A Study of Mitrid Radulae and a Tentative Generic Arrangement of the Family Mitridae

(Mollusca: Gastropoda)

BY

WALTER OLIVER CERNOHORSKY

Vatukoula, Fiji Islands

(47 Text figures)

During the compilation of the faunal monograph on Fijian Mitridae (Cernohorsky, 1965), some difficulty was experienced with the correct generic assignment of certain Fijian mitrids; furthermore, the taxonomic value of certain accepted genera remained obscure.

The works of Thiele (1931) and Wenz (1943) remain the only recent taxonomic treatments on the subdivision of the family, although a recent paper by Cotton (1957) does contain some proposals on the generic division of the Mitridae. The latter work, however, is restricted to genera inhabiting Australian waters, and the excessive number of genera listed (26 genera for 250 species) was based on conchological characters.

Very little work has as yet been done on the anatomy of the Mitridae, and the present tentative arrangement of the group will remain only an incomplete account in this respect. With a broadening knowledge and future research on the family, changes and revisions are to be expected.

This review is mainly concerned with living genera of Mitridae, and extinct genera have been omitted from the synonymy. It should be pointed out that the synonymy of fossil genera, i.e. those regarded as chronological congeners of recent genera, may not be complete; the comprehensive library required to achieve this end is not at the writer's disposal. Furthermore, some conclusions reached, particularly the generic relationship, must for the time being remain hypothetical; additional information and data will of course prevent a stagnancy of the present proposed arrangement.

Dr. Myra Keen, Stanford University, kindly drew my attention to the fact that Mr. Eugene Coan, Stanford University, was presently working on a generic revision of Mitridae in preparation for the "Treatise on Invertebrate Paleontology." It was agreed between Mr. Coan and myself to present this paper as a self-contained unit of analytical conclusions based on anatomy, ecology and external morphology of mitrid mollusks. Mr. Coan's research work appears below and provides a more comprehensive taxonomic treatment of the group, with pertinent information on taxonomy and biblography on Recent and fossil genera.

INTRODUCTION

A generic subdivision of the family based purely on conchological characters must inevitably differ from one based on shell, radula, anatomy, ecology and distribution. Although shell characters are well defined in most cases, they are by no means clear-cut in all species of the respective genera; this is especially noticeable in such related genera as *Vexillum* and *Pusia,* and *Mitra* and *Strigatella.* Species belonging to these genera may not always be correctly assigned to the proper genus on shell morphology alone; since the radulae, however, are often fundamentally different, a generic separation can be achieved through radula examination.

Results of radula studies of mitrids may be found in the works of several authors, e.g. Gray (1853), Troschel (1868-1869), Cooke (1920), Peile (1922, 1936, 1937), Thiele (1931), Habe (1943), Barnard (1959), and Cernohorsky (1965, 1966). The English malacologists Cooke and Peile based their subdivisions of the

family primarily on the radulae of the various mitrid groups. Cooke (*l. c.*) found the radula pattern of mitrids to fall into 12 distinct groups, and Peile (1936) added an additional group to Cooke's subdivision. Cooke (*l. c.*) pointed out that the lateral teeth of Mitridae are of superior value in estimating the relationship of allied groups and species. This is indeed true, since the diverse pattern of the rhachidians may crop up at any time in almost any genus with the exception of *Vexillum* and *Pusia*; the pattern of the laterals, however, is peculiar only to a certain group of species or a certain genus. Cooke (*l. c.*) points out that in this respect the Mitridae fall into line with the allied genera *Fusus* Bruguière, 1792, *Fasciolaria* Lamarck, 1801, *Latirus* Montfort, 1810, and *Peristernia* Mörch, 1852, in all of which the laterals rather than the rhachidians supply the best evidence for classification.

It is unfortunate that the identity of the radulae in Cooke's study must often be suspect. Cooke examined and figured mostly radulae from the Gwatkin collection, and rarely if ever saw the actual shells from which these radulae were removed. In the case of well-known species the identification was most probably correct, but the far from stabilized mitrid nomenclature of the 1920's made an always correct identification impossible. Peile (1936) and Barnard (1959) also commented on the matter of misidentifications among the Gwatkin radulae. Speculations as to the true identity of certain radulae could have been eliminated if an illustration of the species from which the radula was removed had been cited.

HISTORICAL

The Linnaean species of Mitridae were originally placed in the genus *Voluta* Linnaeus, 1758, with the exception of *Pterygia scabricula* (Linnaeus) which was assigned to *Buccinum* Linnaeus. Röding (1798) established the genera *Mitra, Vexillum* and *Pterygia*, although the latter was probably not intended for the group of Mitridae as used at present. Swainson (1831) established the genera *Tiara, Mitrella* (=*Swainsonia* H. & A. Adams) and *Mitreola*. In 1840 the same author drastically reorganized the family and placed the subfamilies Volutinae and Mitrinae in the family Volutidae. The Mitrinae were divided by Swainson into two genera, i. e. *Mitra* and *Tiara,* which in turn were divided into 10 subgenera; the genera *Mitreola, Conoelix* (=*Imbricaria* Schumacher, 1817) and *Mitrella* (=*Swainsonia* H. & A. Adams) were classed as "aberrant genera." From these 15 Swainsonian genera and subgenera, 8 have a basis in radula characters, while one genus (*Mitreola*) based on a fossil species remains of doubtful value.

Cooke (1920) divided the Mitridae into 12 separate groups according to the diverse radula patterns, but provided only very few taxonomic units for the reception of his groups. The majority of his groups is acceptable, with the exception of group 3 (*Mitra coriacea* Reeve, 1845) and group 9 (*M. aerumnosa* Melvill, 1888) which must be synonymized with *Mitra* s. str.

In comparison with its next allied family, the Volutidae, the mitrids remained undivided for a considerable length of time, although their radulae are as diverse as those of the volutids; consequently, the genera *Mitra* and *Vexillum* proved to be the favourite dumping ground for an array of unrelated forms. In contrast to the mitrids, the Volutidae have been subdivided to such an extent that in a recent review of the family (Weaver, 1964) the 209 valid species are assigned to 67 genera; 62 of these have been established for living species only, and on an average the distribution is about three species per genus, while only four species remain in the Linnaean genus *Voluta*. The present tentative division of the family into 12 genera and 4 subgenera may therefore appear somewhat conservative; this arrangement, however, corresponds more or less to our present-day knowledge of the group.

GENERAL

The Mitridae are rhachiglossate prosobranchs of the order Neogastropoda within the superfamily Volutacea. An estimated 85% of all recent species inhabit the Indo-Pacific region, 5% the Mediterranean and East Atlantic regions, while the remainder is distributed over the West Atlantic, Caribbean and Panamic regions. Members of the family prefer warm and temperate waters, and 80% of all species are tropical and subtropical in distribution. The geographical area from Mozambique to Polynesia is the richest in species, with the distributional optimum reaching its apparent saturation point in the Western Pacific arc province and declining in all four directions of the compass.

