the narrow medial fusion in *Terebralia palustris* and *Terebralia sulcata*.

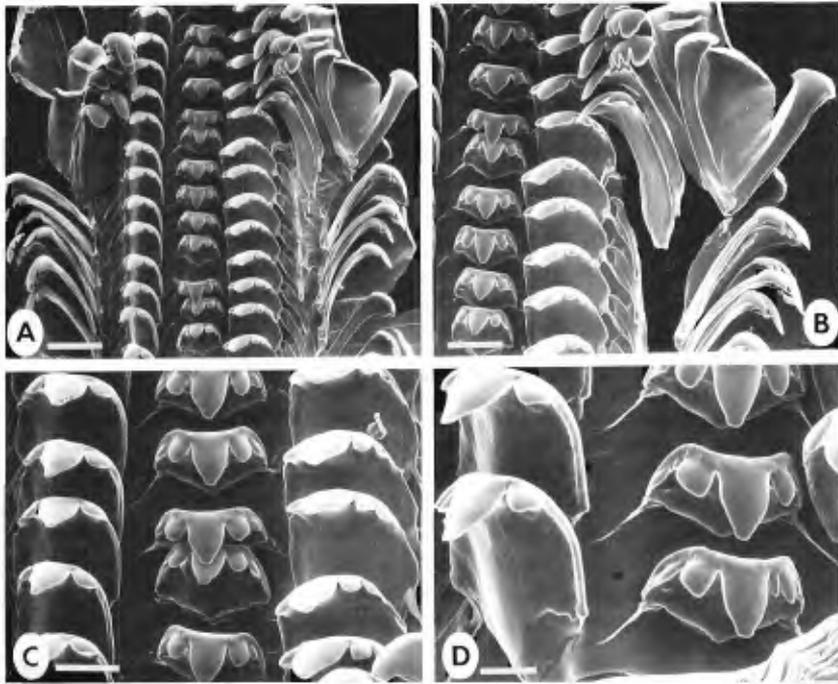


FIG. 11. Radula of *Terebralia semistriata*. A, mid-radular ribbon with marginal teeth spread open; bar = 200 μm . B, half row showing marginal teeth and flange on outer marginal tooth; bar = 80 μm . C, detail of rachidian teeth; bar = 80 μm . D, detail of rachidian and basal plate of lateral teeth; bar = 40 μm .

(Fig. 18F, me). This wide medial fusion effectively closes the oviduct, forming a long medial oviductal passage (sections 2–3, op). The spermatophore bursa (sb) and seminal receptacle (sr) have a common opening.

Reproductive Biology: Nothing is known about the reproductive biology, eggs, or larvae of this species.

Ecology: This species was observed on the surface of open mudflats off the breakwater at Cairns, Queensland, and in the center of the mangroves at Magnetic Island, Queensland. In both places it was found on soft, sticky, cohesive mud.

Fossil Record: Fossils have not been recorded, and the geographic distribution is limited. It is known that the area of Australia in which it is common underwent significant marine regressions in recent geological time, suggesting that *Terebralia semistriata* might have recently evolved.

Distribution: *Terebralia semistriata* has the most limited distribution of any *Terebralia* species, and appears to be confined to trop-

ical Australia and the southern coast of New Guinea (Fig. 13, stars). Although its developmental biology is unknown, its limited distribution suggests that this species might have direct development.

Material Examined: AUSTRALIA: Bay of Rest, North West Cape, Western Australia (USNM 801606); Buccaneer Rock, Broome, Western Australia (USNM 631903); Broome, Western Australia (MCZ 265933); Dampier Creek, Broome, Western Australia (USNM 828829); Mangrove Point, Carnarvon, Western Australia (USNM 828814); Shark Bay, Western Australia (USNM 809759); Point Darwin, Darwin, Northern Territory (MCZ 100958); East Point, Darwin, Northern Territory (MCZ 100958; AMNH 1013); Ludmilla Creek, 6 km N of Darwin, New Territory (USNM 828831); East Arm, 8 km ESE of Darwin, New Territory (USNM 809767); Darwin Harbor, Darwin, New Territory (USNM 867709); Cooktown, Queensland (MCZ 265994); Cairns, Queensland (USNM 794875); Cape Bowling Green, Queensland (USNM 622920); Cockle Bay, Magnetic Id,

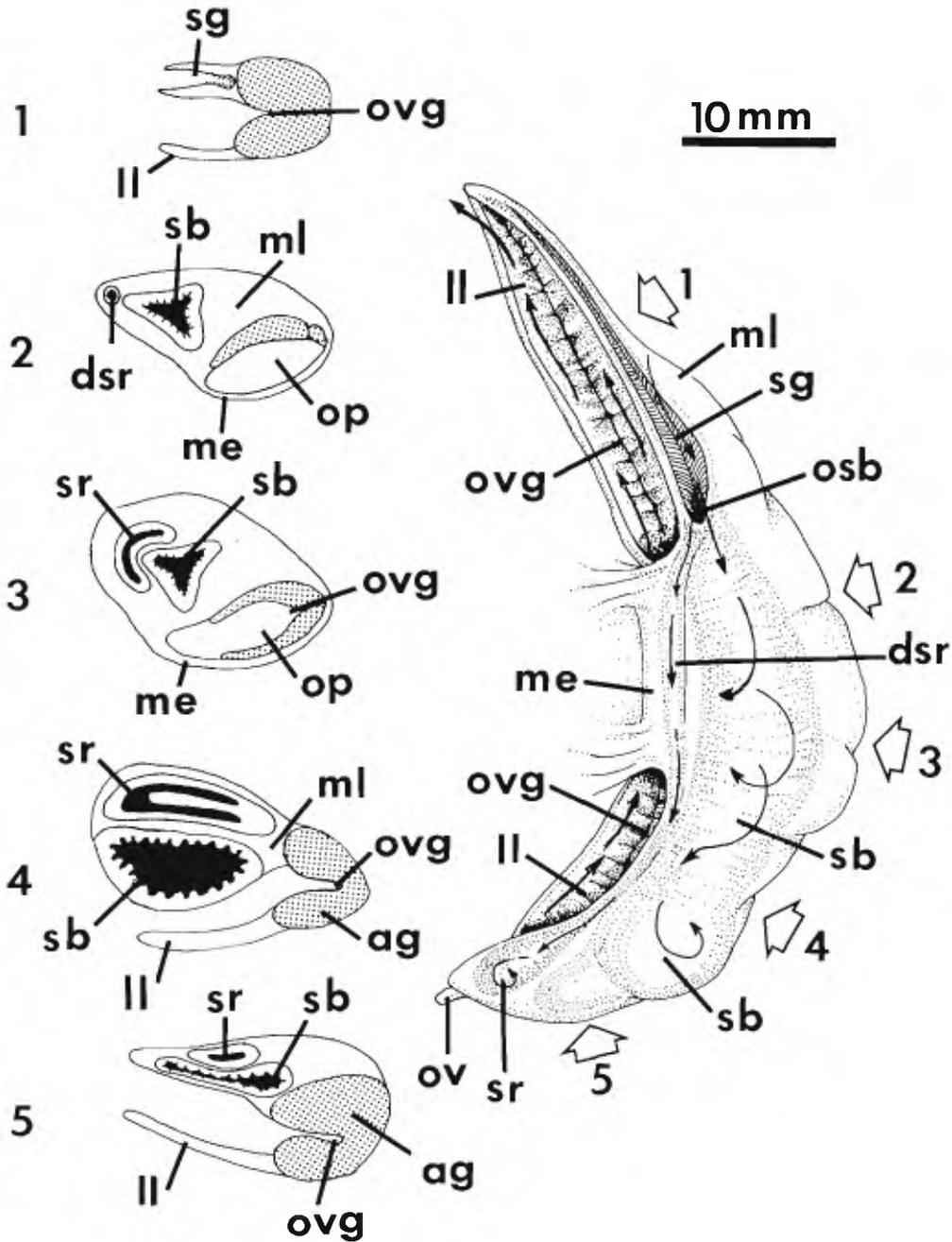


FIG. 12. Diagrammatic figure of pallial oviduct of *Terebralia semistriata*; numbered arrows 1-5 indicate positions of transverse cuts through oviduct represented on left by numerals 1-5. ag, albumen gland; ant, anterior pallial oviduct; dsr, duct of seminal receptacle; ll, lateral lamina; me, medial fusion of pallial oviduct; ml, medial lamina; op, closed oviductal passage; osb, opening to spermatophore bursa; ov, oviduct; ovg, oviductal groove; sb, spermatophore bursa; sg, sperm groove; sr, seminal receptacle.

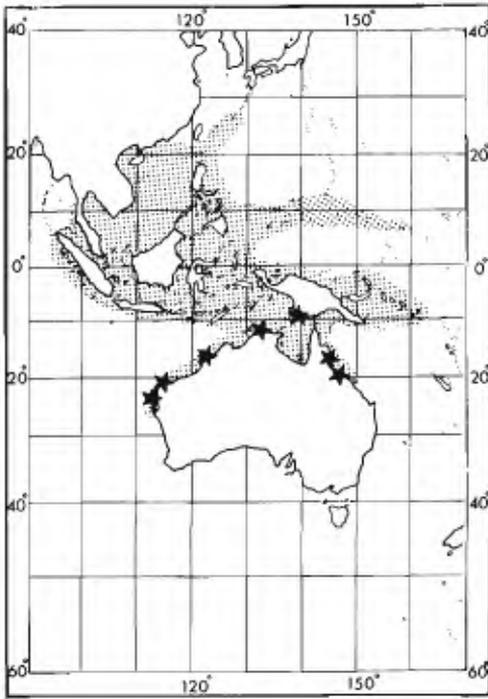


FIG. 13. Geographic distribution of *Terebralia semistriata* (stars) and of *Terebralia sulcata* (shaded area).