In comparison with other groups of mollusca, the Mitridae are geologically speaking a comparatively young family and most probably arose during Cretaceous times from a buccinoid ancestor; they are already well represented in Eocene deposits of Europe and the Lower Mokattam beds (Middle Eocene) of Egypt. Prior to the disappearance of the ancient Tethys sea, Mitridae spread into the West Atlantic and Indo-Pacific regions, and

during Miocene times were well established in South Africa, India, Japan, Australia and Indo-Pacific Islands. With the declining temperatures of the Late Oligocene and Early Miocene and the gradual vanishing of the tropical Tethys fauna, the mitrid genera *Cancilla* and *Vexillum* are dying out in the European region, and the genus *Mitra* has moved toward warmer seas during Pleistocene times. The genera *Strigatella, Pusia* and *Scabricola* are probably later developments of the mitrid branch and may have developed during Early Miocene, while *Swainsonia, Imbricaria* and *Pterygia* are Recent Indo-Pacific offshoots. The genus *Charitodoron* TOMLIN, discovered only in recent years, is somewhat of an enigma in the evolutionary theory of the mitrids, and certainly requires further study; it may well represent the most primitive genus of the family.

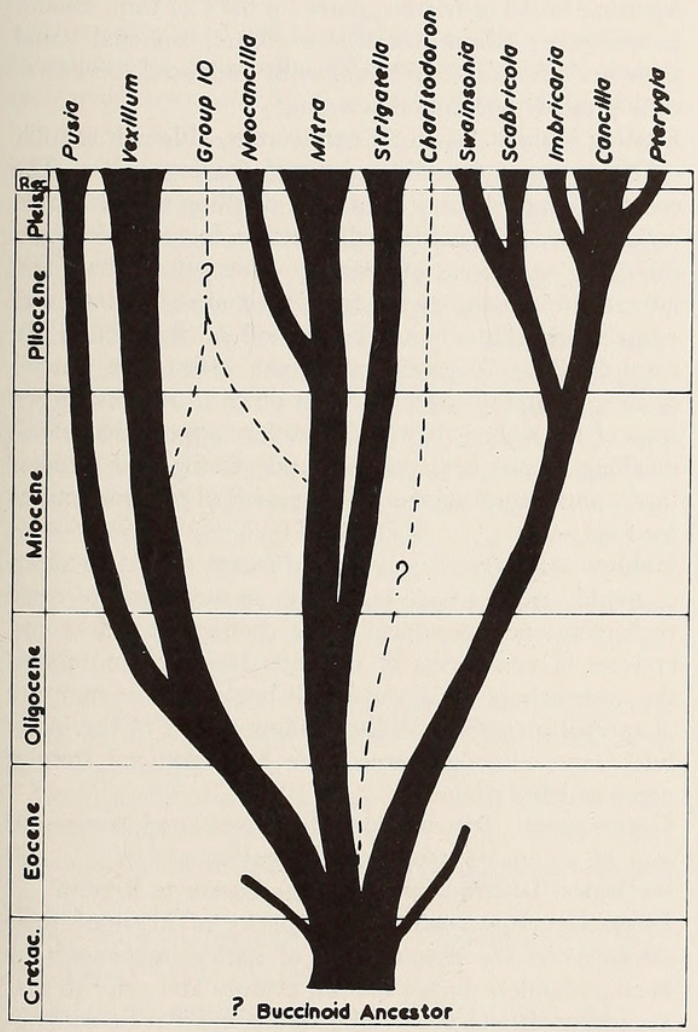


Figure 1

Hypothetical Tree of Origin of the Genera of the Mitridae

Mitrid species of the Early Tertiary are almost entirely extinct, while those of Late Tertiary resemble Recent forms from which they can be separated only infraspecifically. Pleistocene representatives, however, do not appear to differ from Recent living forms.

MATERIAL AND METHODS

Moderately large radulae (3 mm to 8 mm) have been dissected directly from the buccal region of the animal and cleaned from adhering muscle tissue in a 5% cold solution of sodium hydroxide. Smaller radulae (2 mm to 3 mm) have been removed by complete dissection of the buccal bulb region and were soaked in a 5% cold solution of NaOH for 24 hours. Very small radulae (1 mm to 1.5 mm) have been extracted by placing the complete animal in a 10% cold solution of NaOH for 24 hours. Direct dissection and removal of the odontophore is preferable, since potassium hydroxide or sodium hydroxide are not without effect upon chitinous material of the radula, especially in cases where the ribbon is thin and delicate. Hard to find radulae were located by adding a drop of a 1% solution of chlorazol azurine to the macerated material.

A curling of the radula at either end of the ribbon was often experienced. The radula may be successfully straightened by placing the ribbon on the glass-slide with a droplet of water and straightening the first half dozen rows at the nascent end with a needle; the cover-slide is then placed on the flattened portion of the ribbon and gently slid towards the anterior end while at the same time the ribbon is being uncurled with a fine needle from underneath and ahead of the cover slide. Care should be taken in this manipulation as otherwise the ribbon might be severed or teeth displaced.

After cleaning in fresh water, radulae were placed in 70% alcohol for 24 hours, and upon removal dehydrated with 80%, 90% and absolute alcohol. Since most mitrid radulae can be examined unstained, no staining medium has been used as this tends to oxidize in time in tropical climates. Care has been taken in not exerting pressure when placing the cover glass on the slide, since laterals may be splayed and in a different position than is the case in nature.

Volutacea

Mitridae Swainson, 1831

The family is a fairly large one, containing about 500 Recent species. In the present account 4 subfamilies, 12 genera and 4 subgenera are considered.

Animal: Animal with a moderate or large foot, bluntly truncated anteriorly, pointedly rounded posteriorly; in certain sand-dwelling genera the foot extends posteriorly past the apex of the shell. Mantle thin, papillae absent; siphon moderately long or short, thick or slender, simple at distal end; eyes in the form of a simple unicoloured pupil or occasionally ringed, situated near the extremity of the broad base of the tentacles, which may be long or short; proboscis short and thick or long and slender.

Anatomy: The animals are gonochoristic, with the variable penis situated behind the right tentacle; it lies entirely under the mantle facing backwards. Proboscis containing a small odontophore, secured to the wall by a pair of nerve tissues. Salivary glands paired but merging in some subfamilies; a part of the hypobranchial gland is responsible for the purple secretion consisting of the chemical dibromindigotin. A poison gland which is long, slender, smooth and extendable, is present in most subfamilies with the exception of the Vexillinae; the poison gland is fawn coloured and pointed at the distal end in *Mitra clathrus* (Gmelin), and measured 19.0 mm in an animal with a shell 33 mm long. Osphradium well developed in most genera, and an oesophageal caecum ("Vorderdarm" or fore-gut gland of Thiele) is present in all families except the Vexillinae (*fide* Thiele, 1931).