Queensland (USNM 828806); Townsville, Queensland (AMNH 171731); Port Curtis, Queensland (AMNH 14372); Mary River, Hervey Bay, Queensland (MCZ 104650); Long Beach, Kepple Bay, Queensland (MCZ 243490); Rockingham Bay, Queensland (MCZ 104649). NEW GUINEA: Maro River, Merauke, West Irian (MCZ 96915); Merauke, West Irian (MCZ 62358).

Terebralia sulcata (Born, 1778)
(Figs. 14–21)

Murex sulcatus Born, 1778:324 (Holotype: Natural History Museum, Vienna, no. 5260; Type locality not given, here restricted to Ambon); 1780:320–321.

Murex moluccanus Gmelin, 1791:3563 (Type not found: Lister's [1770] pl. 1021, fig. 85 selected to represent lectotype; Type locality: Moluccas).

Strombus mangos Röding, 1798:97 (Type not found: Lister's [1770] fig. 85 here selected to represent lectotype).

Cerithium sulcatum Bruguière [sic]. Kiener,

1841:89–90, pl. 27, figs. 1, 2 (in part, figs. 1, 2 only).

Pyrazus sulcatus (Born). Tapparone Canefri, 1874:41.

Cerithium (*Pyrazus*) *semistriatus* Mörch. Kobelt, 1898:36, pl. 8, figs. 3, 4 (not *semistriata* Mörch, 1852: is *Terebralia sulcata*).

Potamides (*Terebralia*) *tenerrimus* Schepman, 1895:133–135, pl. 6 (Syntypes: [5]: ZMA 2.95.001, largest 10 × 6 mm; Type locality: Roti, Indonesia).

Potamides (*Terebralia*) *tenerrimus* var. *costata* Schepman, 1895:133 (Syntype: ZMA 2.95.002, 19 × 6 mm; Type locality: Roti, Indonesia).

Potamides sulcatus (Born). K. Martin, 1899:211; 1911:21; Lischke, 1914:259; Benthem Jutting, 1929:86.

Potamides (*Terebralia*) *sulcata* (Born). Oostingh, 1925:50.

Terebralia sulcata (Born). Oostingh, 1935:5; Regteren Altena, 1941:17; Benthem Jutting, 1956:442–443.

Potamides (*Terebralia*) *semitrisulcata* (Bolten) Mörch. Odhner, 1917:10.

Synonymic Remarks: Brauer (1878:170) has identified Born's original numbered specimen in the Vienna Museum, which is presumably the holotype of *Terebralia sulcata*. Born's (1780) references to the figures of Lister (1770:1021, fig. 85) and Martini & Chemnitz (1780, figs. 1484, 1485) clearly depict *Terebralia sulcata* of authors, although the Buonanni (1709) figure reference (fig. 68), which is listed first, depicts a short, strongly ribbed shell that only equivocally can be identified with it. *Murex moluccanus* of Gmelin (1791) and *Strombus mangos* of Röding (1798) are synonyms of *Terebralia sulcata*, because both authors referred to the same figure references as did Born (1778). *Strombus semistriatus* was introduced by Röding (1798) as distinct from *Strombus mangos* Röding, 1798, but Gmelin's (1791) *moluccanus* was also cited as a synonym of *Strombus mangos*. Because no figure was cited for *Strombus semistriatus*, this taxon is herein considered a *nomen nudum* (see synonymic remarks under *Terebralia semistriata*). *Potamides tenerrimus* was described from a salt lake on Roti, Indonesia (Schepman, 1895). The syntypes and specimens from the type locality are small, black, slightly deformed and thin-shelled. The same is true for the varietal form named *costata* Schepman, 1895. These

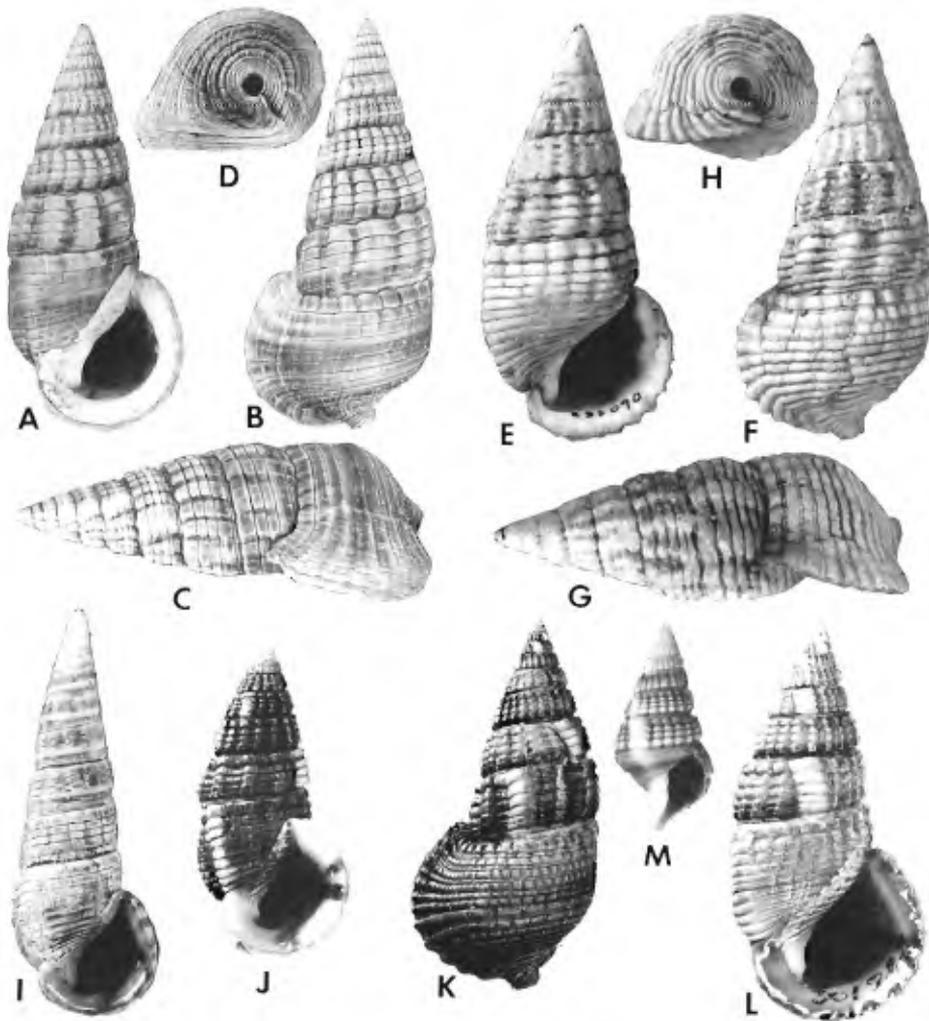


FIG. 14. *Terebralia sulcata*, showing variable shell morphology. A–D, adult shell with strong axial sculpture from Okinawa; 46.9 × 19.5 mm (USNM 671076). E–H, adult shell with strong spiral sculpture from Tawi Tawi Islands, Philippines; 50.9 × 21.4 mm (USNM 233090). I, elongate, narrow adult shell from Hong Kong; 38.9 × 12.7 mm (USNM 858379). J, dwarf adult shell from Palawan, Philippines; 29 × 12.7 mm (USNM 808336). K, L, very inflated adult shell from Burias, Philippines; 45.9 × 21.5 mm (USNM 301727). M, juvenile shell from Masbate, Philippines; 21.2 × 12 mm (USNM 244022).

specimens closely resemble small or immature *Terebralia sulcata*, and are probably ecophenotypes or deformed individuals of this species. Specimens of *Batillaria minima* Mörch, 1852 and *Cerithium lutosum* Gmelin, 1791, from salt lakes in the Bahamas, have similar thin-walled, deformed shells thought to be caused by the atypical, hypersaline environment. The radula depicted by Schepman

(1895, pl. 6) is merely an immature form of the radula of *Terebralia sulcata*.

Description

Shell: Shell (Fig. 14) moderately large, pendant-shaped, reaching 60 mm in length, and comprising about 12 weakly inflated to flat-sided whorls. Protoconch unknown. Early

whorls (Fig. 14M) highly cancellate. Adult shells (Fig. 14A–L) with several wide, randomly placed varices, and sculptured with four or five flattened spiral cords and deeply incised spiral lines overlain by numerous axial ribs, forming overall sculpture of square nodules. Suture deeply incised. Body whorl wide, with expanded thickened outer lip. Aperture wide, ovate, slightly less than one-third the shell length, and with concave columella with broad columellar wash. Outer lip smooth to weakly crenulated, joining (fused to) base of columella just above short, centrally located, tubular siphonal canal (Fig. 14D,H). Body whorl sculptured with numerous beaded spiral cords. Shell dark brown, sometimes with lighter brown bands; varices whitish and beads sometimes light brown. Aperture shiny brown to cream. Operculum corneous, circular, multispiral with central nucleus and ragged edge.

External Anatomy: Animal (from Hong Kong) pigmented with yellow, dusky-brown blotches, flecked with bright yellow dots (Fig. 15A). Snout (sn) long, dark brown to black, with iridescent green, transverse stripes. Cephalic tentacles with broad peduncular bases and slender, long tips. Large black eye at anterior end of each peduncular base. Foot large, with deep groove on posterior propodium corresponding to columellar plait on shell. Sole furrowed with fine longitudinal folds. Opening to anterior pedal gland slit-like, extending posteriorly along two-thirds of sole edge (Fig. 17B, amg). Females with deep ciliated groove (cg) leading from anterior pallial oviduct down right side of foot and around large, pad-like, bulbous, cream-colored ovipositor (ovp) situated near medial foot edge. Small opening in ovipositor leading into glandular chamber inside foot (cross-hatched area). Gonads located in upper visceral coils; ovaries bright green (eggs and spawn masses also green); testis orange-brown. Kidney brown, one whorl long, comprising two lobes: large right lobe consisting of many fine lamellae; smaller left lobe with larger, coarser lamellae. Mantle skirt green, having bifurcate edge; outer (upper) edge scalloped; inner (lower) edge internally fringed with long, spade-shaped papillae having white tips (mp); ventral mantle edge smooth. Deep indentation at mantle edge adjacent to inhalant siphon (inh); exhalant siphon marked by minor indentation. Inhalant siphon thick, muscular, darkly pigmented along external edge, and with large, dark, inner papillae (Fig. 17C).

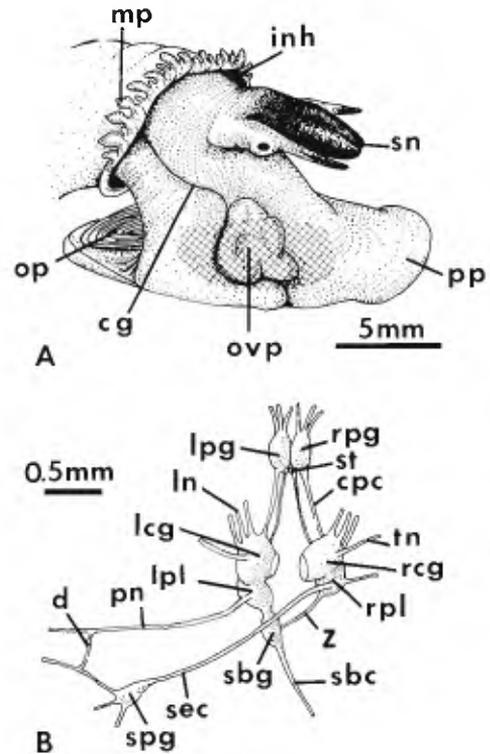


FIG. 15. *Terebralia sulcata*, anatomical features. A, right view of head-foot and mantle edge of female; crosshatched area represents internal ovipositor chamber. cg, ciliated groove; inh, inhalant siphon; mp, mantle papillae; op, operculum; ovp, ovipositor; pp, propodium; sn, snout. B, central nervous system; visceral ganglion and visceral loop not shown. cpc, cerebral pedal connective; d, dialyneury; lcg, left cerebral ganglion; ln, labial nerves; lpg, left pedal ganglion; lpl, left pleural ganglion; pn, left pallial nerve; rcg, right cerebral ganglion; rpg, right pedal ganglion; rpl, right pleural ganglion; sbc, subesophageal connective; sbg, subesophageal ganglion; sec, supraesophageal connective; spg, supraesophageal ganglion; st, statocyst; tn, right tentacular nerve; z, zygoneury.

Inner surface of inhalant siphon darkly pigmented with large, semicircular, unpigmented sensory pit (Fig. 17C) innervated by a pallial nerve. In cross-section, sensory pit comprising thin layer of white tissue underlain by dark pigment (Fig. 17C). Sensory pit located several mm in front of osphradium and ctenidium.

Mantle Cavity: Mantle cavity about two whorls long. Osphradium narrow, ridge-like with many small, tight folds along edge and sunken in trench-like pit. In cross-section, os-

phradium flanked on each side by tuft of ciliated epithelium, innervated by large osphradial nerve located in center of osphradium base. Osphradium 3–4 mm behind mantle edge beginning about 1 mm behind anterior tip of ctenidium. Osphradial length about two-thirds ctenidial length, very narrow, separated from ctenidium by broad membrane. Ctenidium whitish-pink, long, extending length of mantle cavity, very wide and shallow, comprising many thin, crescentic filaments; ctenidial filaments raised and triangular at left leading edge, becoming broad and shallow to right. Anterior ctenidial filaments more acutely triangular than broad, shallow, posterior ones. Tip of leading edge of filament directed to right, with small indentation. Ctenidial filaments each with numerous muscle bundles (strands), and having thin, vitreous rod-like element supporting left leading edge. Hypobranchial gland thick, wide, relatively thin anteriorly, comprised of transverse folds arranged as shallow lamellae posteriorly. Hypobranchial gland partly covering rectum, and secreting copious mucus. Rectum large, very wide, thin-walled, having internal epithelium with many transverse folds. Anus large, at anterior end of rectum. Pallial gonoducts large, open, comprising two laminae with narrow, medial fusion in females.

Alimentary System: Snout (Fig. 15A, sn) broad, bilobed at tip, thick-walled. Buccal hemocoel large, containing massive buccal mass attached to snout wall with numerous muscle bundles. Odontophore long, ovoid. Mouth located on ventral part of snout tip. Oral tube short, with pair of triangular chitinous jaws, each about as wide as width of anterior radula. Radular ribbon (Fig. 16) slightly more than one-fourth shell length, curving under buccal mass, and with pair of long narrow alary processes along anterior third of radular ribbon. Rachidian tooth (Fig. 16C) rectangular, forming semicircle, with narrow basal plate; cutting edge with long central cusp flanked on each side by two denticles. Lateral tooth higher than wide, rectangular with broad basal plate having broad central pillar and short lateral extension; cutting edge with large pointed major cusp and one to three outer denticles. Marginal teeth (Fig. 16A,B) with long narrow shafts and spatulate tips. Inner marginal tooth with broad central cusp, two or three inner denticles, two outer denticles and narrow outer flange. Outer marginal tooth with four cusps and

broad outer flange. Salivary glands originating immediately behind nerve ring, passing through it, comprising pair of tubes, looped along lateral sides of buccal mass, emptying into anterior part of oral cavity. Dorsal food groove in anterior esophagus large, twisting at nerve ring and becoming broad, shallow and ventral in midesophagus. Midesophagus (Fig. 18B, es) broad, dorso-ventrally flattened, and with interior epithelium consisting of numerous fine longitudinal folds and large dorsal fold. Stomach (Fig. 17A) large, occupying about one and one-half whorls of visceral mass. Stomach with esophagus opening (eso) on right anterior side, adjacent to major typhlosole (t) and to large sorting area (sa). Large pad-like ridge arising from broad fold of stomach floor (rp) filling center and posterior of stomach, bordered along its posterior length by deep crescentic groove (cgr) and narrow ridge-like typhlosole (t) traversing its entire length, ending near gastric shield. Single opening to digestive gland (odg) located between typhlosole and ridge. Posterior part of stomach slightly constricted. Central-anterior part of stomach with large chitinous gastric shield (gs). Opening to intestine (int) located in anterior stomach adjacent to, but separate from, style sac opening (oss); style sac and intestine independent of each other. Style sac (ss) embedded in loose, spongy connective tissue anterior to stomach. Internal epithelium of style sac heavily ciliated. Style sac and crystalline style very long, extending from gastric shield, adjacent to kidney, as far anterior as pericardium, parallel to intestine in mid-region of the mantle cavity. Intestine long, looping back over anterior stomach before entering mantle cavity. Rectum (Fig. 18A–E, r) very wide, about one-fourth ctenidial width, having thick walls, and compressed into flattened tube; rectum having interior epithelium with thin ventral channel bordered by one wall with numerous transverse, leaflet-like folds, and by another with wide thickened transverse ridges. Fecal pellets each compressed into long ovoid shape, stacked in large groups. Anus slightly detached from mantle wall, with broad opening.

Reproductive System: Pallial oviduct (Fig. 18F) open along most of its length, but with narrow medial closure. Pallial oviduct consisting of two long, wide, thickened laminae: lateral lamina attached to mantle wall (ll), and free, medial lamina (ml). Laminae fused me-

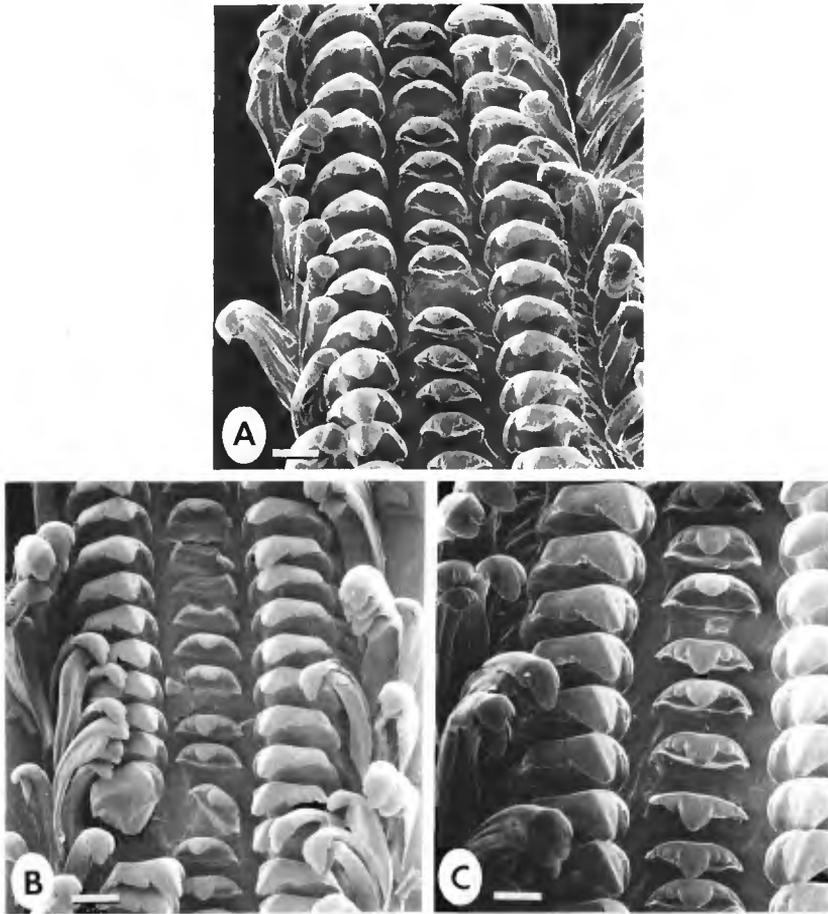


FIG. 16. *Terebralia sulcata*, scanning electron micrographs of radula from Hong Kong (USNM 858379). A, radular mid-section with marginal teeth spread open; bar = 15 μm . B, mid-section of radular ribbon with marginal teeth partly opened showing basal plate of lateral tooth; bar = 20 μm . C, detail of half row showing rachidian teeth; bar = 10 μm .