Radula: Radula of the rhachiglossan type, consisting of various patterns in different genera but primarily of triserial construction, with only one genus (*Pterygia*) lacking laterals. Radula moderately short, ranging from 1 mm to 10 mm (3% to 35% of shell-length) and fairly narrow, i. e. from 9% to 30% in width of total ribbon length; the ribbon is variable in colour, but generally translucent white, yellow, amber or rusty-brown. The rhachidian teeth range from unicuspid to multicuspid, while the laterals are undergoing reduction and in the subfamily Vexillinae are reduced to simple "sickle-shaped" teeth. A similar diversity of the rhachidians can be observed in the Volutidae, where characters vary from the multicuspid rhachidian of *Voluta* Linnaeus, tricuspid rhachidian of *Aulica* Gray, 1847, and *Cymbiola* Swainson, 1831, to the unicuspid rhachidian of *Amoria* Gray, 1855. In the Mitridae there is a definite correlation between the length and number of teeth of the ribbon as compared to shell-length.

Shell: Shell from 5 mm to 170 mm in size, variable in shape, but generally fusiform, turreted, pyriform ovate or cylindrical. Whorls number from 6 to 13, nuclear whorls from 1 to 3½ and are generally glassy and smooth. Shell either smooth or sculptured with axial plicae, transverse ridges, grooves, pits or nodules. Columella usually calloused and with from 2 to 9 oblique plicae; in the genus *Charitodoron* Tomlin, 1932, the columella is smooth. Aperture broad or narrow, outer lip thick or thin, smooth or nodulose; labrum smooth or lirate, siphonal canal short and truncated or prominently produced, periostracum present, operculum wanting.

Feeding Habits: Primarily carnivorous, although radular evidence suggests a divergence of feeding habits. The construction of the radula of sand-dwelling mitrids would make the radula particularly suitable for a tearing and shredding technique of feeding; more often than not, laterals are missing in the front rows of the ribbon, and cusps of rhachidians are broken off at their bases. In coral-dwelling *Strigatella* and some *Mitra,* the rhachidians and laterals are both worn down in the first dozen rows of the ribbon. It would therefore appear that coral-dwelling species are sweeping and grazing over detritus layers of the coral substratum in search of microorganisms for food.

Habitat: Mitridae are generally found buried in clean or muddy sand of wide lagoons or in sand-pools of coral reefs; some genera appear to be confined to cracks and crevices of coral reefs of the intertidal zone or inhabit the underside of coral and basalt boulders. The majority of species is confined to the shallow waters of the intertidal zone, although some have been dredged from a depth of 940 fathoms.

Geographical Distribution: In warm and temperate seas of all major geographical provinces.

Geological Distribution: From the Eocene to Recent.

Economic Importance: Large species of Mitridae were employed in the manufacture of native implements by Pacific islanders during the last century and prior to that as hand-tools and net-weights by various Pacific communities; otherwise there seems to be little commercial use for this family of mollusks.

Mitrinae Swainson, 1831

(Mitrianae, Mitranae, Mitriana Swainson, 1831 — emended to Mitrinae Swainson, 1840)

This subfamily includes one of the oldest surviving genera and its offshoots and is divided into 5 genera and one subgenus.

The radula is triserial, rhachidians are small and variable in shape, with from 3 to 12 cusps, laterals variable

in form and with 10 to 45 cusps; extendable poison gland present in members of this subfamily. Eggs laid in vase-shaped egg-capsules, 15 to 40 scattered over the substratum; each capsule contains from 300 to 500 white, cream-coloured or translucent-yellow eggs.

Mitra Röding, 1798

Mitra Röding, 1798, Mus. Bolten., p. 135 – Type species by subsequent designation (Winckworth, 1945) *Voluta episcopalis* Linnaeus, 1758 = *Mitra mitra* (Linnaeus).

Shells 10 mm to 170 mm in size, generally ovate, elongate-ovate or fusiform, smooth or spirally grooved, ridged or pitted, aperture variable, outer lip smooth or crenulate, labrum smooth, columella with 3 to 7 plicae, siphonal canal short or moderately long; shell generally covered with a moderately thick epidermis.

Radula with three teeth per row, rhachidian moderately small, quadrate, rectangular, trapezoidal or triangular, concave, with 3 to 12 cusps. Laterals ranging from two to four times the width of rhachidians, short and broad, comb-like, with a convexity at the base and with from 10 to 45 prominent cusps distributed over the entire width of the plate. The ribbon has a width of 16% to 30% of total ribbon-length, and from 9% to 12% of total shell-length; the number of rows per 1 mm of ribbon length varies from 15 to 33, and from 16 to 30 per 10 mm of shell length.

Habitat is in sand or sand substratum under coral rocks or in cracks and crevices of coral rocks, from shallow to deeper water.

Geologic distribution is from Eocene to Recent. Since Pliocene times the genus occurs only in the Indo-Pacific, Panamic, Caribbean, Atlantic and Mediterranean regions.

Mitra mitra (Linnaeus, 1758), Cernohorsky, 1965, The Veliger **8** (2): 91; plt. 13, fig. 1.

Radula of specimen from the Fiji Islands: Radular ribbon white in colour, 5.1 mm long and 0.8 mm wide in shell 50 mm in length; fully-formed rows number 76 (+ 5 nascentes), with the front three to four rows of teeth equally worn. Rhachidians with five prominent cusps, central cusp more massive and longer than side-cusps. Laterals 2½ times as broad as rhachidians, comb-like and with 13 to 15 cusps distributed over the entire width of the lateral plate; the last three to four cusps often appear as small denticles.

Proboscis extremely long in comparison to shell size, and was found to measure 37 mm in a 50 mm long specimen.

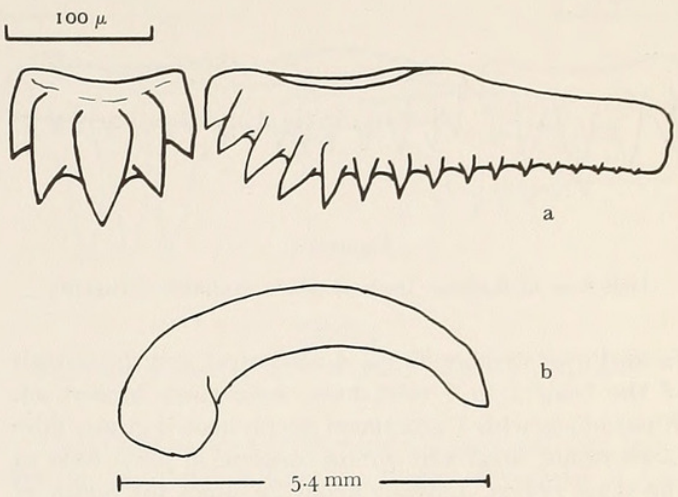


Figure 2

a: Half-Row of Radular Teeth of *Mitra mitra* (Linnaeus)
b: Lateral View of Penis

Mitra idae Melvill, 1893; Shikama, 1963, plt. 74, fig. 16.

Radula of specimen from Point Conception, California: Radular ribbon amber in colour, 6.8 mm long and 1.5 mm wide in shell 54 mm in length; fully-formed rows number 98 (+ 4 nascentes), rhachidians of the front 13 to 14 rows of teeth badly worn; laterals equally worn in front

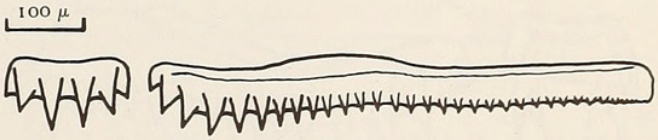


Figure 3

Half-Row of Radular Teeth of *Mitra idae* Melvill

16 rows, with the four large cusps facing the rhachidians either worn down or broken off. Rhachidians with 6 prominent cusps, two central cusps about equal-sized. Laterals four times the width of rhachidians, with 32 cusps distributed over the entire width of the plate, last 6 cusps appearing as weak denticles.

The radula of *Mitra idae*, the type of *Atrimitra* Dall, 1918, resembles that of *M. stictica* (Link, 1807). *Atrimitra* Dall should be placed in the synonymy of *Mitra* s. str.

Mitra cardinalis (Gmelin, 1791); Cernohorsky, 1965, The Veliger **8** (2): 82; plt. 13, fig. 2.

Radula of specimen from Fiji: Radular ribbon white, 4.2 mm long and 0.94 mm wide in shell 41 mm long; fully

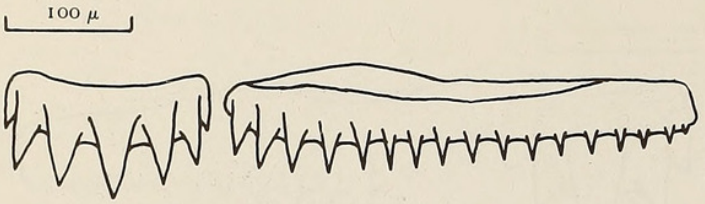


Figure 4

Half-Row of Radular Teeth of *Mitra cardinalis* (Gmelin)

formed rows number 58 (+ 4 nascentes) and the laterals of the front 3 to 4 rows have some cusps broken off. Rhachidians with 7 prominent deeply-rooted cusps; side-cusps rather small and almost obsolete in some rows of the same ribbon. Laterals about 2¼ times the width of rhachidians, with 16 to 17 cusps distributed over the entire width of the lateral plate.

Mitra eremitarum Röding, 1798; Cernohorsky, 1965, The Veliger 8 (2): 87; plt. 13, fig. 3.

Radula of specimen from Fiji: Radular ribbon amber in colour, 3.8 mm long and 0.56 mm wide in shell 49 mm in length; fully-formed rows number 68 (+ 1 nascent) and the front 12 to 14 rows of teeth are badly worn.

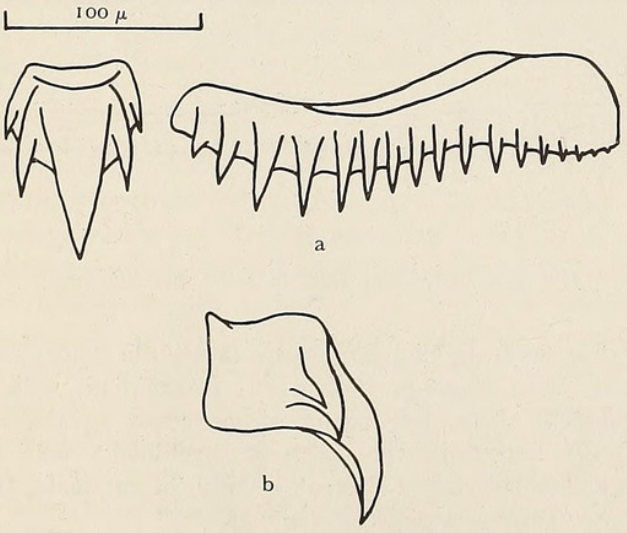


Figure 5

a: Half-Row of Radular Teeth of *Mitra eremitarum* Röding
b: Lateral View of Rhachidian

Rhachidians dark amber in colour, with 5 cusps, central cusp large and massive, side-cusps smaller and slender. Laterals greyish-white, about 3 times the width of rhachidians with 16 to 17 cusps distributed over the entire width of the lateral plate.

The proboscis is very long, measuring 37 mm in a shell 49 mm in length. Cooke's figure of the radula of *Mitra adusta* Lamarck (1920, fig. 1) is appreciably different and most probably originated from a different species.

Mitra fraga Quoy & Gaimard, 1833; Cernohorsky, 1965, The Veliger 8 (2): 89; plt. 16, fig. 42.

Radula of specimen from Fiji: Radular ribbon translucent-white, 1.1 mm long and 0.25 mm wide in shell 12 mm in length; fully formed rows number 34 (+ 3 nascentes) and the front two to three rows of teeth are badly worn. Rhachidians with 7 fairly prominent cusps, central

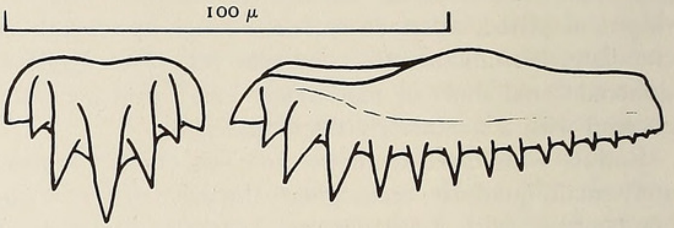


Figure 6

Half-Row of Radular Teeth of *Mitra fraga* Quoy & Gaimard

cusp the longest. Laterals about 2 to 2⅕ times the width of rhachidians, with 13 to 15 cusps distributed over the entire width of the plate; cusps diminish in size toward the end where they appear as small denticles.

Mitra stictica (Link, 1807); Cernohorsky, 1965, The Veliger 8 (2): 98; plt. 14, fig. 15.