dially with thin sheet of mantle tissue binding together edges (me). Oviductal groove (ovg) at attached base of glandular portions of both laminae and bordered with many transverse ridges. Albumen gland (ag) white, opaque, beginning at posterior and extending anteriorly to mid-pallial oviduct; darkly pigmented capsule gland (cg) anterior to albumen gland. Long sperm gutter (Figs. 18F, 19A, sg) located along edge of anterior medial lamina, opening into narrow bifurcate duct, leading into spermatophore bursa (Figs. 18F, 19D,E, sb) and seminal receptacle (Fig. 18F, sr). Sperm gutter highly ciliated, having many fine longitudinal folds. Spermatophore bursa (Fig. 18C–F, sb) large, elongate, lying in left, outer,

posterior portion of non-glandular region of medial lamina. Spermatophore bursa interior epithelium bright yellow, ciliated, finely folded (Fig. 19D,E, sb), containing as many as three spermatophores. Seminal receptacle (Fig. 18C,D,F, sr) small, elongate, located in right inner wall of posterior medial lamina adjacent to spermatophore bursa. Seminal receptacle with large medial lobe having internal ciliated epithelium transversely folded. Oriented eupyrene sperm embedded in wall of seminal receptacle (Fig. 19E,F, sr). Non-glandular portion of lateral lamina (Fig. 18F, ll) consisting of thin sheet of tissue attached to floor of mantle cavity on right side of foot. Deep ciliated groove (Fig. 15A, cg) emerging from an-

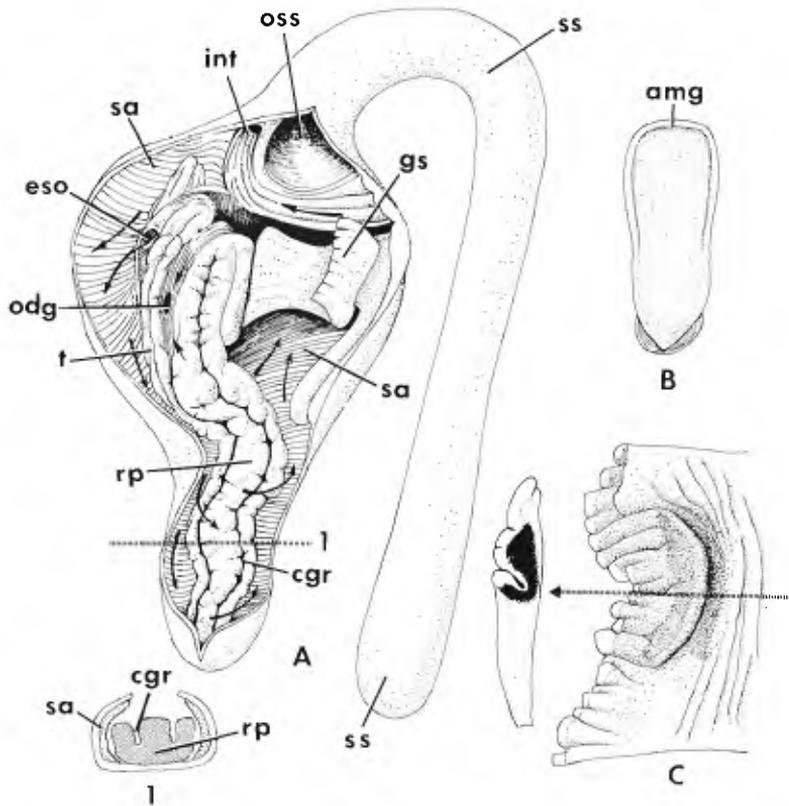


FIG. 17. *Terebralia sulcata*, anatomical features. A, diagrammatic representation of stomach; style sac folded back. cgr, crescentic groove; eso, opening of esophagus; gs, gastric shield; int, opening to intestine; odg, opening to digestive gland; oss, opening to style sac; rp, ridge-like pad; sa, sorting area; ss, style sac; t, typhlosole; 1, transverse cross-section through posterior stomach, shown below. B, sole of foot showing extent of opening to anterior mucous gland (amg). C, pallial light-sensitive organ at edge of inhalant siphon; arrow denotes plane of section through organ shown to left.

terior pallial oviduct, running down right side of foot to white, bulbous ovipositor (Fig. 15A, ovp; 20A,B). Ovipositor with small opening (Fig. 20D,E) leading to narrow, interior, glandular chamber (Fig. 20F) and secreting milky, viscous fluid. Glandular tissue of ovipositor staining darkly in section. Ovipositor chamber a narrow slit, circular in cross-section (Fig. 20F,G), formed within thick glandular tissue, divided by longitudinal ridge emerging from anterior base of ovipositor on thin connecting ridge; epithelium of ovipositor chamber ciliated. Ovipositor gland producing milky fluid, becoming viscous and swelling upon contact with water.

Ovary green, producing bright green eggs about 200 μm in diameter. Eggs surrounded by albumen and encapsulated, attaining diameter of 220 μm , arranged into long, twisted

gelatinous strings in pallial oviduct, and emerging from it into ciliated groove (Fig. 15A, cg) on right side of foot, and moving down to large, glandular ovipositor near foot edge (Fig. 15A, ovp). Ovipositor secreting gelatinous material surrounding egg capsules (Fig. 21F), forming elongate, thin, jelly tube, about 2.5 mm wide, encased within parchment-like outer membrane, joined along its length by longitudinal suture (Fig. 21E). Elongate gelatinous tube containing egg capsules folded into loose coils forming twisted spawn mass about 40 mm long (Fig. 21D) and about 135 cm in length when unraveled. Spawn mass containing about 7,000 egg capsules, deposited on substrate, covered with adhering detrital particles and sand grains.

Male pallial gonoduct open, comprised of two laminae; thin and pink anteriorly, thick