Radula of specimen from Fiji: Radular ribbon light brown in colour (nascentes end white), 6.1 mm long and 1.9 mm wide in shell 66 mm in length; fully formed rows

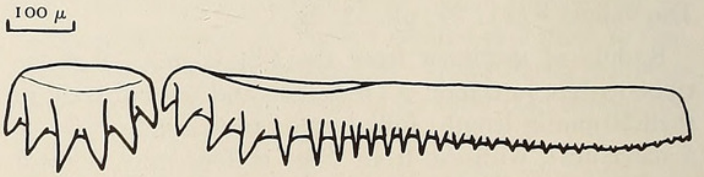


Figure 7

Half-Row of Radular Teeth of *Mitra stictica* (Link)

number 77 (+ 4 nascentes), and the front 10 rows are badly worn, especially the rhachidians. Rhachidians with 6 prominent cusps, with the two central cusps equal in size. Laterals about 3½ times the width of rhachidians, with 26 to 30 cusps which decrease in size towards the

end and are distributed along the entire width of the plate.

Proboscis flesh-coloured, 55 mm long in shell 66 mm in length.

The genera *Tiarella* SWAINSON, 1840 and *Papalaria* DALL, 1915, established for the group of species comprising *Mitra papalis* (LINNAEUS), *M. stictica* (LINK), *M. cardinalis* (GMELIN), etc., should be placed in the synonymy of *Mitra* s. str.

Mitra ferruginea LAMARCK, 1811; CERNOHORSKY, 1965, The Veliger **8** (2): 88; plt. 13, figs. 7, 7 a.

Specimen from Fiji: Radular ribbon translucent white, 3.1 mm long and 0.44 mm wide in shell 48 mm in length; fully formed rows number 88 (+ 3 nascentes), and wear

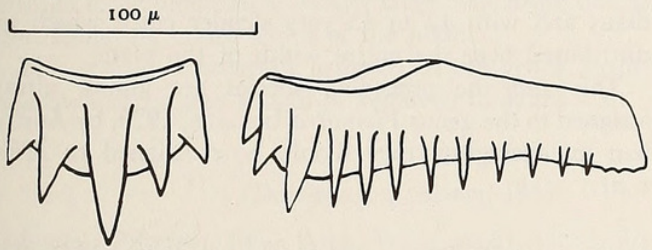


Figure 8

Half-Row of Radular Teeth of *Mitra ferruginea* LAMARCK

is discernible on the front rows of the ribbon. Rhachidians with 5 massive cusps, central cusps the longest. Laterals with 11 to 13 cusps, last 2 to 3 cusps appearing as minute denticles.

COOKE (1920) placed this species in section 3 of group 1; the rhachidian depicted in COOKE's figure (fig. 3) shows a rhachidian with 6 equal-sized slender cusps and hardly resembles the rhachidian of *Mitra ferruginea* examined in this study.

Mitra cucumerina LAMARCK, 1811; CERNOHORSKY, 1965, The Veliger **8** (2): 87; plt. 17, figs. 50, 50 a.

Specimen from Fiji: Radular ribbon translucent-white in colour, 2.5 mm long and 0.45 mm wide in shell 25 mm in length; fully formed rows number 37 (+ 3 nascentes) and front rows of teeth hardly show any wear at all. Rhachidians with 3 prominent deeply-rooted cusps, central cusps slightly larger. Laterals about 1½ times the width of the rhachidians with about 11 cusps; the first cusp is beak shaped and facing the rhachidian, while the ultimate $\frac{1}{6}$ of the plate is bare.

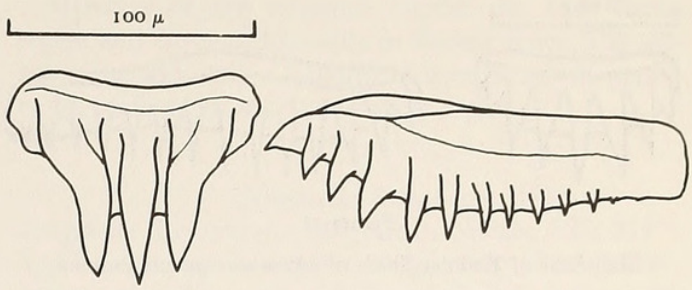


Figure 9

Half-Row of Radular Teeth of *Mitra cucumerina* LAMARCK

The radula of *Mitra cucumerina* is quite different from that of *M. chrysalis* REEVE, although the shells of the two species are somewhat similar. In *M. chrysalis* the rhachidians have 8 to 10 long and slender cusps while the cusps on the laterals are more numerous.

Mitra auriculoides REEVE, 1845; CERNOHORSKY, The Veliger **8** (2): 109; plt. 18, fig. 61.

Specimen from Fiji: Radular ribbon translucent-white, 1.4 mm long and 0.21 mm wide in shell 15 mm in length; fully formed rows number 57 (+ 3 nascentes), and the front 2 to 3 rows are worn. Rhachidians with 8 moderately long cusps, the 4 central cusps about equal in length.

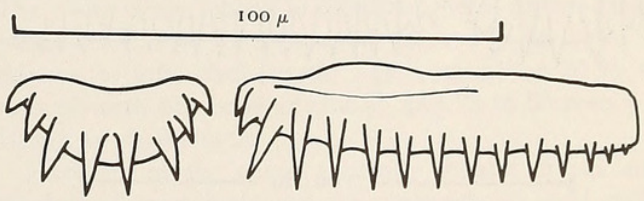


Figure 10

Half-Row of Radular Teeth of *Mitra auriculoides* REEVE

Laterals twice the width of the rhachidians with 13 to 15 cusps distributed over the entire width of the plate, gradually decreasing in size.

This species is almost always assigned to the genus *Strigatella* SWAINSON; however, the radula proves it to be a *Mitra*.

Mitra ostergaardi PILSBRY, 1921; J. CATE, 1962, The Veliger **4** (3): 143; plt. 33, fig. 3; plt. 35, fig. c.

Specimen from Kailua Bay, Oahu, Hawaii: Radular ribbon translucent-white, 3.2 mm long and 0.62 mm wide in shell 28 mm in length; fully formed rows number 64

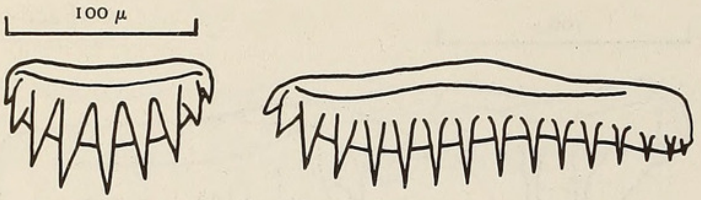


Figure 11

Half-Row of Radular Teeth of *Mitra ostergaardi* PILSBRY

(+ 3 nascentes) and no appreciable wear is discernible on the front rows of teeth. Rhachidians with 8 to 9 moderately slender cusps. Laterals about twice as broad as rhachidians, with 14 to 16 slender cusps which are distributed over the entire width of the lateral plate.

Mitra nigra (GMELIN, 1791); ALLAN, 1959, Austral. shells, plt. 26, fig. 17 (as *Vicimitra contermina* IREDALE).

Specimen from Redhead, Bendalong, N. S. W., Australia: Radular ribbon amber in colour, 5.1 mm long and 1.2 mm wide in shell 44.0 mm long; fully formed rows number 82 (+ 2 nascentes) and front rows of teeth show considerable wear. Rhachidians with 9 deeply rooted

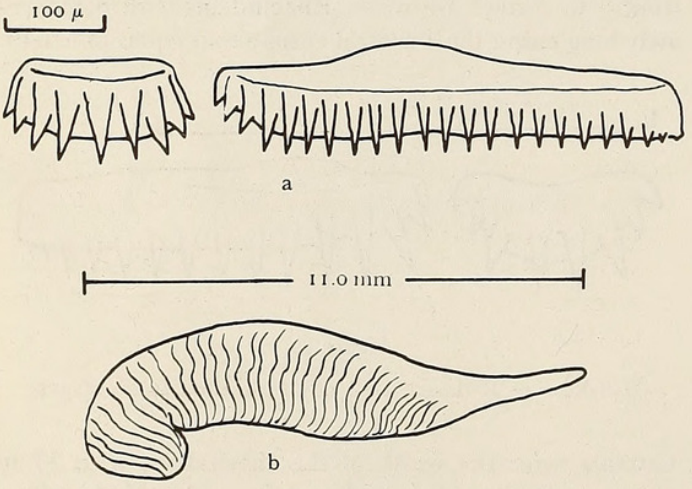


Figure 12

a: Half-Row of Radular Teeth of *Mitra nigra* (GMELIN)
b: Lateral View of Penis

cusps, with the 3 central cusps being equal in size. Laterals about twice the width of rhachidians with 22 to 23 long and slender cusps, which are distributed along the entire width of the plate.

The proboscis measured 34 mm and the penis 11 mm, both in extended position.

Mitra glabra SWAINSON, 1821; ALLAN, 1959, plt. 26, fig. 18 (also REEVE, 1844, pl. 6, sp. 43).

Specimen from Redhead, Bendalong, N. S. W., Australia: Radular ribbon amber in colour, 6.1 mm long and 2.0 wide in shell 65 mm in length; fully formed rows number 92 (+ 3 nascentes), and some wear is visible on

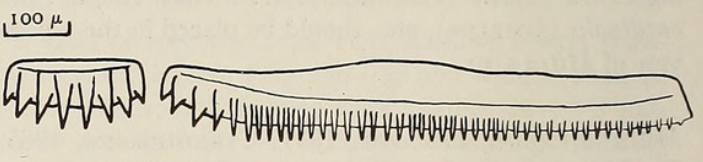


Figure 13

Half-Row of Radular Teeth of *Mitra glabra* SWAINSON

the front rows of teeth. Rhachidians with 8 to 10 deeply rooted cusps. Laterals about 4 times the width of rhachidians and with 42 to 45 very slender cusps which are distributed over the entire width of the plate.

This and the preceding species are almost always assigned to the genus *Vicimitra* IREDALE, 1929, by Australian malacologists; they should be reassigned to *Mitra* s. str.

Mitra variabilis REEVE, 1844; CERNOHORSKY, 1965, The Veliger 8 (2): 100; plt. 14, fig. 16.

Specimen from North-West Island, Queensland, Australia: Radular ribbon translucent white, 2.7 mm long and 0.5 mm wide in shell 32 mm in length; fully formed

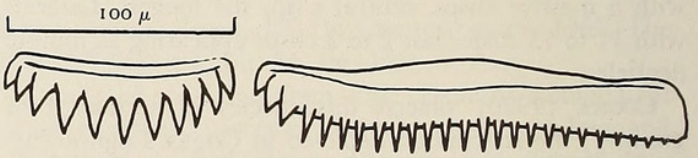


Figure 14

Half-Row of Radular Teeth of *Mitra variabilis* REEVE

rows number 124 (+ 7 nascentes) and no appreciable wear was evident on the front rows of the ribbon. Rhachidians wide and short with 11 moderately long cusps. Laterals about twice the width of rhachidians with 24 to 26 slender cusps which are distributed along the entire width of the plate.

Mitra hirasei (PILSBRY, 1904); SHIKAMA, 1963, Shells world ill. col., plt. 74, fig. 2.

Specimen from Kiushio Island, Japan: Radular ribbon translucent white, ultimate 15 rows (nascentes excluded)

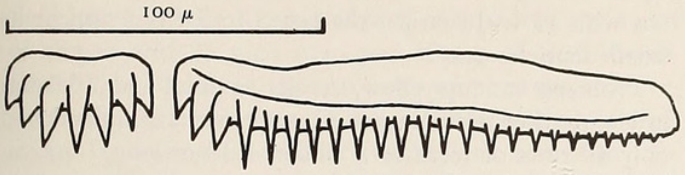


Figure 15

Half-Row of Radular Teeth of *Mitra hirasei* (Pilsbry)

orange-brown in colour, 1.3 mm long and 0.38 mm wide in shell 27 mm in length; ribbon consisting of 88 rows (+ 5 nascentes), and no appreciable wear is evident on the front rows of teeth. Rhachidians with 7 deeply rooted cusps; laterals about 3 times the width of rhachidians, with 23 to 25 moderately slender cusps which are distributed along the entire width of the plate.

This species is generally assigned to the genus *Scabricola* Swainson, and should be removed to *Mitra* s. str.

(Dibaphus) Philippi, 1847

Dibaphus Philippi, 1847, Arch. Wieg., p. 61, plt. 3, figs. 1 - 3. – Type species by monotypy *Conus edentulus* Reeve, 1844, *ex* Swainson MS, = *Mitra (Dibaphus) edentula* (Reeve).

The shells of this subgenus are generally 25 mm to 45 mm in length, cylindrical and cone-shaped, spire short, aperture long and narrow, columella with several plicae anterior of which appears to be the continuation of the spiral ridges on the body whorl; sculpture consists of small and angulate transverse grooves or ridges, interstices cancellate with axial striae.

The radula is similar to that of *Mitra* s. str., but not sufficiently different to merit generic rank. For figure of radula see Cooke, (1920, p. 409, fig. 4).

The species of the subgenus inhabit the underside of dead coral boulders on reef flats.

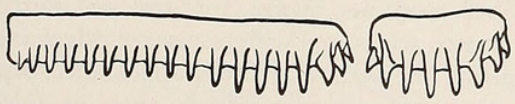


Figure 16

Half-Row of Radular Teeth of
Mitra (Dibaphus) edentulus (Reeve)
[after Cooke, 1920, text figure 4 – no magnification]

Members of the subgenus inhabit the Indo-Pacific region and developed possibly in Recent times. The subgenus includes only a handful of species, which appear to be confined to the Indo-Pacific region.