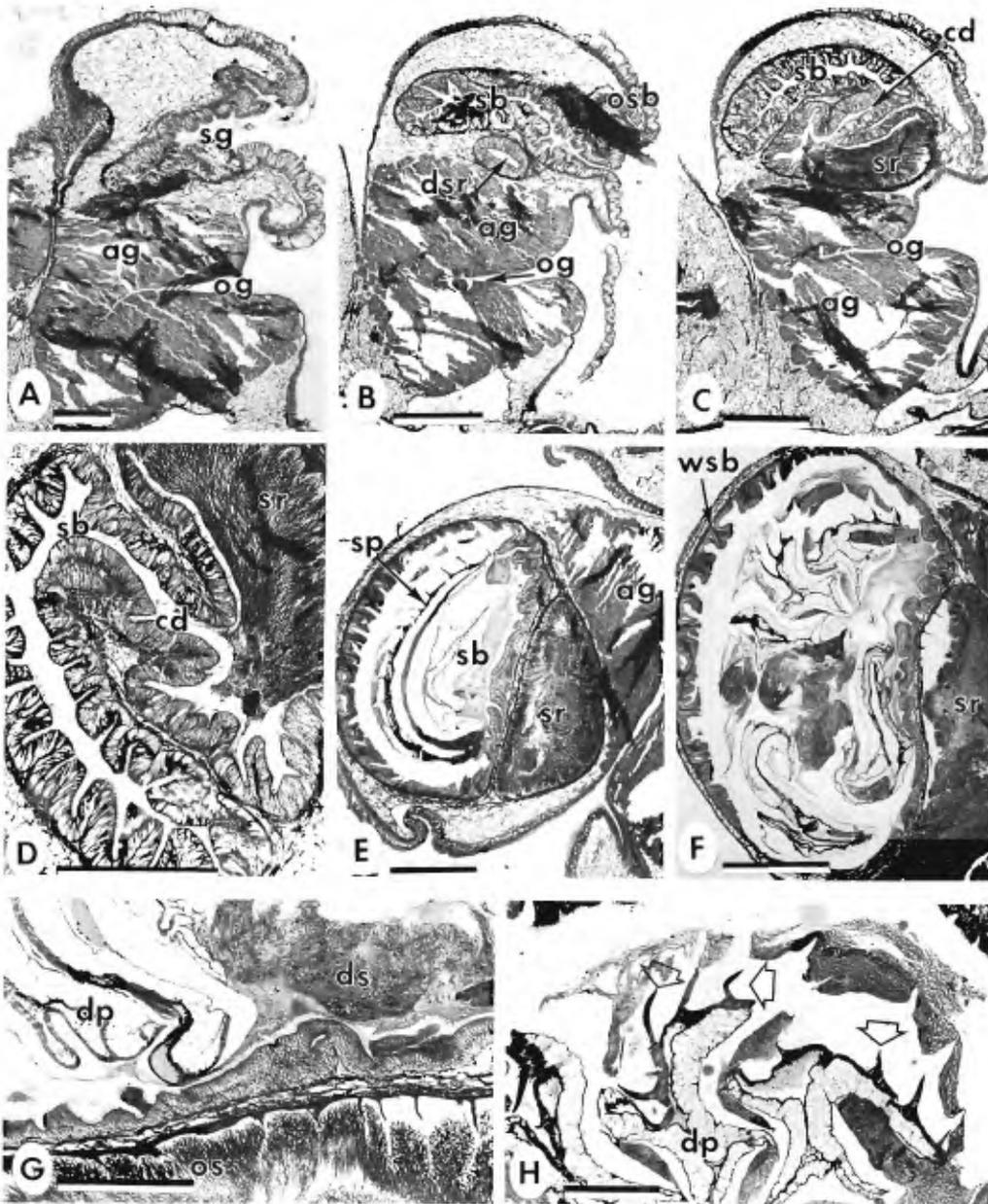


FIG. 19. *Terebralia sulcata*. histological sections through pallial oviduct. A, mid-oviduct showing sperm gutter (sg), oviductal groove (og) and albumen gland (ag); bar = 0.5 mm. B, mid-oviduct showing opening to spermatophore bursa (osb), anterior spermatophore bursa (sb), duct to seminal receptacle (dsr), albumen gland (ag) and oviductal groove (og); bar = 0.5 mm. C, posterior seminal receptacle showing connective duct (cd) between spermatophore bursa (sb) and seminal receptacle (sr); bar = 0.5 mm. D, oriented sperm in seminal receptacle (sr) and connective duct (cd) to spermatophore bursa (sb); bar = 0.2 mm. E, section through bursa (sb) and seminal receptacle (sr) showing spermatophore (sp), *in situ*; bar = 0.5 mm. F, bursa containing disintegrating spermatophore and showing details of ridged epithelium lining bursa (wsb); bar = 0.5 mm. G, detail of epithelium separating seminal receptacle from bursa; note disintegrating spermatophore (dp), dispersed sperm (ds) in bursa and oriented sperm (os) in receptacle; bar = 0.2 mm. H, cross-section through disintegrating spermatophore (dp) showing keels (arrow heads); bar = 0.1 mm.

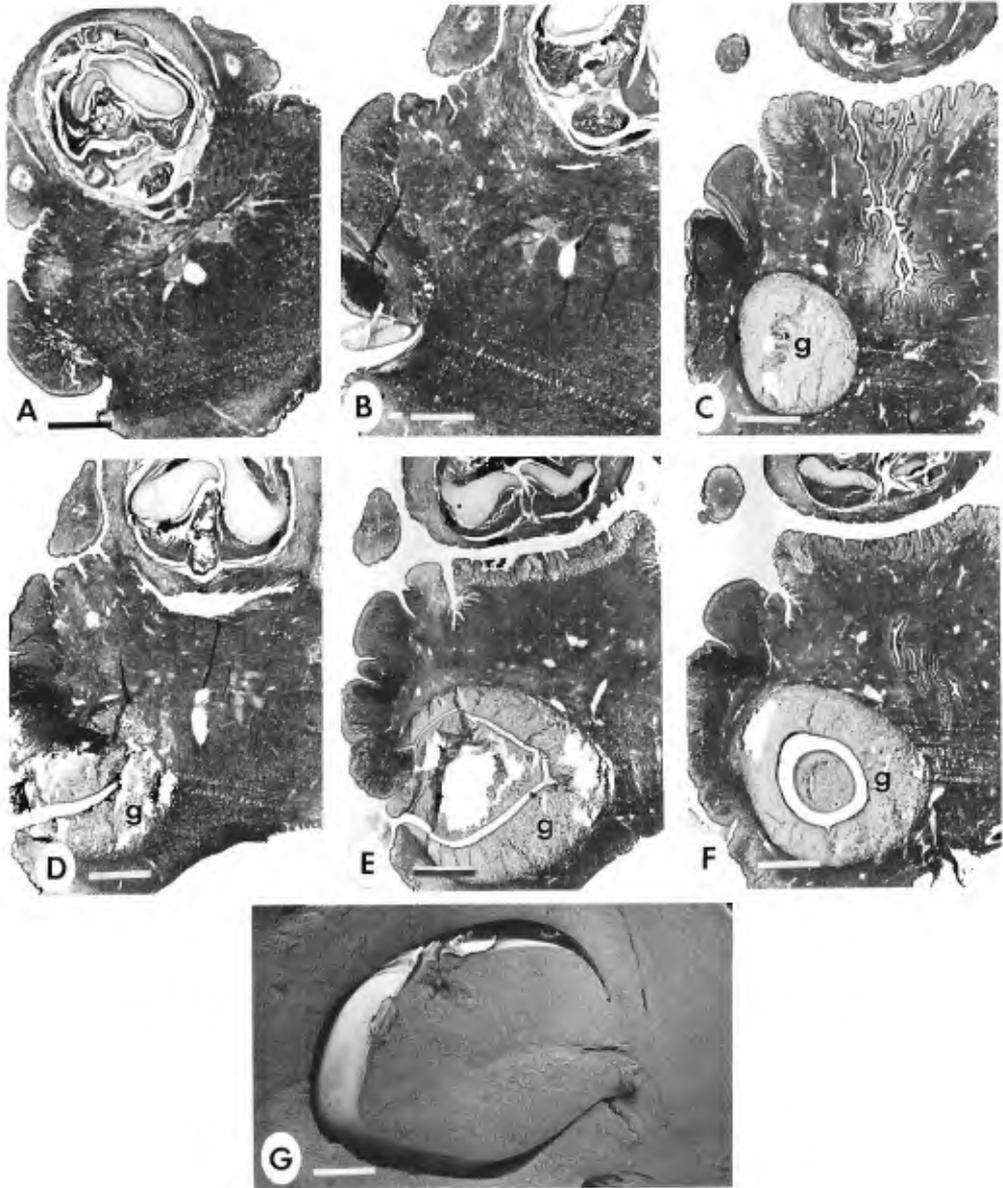


FIG. 20. *Terebralia sulcata*. histological sections of head-foot. A-F, transverse sections through head-foot, anterior to posterior, showing external ovipositor gland (g) (A, B) and its interior chamber (F); note opening into gland (D) and formation of lumen (E, F); bars = 2 mm. G, section through critical point dried ovipositor gland showing lumen and plug-like longitudinal extension emerging from base of gland; bar = 1 mm.

glia (lpg, rpg) closely joined, each with basal statocyst (st); each ganglion giving rise to three nerves innervating foot. Pedal-cerebral connectives (cpc) moderately short and thick;

pedal-pleural connectives thin, adjacent to pedal-cerebral connectives. Subesophageal ganglion with zygoneurous connection (z) to right pleural ganglion. Supraesophageal con-

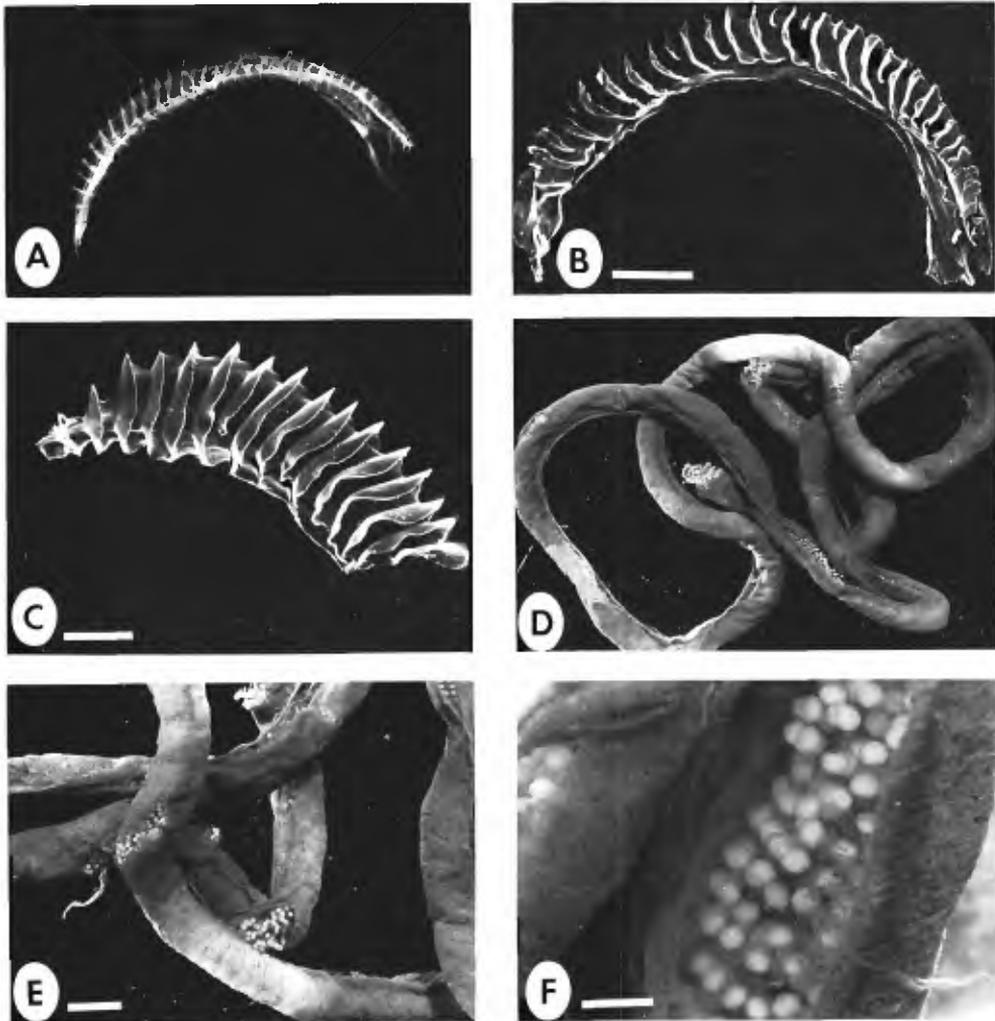


FIG. 21. *Terebralia sulcata*. A, spermatophore (removed from bursa) in sea water; 5.4 mm long. B, C, critical point dried spermatophores, SEM; bars = 900 μm and 300 μm , respectively. D, coiled spawn mass; 30 mm long. E, F, detail of spawn mass showing outer opaque covering of jelly string and numerous egg capsules within; bar = 2 mm.

nective (sec) long; dialyneurous connection (d) between supraesophageal nerve and left pallial nerve (pn). Subesophageal ganglion (sbg) with very short connective to left pleural ganglion. Long visceral loop; visceral ganglion in floor of posterior mantle cavity.