Strigatella Swainson, 1840.

Strigatella Swainson, 1840; Treat. Malac., **127**: 319. – Type species by subsequent designation (Gray, 1847) *Mitra zebra* Lamarck, 1811 = *Strigatella paupercula* (Linnaeus, 1758).

Shells small or moderate in size, ovate or elongate-ovate, heavy and solid; sutures plain or coronate, whorls smooth or sculptured with striae, granules or pits; aperture narrow, outer lip thick, smooth or crenulate, generally with a prominent callus on outer lip; labrum smooth, columella with 3 to 5 plicae, anterior canal short; shell with periostracum.

The animal has generally a light-coloured sole of the foot, while the dorsum of the foot is light or dark brown. Foot, siphon, tentacles and eyes are smaller than is the case in Vexillinae.

The rhachidians are variable in pattern and similar to those of *Mitra* s. str.; in the type species the two central cusps are equal in size. Laterals are generally 2 to 3 times as broad as the rhachidians, cleaver-shaped, concavely depressed at the beginning, and with the last quarter or one-third of the lateral plate always bare of teeth. The width of the ribbon in relation to total ribbon-length varies from 9% to 20%, and from 7% to 21% in relation to total shell-length. There are about 20 to 45 rows of teeth per 1 mm of ribbon, and 25 to 50 rows per 10 mm of shell-length.

Members of the genus generally inhabit cracks and crevices of coral reefs and the underside of coral rocks in the intertidal zone.

The genus is distributed over the Indo-Pacific, Panamic, Caribbean and Atlantic regions. The genus probably developed during the Miocene.

The radula of *Strigatella* is similar in pattern to *Mitra* s. str., but differs in that the inner part of the laterals is arched and concavely depressed, while the outer part of the plate is straight; the teeth become small denticles towards the outer half of the plate, and become obsolete or absent on the ultimate third or quarter of the plate.

Mitreola monodonta (Lamarck, 1803), the type species of *Mitreola* Swainson, 1832, is rather similar to members of the Recent genus *Strigatella*. The mammillate protoconch and heavily calloused columella of *M. monodonta* should provide the necessary excuse to separate the fossil genus *Mitreola* from the Recent *Strigatella*; genera

based on fossil type-species are after all malacologically undesirable for living groups of species.

Strigatella paupercula (Linnaeus, 1758); Cernohorsky, 1965, The Veliger **8** (2): 112; plt. 17, fig. 59.

Specimen from Fiji: Radular ribbon translucent-white, 3.6 mm long and 0.52 mm wide in shell 17 mm in length; fully formed rows number 82 (+ 3 nascentes), and the front 10 rows of teeth are badly worn and mutilated.

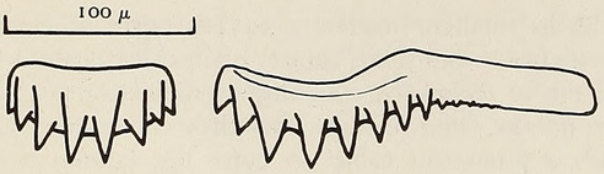


Figure 17

Half-Row of Radular Teeth of *Strigatella paupercula* (Linnaeus)

Rhachidians with 6 main cusps and 2 small accessory denticles which are obsolete in some rows on the same ribbon. Laterals about 2¼ times the width of the rhachidians with 8 to 9 fairly strong cusps and 3 to 4 small denticles; the ultimate third of the plate is bare.

Strigatella retusa (Lamarck, 1811); Cernohorsky, 1965, The Veliger **8** (2): 113; plt. 18, fig. 64.

Specimen from Fiji: Radular ribbon translucent-white, 2.2 mm long and 0.2 mm wide in shell 30 mm in length; fully formed rows number 102 (+ 4 nascentes). Rhachidians with 8 moderately long cusps, 2 central cusps equal in length. Laterals 2½ times the width of rhachidians with 13 to 14 cusps; the last 3 to 5 cusps appear as small denticles only.

Proboscis creamy-yellow, slender at distal end, 19.0 mm in length after preservation. One specimen examined had only 49 rows of teeth in a ribbon 1.2 mm long.

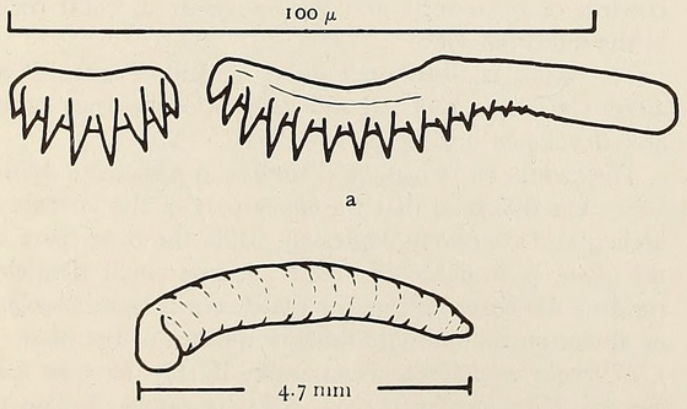


Figure 18

a: Half-Row of Radular Teeth of *Strigatella retusa* (Lamarck)
b: Lateral View of Penis

Strigatella ticaonica (Reeve, 1844); Cernohorsky, 1965, The Veliger **8** (2): 99; plt. 14, fig. 14.

Specimen from Fiji: Radular ribbon light amber in colour, 2.9 mm long and 0.47 mm wide in specimen 23.0 mm in length; fully formed rows number 88 (+ 4 nascentes) and the rhachidians in the first two front rows have the cusps worn away. Rhachidians are roughly rectangular and equipped with 7 prominent deeply rooted cusps; the side-cusps become very small in some rows of the same ribbon. Laterals about 2½ times the width of rhachidians, concavely depressed towards centre of ribbon, and with 10 to 12 strong cusps; the last 3 to 4 cusps usually appear as small denticles, and the ultimate third of the plate is bare.

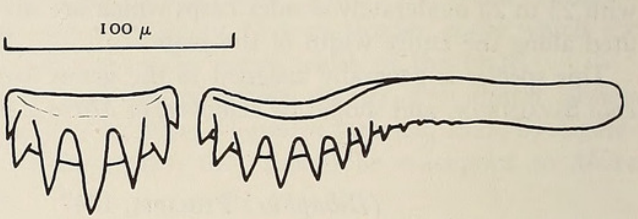


Figure 19

Half-Row of Radular Teeth of *Strigatella ticaonica* (Reeve)

This species is generally placed in the genus *Mitra*, from which it should be removed and assigned to *Strigatella*.