Remarks

Shell: Of all the mangrove snails described herein, *Terebralia sulcata* has the thinnest shell, although it is by no means fragile. This

shell is easily distinguished from that of *Terebralia semistriata* (Fig. 10), its morphologically similar congener, by its smaller size, cancellate sculpture, and particularly by its prominent axial ribs. Shell size is very variable: some populations comprise only dwarfed individuals (Fig. 14J). Shell shape is also variable, especially between populations: shells can be very squat and wide (Fig. 14K,L) or extremely tall and slender (Fig. 14I). Shell sculpture is highly variable, especially in

the number and prominence of axial ribs. In some phenotypes the spiral cords are flat and the shell appears nearly smooth, sculpture consisting of incised spiral and axial lines (Fig. 14A–C,I); other phenotypes have strongly developed spiral cords and axial ribs and appear very cancellate (Fig. 14J–L). Juvenile snails have fine cancellate sculpture and deeply incised sutures (Fig. 14M). As in other *Terebralia* species, there are two plaits on the columellar pillar, extending up the entire shell, and opposite these, on the inner shell wall, there are teeth wherever an external varix has been formed. The shells of both *Terebralia* species are notable for the complete to nearly complete peristome, due to the fusion of the anterior outer lip to the anterior siphonal canal, and for the straight, short, tubular siphon, opening through the middle of the shell base (Fig. 14D,H). The complete peristome allows the animal to clamp down firmly on the substrate, and avoid desiccation and predators while maintaining communication with the external environment through the tubular siphon.

Anatomy: The darkly pigmented snout (Fig. 15A, sn) is one of the distinguishing features of this species. Although it can be considerably extended, the snout does not have the length or elasticity of the supple snout of *Telescopium*.

The semicircular slit that forms a shallow pit on the underside of the inhalant siphon (Fig. 17C) is very similar to that of *Terebralia palustris*. Histological sections show that this siphonal area is highly innervated, and although there is no evidence of a pallial eye as found in some other potamidids, this pit probably functions as a light-sensory organ. It is undoubtedly homologous with the mantle eyes and light-sensory organs of other potamidids, for it is in the same place and innervated with the same nerves; it cannot compare in complexity with the well-developed pallial eye of *Cerithidea* and *Tympanotonus* species (Houbrick, 1984, 1988). Prior to extending its head-foot from the shell, the animal extrudes the sensory pit of the mantle from the tube-like anterior canal of the shell (Fig. 14D,H), allowing it to detect shadows and movement.

The osphradium resembles that of *Telescopium* in being sunken in a pit. A histological cross-section of this organ has been depicted by Maeda (1986, pl. 1, fig. 2), who, in his survey of cerithioidean groups, desig-

nated this kind of osphradium a Type-1 osphradium (Maeda, 1986:35).

The radula of *Terebralia sulcata* (Fig. 16A–C) most closely resembles that of *Terebralia semistriata* (Fig. 11A–D), but differs in having a narrower lateral lamella on the outer margins. Unlike the situation in *Terebralia palustris*, there is no ontogenetic change in radular morphology. The midesophagus is broad, and, as in *Telescopium*, is not developed into an esophageal gland. A crop occurs in *Cerithidea* species (Houbrick, 1984), and a well-developed esophageal gland occurs in members of the family Cerithiidae (Houbrick, 1988). The raised pad on the ventral floor of the stomach (Fig. 17A, rp) is very large and unusual among cerithioideans. Ciliary movements in the stomach suggest that particles entering the stomach from the esophagus are moved in the crescentic groove (cgr) from the posterior stomach around the central pad to the opening to the digestive gland (odg), and onto the gastric shield (gs) and the rotating end of the crystalline style. It is here that amylase is thought to be secreted as part of the digestive process. The wide, thick-walled rectum, with its elaborately folded interior epithelium, probably absorbs fluids from the fecal bolus, and molds and forms the fecal pellets.

Reproductive Biology: Nothing has been recorded in the literature about the reproductive biology, spawn or development of this species; thus a study of reproductively mature animals was undertaken in Hong Kong. The large cream-colored, pad-like ovipositor usually bulges from the surface of the anterior right side of the foot in ripe females, and is much like the ovipositor of *Terebralia palustris*. The small opening at the posterior of the ovipositor (Fig. 20D,E) extends well into the foot, in which it forms a cylindrical chamber (Fig. 20F) that appears to produce a gelatinous substance probably applied during final formation and deposition of the egg mass. The chamber has a longitudinal plug emerging from its posterior wall and filling the lumen so that the cavity itself is narrow (Fig. 20F,G). In section, the extensive glandular part of the ovipositor consists of spongy-looking cells with small nuclei (Fig. 20C–F, g). The epithelium of the chamber consists of a layer of elongate cells having long, darkly staining nuclei, and is ciliated, thus indicating an ectodermal origin. The ovipositor and chamber are similar in origin and placement, and prob-

ably homologous with similar structures described in other cerithioidean taxa (Houbrick, 1988:98, 101), but in *Terebralia*, the chamber does not function as a brood pouch. The ovipositor and chamber of *T. sulcata* are morphologically very similar to those described in *Diastoma melanioides* (Reeve, 1894), of which the chamber might or might not be a brood pouch.

Spawn masses deposited by *Terebralia sulcata* in Hong Kong during March occurred on the roots of mangroves, and were cryptic, being covered by detrital particles (Yipp, pers. comm.). If the detrital particles are scraped from the jelly strings, the developing embryos appear bright green, matching the color of the ovaries of ripe female snails. Although the developmental biology of *Terebralia sulcata* is unknown, its egg capsules are about equal in size to those of *Telescopium telescopium*, which is known to have free-swimming larvae; thus, it can be reasonably assumed that *Terebralia sulcata* also has free-swimming larvae.

Terebralia sulcata is unusual in having an ornate, complexly sculptured spermatophore (Fig. 21A–C). The numerous parallel transverse ridges on the spermatophore apparently anchor it in the bursa (Fig. 19E,F). This kind of spermatophore sculpture may prove to be distinctive of the genus. Within a spermatophore, a narrow elongate chamber holds both euspermatozoa and paraspermatozoa and other acellular elements of unknown composition. Longitudinal sections through a disintegrating spermatophore, *in situ* in the spermatophore bursa (Fig. 19E–H), show that the walls of the spermatophore are compartmentalized and composed of a spongy, acellular, chitinous substance. The sections indicate that the sperm are liberated into the bursa as the walls of the spermatophore disintegrate. The paraspermatozoa are probably resorbed in the bursa, for only euspermatozoa are found in the seminal receptacle.

The nervous system of *Terebralia sulcata* (Fig. 15B) differs little from that of *Telescopium*, although the supraesophageal connective and left pallial nerve are shorter. Bouvier (1887:144–145, pl. 7, fig. 30) has described and illustrated in great detail the nervous system of *Terebralia sulcata*.

Ecology: *Terebralia sulcata* is a hardy generalist, able to tolerate desiccation and a wide range of substrate types, and is able to ingest roughly equal portions of algae and vascular

plants as well as large quantities of detritus and sand. In Hong Kong, Yipp (1980:705) identified four categories of plant materials, microalgae, filamentous algae, macroalgae and vascular plants, all of which underwent reduction on passage through the gut, with the possible exception of the filamentous algae.

In contrast to *Terebralia palustris*, which is a much larger snail and which occurs on fine mud substrates, *Terebralia sulcata* prefers coarser substrates and attains its highest densities on them. I observed a population of this species in a stand of dwarf mangroves in Hong Kong, a habitat that has been thoroughly described by Morton & Morton (1983:222–223). This population, which also has been studied by Wells (1983) and Yipp (1980), occurs on intertidal sand and rocky habitats throughout the salt marsh and on the roots of the dwarf mangroves. Other Hong Kong populations of *Terebralia sulcata* occur in protected bays on similar substrates from which mangroves are absent (pers. obsr.; Wells, 1983:145). In contrast to the Hong Kong populations, Wells (1983:152) showed that this species is found only in mangroves in Western Australia and suggested that habitat segregation might differ in various regions. For instance, in the mangroves of the Bay of Rest, Western Australia, Wells (1980:2) found *Terebralia sulcata* was widely distributed throughout the seaward mangroves, *Rhizophora stylosa* and *Avicennia marina*, where it was common among the pneumatophores of the latter; however, in a mangrove forest in the Kimberly area, Western Australia, *Terebralia sulcata* was narrowly restricted to the floor of the *Aegialitis* zone (Wells & Slack-Smith, 1981). Wells (1986:88) remarked that of the mollusks living among *Avicennia* in the Bay of Rest, Western Australia, *Terebralia sulcata* dominated in terms of density and biomass, forming 50 percent of the total numbers and 85 percent of total biomass. Wells might not have discriminated *Terebralia sulcata* from *Terebralia semistriata*; consequently, his conclusions about habitat segregation might be erroneous and should be reconsidered. In Java, Benthem Jutting (1956:443) recorded this species living on mudflats, often attached to branches and roots of mangroves or on stones. It is likely that the microhabitat of this generalist species varies throughout its geographic range.

Little has been written about the predators of this species. Wells (1986:88) has sug-

gested that in the Bay of Rest, Western Australia, *Terebralia sulcata* commonly lives among *Avicennia* pneumatophores for protection from predatory rays, which are largely unable to feed among them. A small copepod lives in the mantle cavity of the Hong Kong populations (pers. obsr.).

Fossil Record: *Terebralia sulcata* can be traced from the Late Miocene to the present and is well represented in the fossil records. Neogene records include Java, Sumatra, Nias, Timor, New Guinea and the Philippines (Regteren Altena, 1941:17). This species has been recorded as a Miocene fossil from Eniwetok Atoll, Marshall Islands (Late Miocene; Ladd, 1972:27), from Java (Late Miocene; K. Martin, 1899:211; Wissema, 1947:48) and from the Philippines (Wissema, 1947:48). There are Pliocene records from Java (K. Martin, 1899:211; Wissema, 1947:48), Sumatra (Wissema, 1947:48; Vlerk, 1931:25), Timor (K. Martin, 1899:211; Tesch, 1920:57, pl. 131, figs. 183,184; Vlerk, 1931:25; Wissema, 1947:49), New Guinea (Wissema, 1947:49) and the Philippines (Wissema, 1947:49). Pleistocene records from Java were cited by Wissema (1947:49). There are also Holocene records from Nias and the Celebes (Wissema, 1947:49) and from Taiwan (Regteren Altena, 1941:17). During this study, fossils of *Terebralia sulcata* from Niue were examined, indicating a previously wider geographic extension into the southern Pacific.

Distribution: The easternmost extension of this species in the Pacific Ocean is in the western Caroline Islands and in Guam (Roth, 1976:8). *Terebralia sulcata* is common throughout the western Pacific from the Ryukyus south to Taiwan, China, Viet Nam, and throughout the Philippine archipelago (Fig. 13, shaded area). It also occurs in Borneo, New Guinea, and throughout tropical Australia. *Terebralia sulcata* is common throughout the Indonesian Archipelago, the Malayan peninsula, and in the estuaries and mangroves of Viet Nam, but according to Brandt (1974:195), has never been found alive in Thailand.

Material Examined: MALAYSIA: Kranji, Singapore (ANSP 239547; USNM 631935, 794078); Pulau Hanto, SW of Keppel Harbor, Singapore (USNM 660843). VIET NAM: Quiuhon (AMNH 86016). INDONESIA: Pulau Bai, Batu Gp, off Sumatra (USNM 654608); Pulau Siburu, N of Sipora, SW Sumatra (USNM 654700); Koeta Beach, Bali (USNM

617606); Limbe Id, Gulf of Tomini, Celebes (USNM 243938); Pasir Putih, Jailolo District, Halmahera, Moluccas (USNM 837034, 863460); Dorosago, Maba District, Halmahera, Moluccas (USNM 837084); W side Mitak Id, Jamdena Strait, Tanimbar, Moluccas (USNM 747535); mouth of Maikoor River, Aru, Moluccas (USNM 755616). NEW GUINEA: Sowek, Soepoeri Ids, Schouten Ids, West Irian (ANSP 207871; USNM 835664); Ave Id, Geelvink Bay, West Irian (AMNH 128264). BORNEO: Tanjung Aru, Jesselton, N Borneo (USNM 658482); Port Essington, N Borneo (ANSP 225722); Po Bui Id, Sandakan, N Borneo (USNM 232866; AMNH 150829); Stanati, Kudat District, N Borneo (USNM 632194); N side Malawi Id, N Borneo (AMNH 106821); Taganak Id (USNM 243940). AUSTRALIA: Rowley Shoals, off Broome, Western Australia (USNM 847084); Bay of Rest, North West Cape, Western Australia (USNM 801606); creek, Darwin Harbor, New Territory (USNM 867710); Ludmilla Creek, 6 km N of Darwin, Northern Territory (USNM 828813); East Arm, 8 km of ESE of Darwin, Northern Territory (USNM 828812); Bickerton Id, Gulf of Carpentaria, New Territory (USNM 602227); Thursday Id, Torres Strait, Queensland (USNM 613611, 603512; ANSP 242444). PHILIPPINES: Port Matalvi, Luzon (USNM 243616); Batangas, Luzon (USNM 233244); Port San Vicente, Palaui Id, Luzon (USNM 232966); Kawit, Luzon (USNM 599751); Dumurug Id, Masbate (USNM 244022); Puerto Galero, Mindoro (USNM 777282); Alimango River, Burias (USNM 301727, 301726); Cebu, Cebu (USNM 419342); Siasi, Jolo (USNM 233234); Batag Id, Samar (USNM 472943); Puerto Princessa, Palawan (USNM 239799); Palawan (FSM 4168); Viejo Victorias, Negros (USNM 313250); Zamboanga, Mindanao (USNM 244035); Siminor Id, Tawi Tawi Gp (USNM 233090); Tataan, Simaluc Id, Tawi Tawi Gp (USNM 243699). CHINA: Tai Tam Harbor, Hong Kong (USNM 858379, 862676); Ting Kok, Tolo Harbor, New Territories, Hong Kong (USNM 858420). RYUKYUS: Okinawa (USNM 671076); Naha, Okinawa (USNM 632448); Orawan, Okinawa (USNM 593554); Saedake, Okinawa (AMNH 171733); Aha, Okinawa (AMNH 171732). CAROLINE ISLANDS: Timil Harbor, Yap (USNM 485811); Yaptown, Yap (USNM 634251, 485850); Yap (USNM 634415); Garumisukan River, Karamando Bay, Babelthuap, Palau (USNM 620862; ANSP 200599); Babelthuap Id,

TABLE 1. Character comparison of *Telescopium* with *Terebralia*.

<i>Telescopium</i>	<i>Terebralia</i>
Shell	
1. shell aperture tangential	shell aperture normal
2. peristome closed	peristome open
3. one columellar fold	two columellar folds
4. palatal teeth absent	palatal teeth present
5. no varices on shell	varices present
Anatomy	
6. snout very long, supple	snout short, robust
7. snout tip with pad	snout tip without pad
8. foot groove in both sexes	foot groove in females only
9. ovipositor small	ovipositor large
10. ovipositor lacking chamber	ovipositor with chamber
11. weak papillae on mantle edge	large papillae on mantle edge
12. osphradium in deep trench	osphradium not in trench
13. osphradium 1/4 gill length	osphradium 2/3 gill length
14. osphradium next to ridge	no ridge
15. radula & buccal mass small	radula & buccal mass large
16. oviduct open	oviduct with medial fusion
17. oviductal groove complex	oviductal groove simple

Palau (USNM 631786); Koror, Palau (USNM 636196; AMNH 92748); Ngesias Village, Peleliu Id, Palau (USNM 656526); Arakitaoch Stream, Palau (USNM 656505); Ponape (AMNH 218504).

DISCUSSION

Comparisons of the morphologies, life histories and ecology of the species comprising the genera *Telescopium* and *Terebralia* and their relationships to other members of the Potamididae follow. The major characters distinguishing the two genera are presented in Table 1.

Juveniles of large mangrove-dwelling snail taxa, although superficially similar to one another, can be distinguished easily: *Telescopium* juveniles (Fig. 1H) are conical, sculptured with many spiral cords, and entirely lacking axial sculpture; *Terebralia palustris* juveniles (Fig. 7I,J) are fusiform, have incised sutures, and are sculptured with wide, flat axial ribs; *Terebralia sulcata* juveniles (Fig. 14M) are fusiform, inflated, and have a deeply incised suture and a cancellate, beaded appearance; *Terebralia semistriata* juveniles have stocky, inflated shells with weak sutures, and in early stages have dominant axial sculpture (Fig. 10G), which later becomes more cancellate (Fig. 10H).

Pallial siphonal eyes and light-sensory organs are common among members of both the

Potamididae and other cerithioidean families. These pallial structures are thought to be homologous because they all have the same location and innervation (Houbrick, 1984:10–11). Most members of the family Potamididae appear to have pallial light-sensory organs located on the underside of the inhalant siphon. A deep sensory pit (presumably light-sensitive) in the inhalant siphon (Fig. 17C), occurs in *Terebralia* species. In *Telescopium* this structure is even more highly developed and contains a lens. A fully developed pallial eye with lens and cornea occurs in *Cerithidea* species (Houbrick, 1984:10–11) and in *Tympanotonus fuscatus* (Linné, 1758) from West Africa (Johansson, 1956). In the family Batillariidae, pallial light-sensitive organs have been observed only in *Pyrazus ebininus* (Bruguière, 1792) (see Tenison-Woods, 1888: 175). Similar organs have also been found in species of *Rhinoclavis* Swainson (Houbrick, 1978) and of *Gourmya* (Houbrick, 1981b: 5–6), both of the family Cerithiidae Férus-sac.

The very long snout of *Telescopium* (Fig. 3B, sn) is comparable to the long extensible snouts seen in some *Cerithidea* species (Houbrick, pers. obsr.), but the radula is very small and weak. In contrast, the snout of *Terebralia* species (Fig. 15A, sn) is more robust, broader, somewhat shorter, and darkly pigmented, and contains a long, robust radula.

Both *Telescopium* and *Terebralia* species have propodial mucous glands with slit-like openings that are unusual in extending back

to the middle of the foot (Figs. 3B, 17B, amg). This also occurs among members of the Planaxidae (Houbrick, 1987:445).

In contrast to *Terebralia* species, the ovipositor of *Telescopium telescopium* (Fig. 3A, ovp) is much smaller, located closer to the edge of the sole, and lacks an inner chamber. The posterior location of the ovipositor in *Telescopium* is unusual: in species of *Cerithidea* (see Houbrick, 1984) and in *Terebralia*, it is situated more medially on the foot (Fig. 15A, ovp). The very large ovipositor with interior chambers (Fig. 20) in female *Terebralia* species is an unusual structure, but not unique among cerithioideans, for a similar chamber in *Diastoma* has been found (Houbrick, 1981c:607–608). It is thought that secretions from these internal glandular chambers contribute to the coating of the spawn mass during deposition. The ovipositors with chambers in the foot of *Terebralia* species are homologous with, and a morphological step toward, the cephalic brood pouches seen in planaxids, thiarids, siliquarids and fossarids (Houbrick, 1988:101). Cephalic brood pouches among cerithioideans appear to be modifications of the invaginated ectodermal ovipositor glands.

Reduction of the ctenidium occurs among Potamididae, especially in the more highly amphibious forms. The ctenidial filaments of *Terebralia* species are much reduced in height, and in *Telescopium telescopium* they have become a series of fine ridges (Fig. 2F,G, ct). The extreme of this trend occurs among some members of the genus *Cerithidea* Swainson, 1840, in which ctenidia are so greatly reduced and degenerate that they are virtually absent in several species (Houbrick, 1984:11).

Radular patterns of Potamididae members are all similar in that the rachidian tooth lacks basal cusps, the lateral extensions of the lateral tooth are of short to medium length, and the flanges of the inner and outer marginal teeth are of equal length. In contrast, batillariids have basal cusps on the rachidian, very long extensions on the lateral tooth, and the flange on the outer tooth is much shorter than that of the inner tooth.

Perhaps the most striking internal anatomical feature of the large potamidids is the long style sac (Fig. 17A) and crystalline style, which protrude anteriorly as far as the posterior mantle cavity. Berkeley & Hoffman (1834: 436) were puzzled by the style in *Telescopium*, describing it as ". . . a cylindrical body consisting of a rather firm transparent jelly . . .," and suggested that it secreted

something necessary for the eggs. Very long styles also occur among the Strombidae. The style of *Telescopium* is undoubtedly the longest seen among potamidids, but in general form is similar to those of *Terebralia* species (this paper) and *Cerithidea* species (Houbrick, 1984:7). All of the large potamidid taxa with very long crystalline styles also lack esophageal glands. Species of *Cerithidea* Swainson, 1840, also lack an esophageal gland, but have instead a dilated mid-esophagus, which presumably functions as a crop (Houbrick, 1984:5). Driscoll (1972:384) suggested a functional relationship between style length and the composition of ingested food, but this does not seem to be the case because *Telescopium* ingests very fine particulate matter, while *Terebralia* eats fallen mangrove leaves, and both taxa have long styles. The long style sac and the lack of an esophageal gland are synapomorphies defining the family Potamididae (see Houbrick, 1988).

The large raised pad dominating the floor of the stomach (Fig. 17A, rp) and the crescentic groove (cgr) bordering the pad are notable features of *Telescopium* and *Terebralia* species. Seshaiya (1932:174) pointed out that the pad ("fleshy ridges") in the stomach is the result of the typhlosole-like foldings of the ventral wall of the stomach. He noted that an examination of the stomachs of many style-bearing taxa does not lend support to the view that the crescentic groove on the stomach floor is a vestigial spiral caecum.

Among cerithioideans, the pallial oviduct morphology of *Telescopium* is by far the most unusual and atypical. The complexity of the gutter system in the laminae (Fig. 5C,D) is equaled only by that of *Modulus modiolus* (Houbrick, 1980:130, fig. 8). The numerous, thick transverse ridges on the glandular portions of the laminae bordering the oviductal groove (Fig. 5C,D, ovd) occur elsewhere only in turritellid pallial oviducts (Carrick, 1980: 245). The partial medial fusion (Figs. 12, 18F, me) of the pallial gonoducts of *Terebralia* species is unique among cerithioideans, but in other respects the gonoducts are typical of the superfamily. Complete fusion of the pallial oviducts occurs only in some thiarids such as *Thiara* Röding, 1798, *Tarebia* H. & A. Adams, 1854, and *Melanoides* Olivier, 1804.

The spawn masses of members of both genera appear to be similar in morphology, and contain many small egg capsules typical of species having free-swimming larval stages. The wide distributions of species in both genera reflect good dispersal ability.

Nearly all cerithioideans are thought to produce spermatophores, although few have been described in detail. The only cerithioidean spermatophore studied under SEM is that of *Modulus modulus* (Linné) (Houbrick, 1980: 127–129, figs. 6, 7), which is spindle-shaped, unsculptured and composed of a microscopic fibrous matrix. Spermatophores have been recorded in numerous cerithioidean families (for summary, see Houbrick, 1988:111) and are usually simple, ovoid or crescentic structures having smooth surfaces and a few longitudinal keels. The spermatophore of *Terebralia sulcata* (Fig. 21A–C) is by far the most elaborate observed among cerithioideans.

The nervous systems (Figs. 3C, 15B) of all the large potamidids in this review are similar, differing only in minor details, such as the length of the supraesophageal connective and the length of labial nerves. Zygoneury and dialyneury are well established in both genera. The well-developed triple nerves emanating from each pedal ganglion extend forward into the foot and innervate the ovipositor and glandular portions of the propodium. The major ganglia of the central nervous system are closely concentrated with the exception of the supra- and subesophageal and visceral ganglia, which are separated from the central nervous system by long connectives. The potamidid nervous system is thus unusual in being simultaneously “close” and “loose.”

All four of the potamidid taxa described in this study might occur in sympatry, but they usually differ in microhabitat. *Terebralia palustris*, the most widely distributed species, occurs with *Terebralia sulcata* and *Telescopium telescopium* in many parts of its range. Adult *Telescopium telescopium* and *Terebralia palustris* are frequently together on the mud, but have very different diets. *Terebralia palustris* prefers the shade of the mangrove canopy and is somewhat segregated from *Telescopium telescopium*, which appears to prefer a more open habitat. In the Bay of Rest, Western Australia, Wells (1980: 2) found that *Terebralia palustris* was narrowly confined to the upper limit of the mangroves, whereas *Terebralia sulcata* was more widely distributed and occurred in the lower limit of the mangroves. In addition, the two congeners preferred different sediment grain sizes. Densities of *Terebralia palustris* were greatest in fine mud, while *T. sulcata* had its greatest densities in coarser sediments. Wells (1980:4) pointed out that although *Terebralia palustris* occurs amongst mangroves of the genera *Bruguiera*, *Cerriops* and *Avicen-*

nia, it avoids *Rhizophora stylosa*, and suggested that the *Rhizophora stylosa* sediments were probably too acidic for it. Although the two common *Terebralia* species might occur in sympatry, Wells (1980:1–2) pointed out that there are wide geographic gaps in the distributions of *Terebralia sulcata* and *Terebralia palustris*. As mentioned earlier, Wells might not have been aware of the existence of *Terebralia semistriata*, which is very common in the mangroves of this region, and might have lumped it with *Terebralia sulcata*. *Terebralia semistriata* occurs on soft mud; I have found it on mudflats of the Queensland coast devoid of mangroves.

Terebralia is both the more species-rich and the older of the two genera, having a fossil record beginning in the Early Miocene. In terms of numbers of species, it appears to have reached its acme during the Middle to Late Tertiary, but now is represented by only three living species. In contrast, *Telescopium*, which can be traced back only as far as the Late Miocene, appears to have been a species-poor, highly apomorphic genus, represented today by only one living species.

In a previous phylogenetic analysis of fifteen families of the superfamily Cerithioidea, I suggested that each of the subfamilies thought to comprise Potamididae, the Batillariinae and Potamidinae, be accorded full familial status (Houbrick, 1988:114, 117). The morphological characters of *Telescopium* and *Terebralia* species described herein emphasize even more the great differences between these potamidid genera and the batillariids. It is therefore formally proposed that the *Batillaria* group be excluded from the family Potamididae and be raised to familial rank as the Batillariidae. This action eliminates subfamilial categories from the Potamididae.

The suggestion that the *Cerithidea* group be accorded familial status (as Cerithideidae; Houbrick, 1988:118) is herein revoked. Many shared anatomical characters such as those of the alimentary system, mantle cavity organs, and pallial eyes, unite *Cerithidea* with *Telescopium* and *Terebralia* in the Potamididae. *Cerithidea* differs from other potamidids in having two seminal receptacles, hardly reason for familial recognition.

The exact phylogenetic relationship of *Telescopium* and *Terebralia* to the potamidid genera *Cerithidea* Swainson, 1840, *Pirenella* Gray, 1847, and *Tympanotonus* Schumacher, 1817, cannot be ascertained until anatomical study of the two latter genera is undertaken. The standing of Potamididae and Batillariidae

in relation to other closely related families within Cerithioidea awaits a more formal phylogenetic analysis of these groups in conjunction with other unstudied cerithioidean families.

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