Neocancilla Cernohorsky, gen. nov.

Neocancilla papilio (Link, 1807) hereby designated as type species.

Type species: *Voluta papilio* Link, 1807.

Shell: Shell moderate in size, fusiform and fairly solid, whorls convex, sculptured with transverse ridges and axial striae, giving the shell a scabrous appearance. Aperture moderately narrow, labrum smooth, outer lip thickened, crimped or obsoletely crenulate, columella plicate, siphonal canal produced.

Animal: Foot moderately large, varicoloured; eyes, proboscis and siphon moderately well developed.

Radula: Radular ribbon about 10% in width in relation

to total ribbon length, and 13% in width in relation to shell length; about 20 rows of teeth are present per 1 mm of ribbon and 23 such rows per 10 mm of shell-length. Rhachidians bicuspid, the two cusps equal in size, massive, generally flanked by one or two small denticles; laterals about 1½ times the width of rhachidians, somewhat degenerate in appearance, with 5 to 7 cusps and 2 to 3 small denticles.

Habitat: In sand only, in shallow and deeper water.

Geographical Distribution: Indo-Pacific, ? Caribbean region.

Age: Recent.

Discussion: The radula pattern of this group of species differs widely from other groups and is thus separated as a new genus. Cooke (1920) placed shells with a similar radula pattern in his group No. 7 but did not provide a taxonomic name for it.

Neocancilla papilio (Link, 1807); Cernohorsky, 1965, The Veliger **8** (2): 93; plt. 14, fig. 22.

Specimen from Fiji: Rhachidians of radular ribbon rusty-brown, laterals thin and greyish-white, ribbon 3.9 mm long and 0.42 mm wide in shell 33.0 mm in length; fully formed rows number 52 (+ 14 nascentes) and only

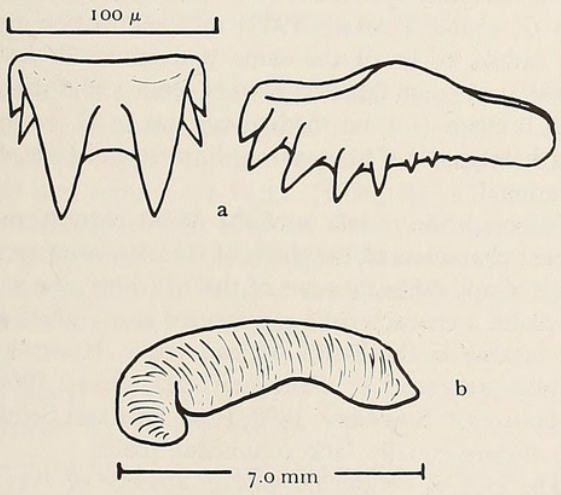


Figure 20

a: Half-Row of Radular Teeth of *Neocancilla papilio* (Link)
b: Lateral View of Penis

the first 2 to 3 front rows of teeth are slightly worn. Rhachidians about rectangular in shape, with 2 long and massive cusps and a pair of small overlapping side cusps on either side. Laterals 1½ times the width of rhachidians, with about 8 cusps, last 2 to 3 cusps generally very small.

Proboscis measured 10 mm after preservation.

Neocancilla langfordiana (J. Cate, 1962), The Veliger **5** (2): 80 - 83; plts. 10, 11.

Specimen from Waianae, Oahu, Hawaii: Radular ribbon consisting of rusty-brown rhachidians and thin whitish laterals; ribbon 2.8 mm long and 0.34 mm wide in

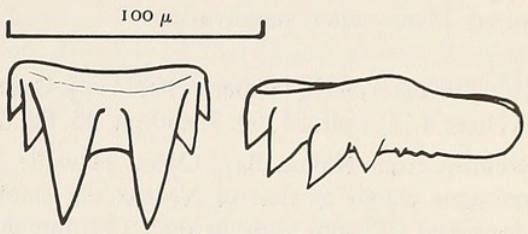


Figure 21

Half-Row of Radular Teeth of *Neocancilla langfordiana* (J. Cate)

shell 25.0 mm in length; fully formed rows number 38 (+ 8 nascentes) and the front rows of teeth displayed a negligible amount of wear. The pattern of rhachidians and laterals is very similar to that of *Neocancilla papilio* from the Fiji Islands, and the radulae also agree in many other aspects. The shells of the two species are rather similar, and both may prove to be conspecific.

Neocancilla clathrus (Gmelin, 1791); Cernohorsky, 1965, The Veliger **8** (2): 103; plt. 14, fig. 25.

Specimen from Fiji: Radular ribbon amber in colour, rhachidians rusty-brown, end of laterals thin and white, ribbon 4.3 mm long and 0.4 mm wide in shell 32.0 mm in length; fully formed rows number 77 (+ 8 nascentes),

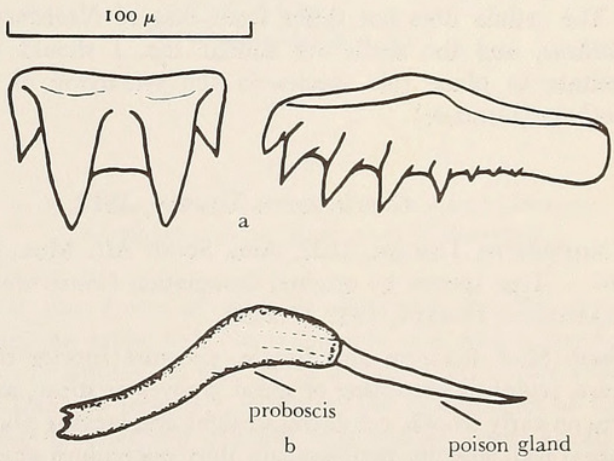


Figure 22

a: Half-Row of Radular Teeth of *Neocancilla clathrus* (Gmelin)
b: Proboscis with Poison Gland in Extended Position

the front 3 rows of teeth being worn. Rhachidians roughly rectangular in shape, equipped with 2 long and massive cusps and 2 shorter solid side-cusps. Laterals 1½ times the width of rhachidians, furnished with 8 cusps; the ultimate 3 cusps are very small and appear as denticles throughout all rows of the ribbon.

The proboscis is orange-brown flecked with cream, and measured 15 mm after preservation.

Neocancilla emersoni (PILSBRY, 1921); J. CATE, 1962, The Veliger 4 (3): plt. 34, fig. 2, and plt. 35, fig. d.

Specimen from Kailua Bay, Oahu, Hawaii: Radular ribbon same colour as that of *Neocancilla clathrus,* 1.7 mm long and 0.22 mm wide in shell 15.0 mm in length; fully formed rows number 62 (+ 4 nascentes), front rows somewhat worn and laterals fractured. Rhachidians with

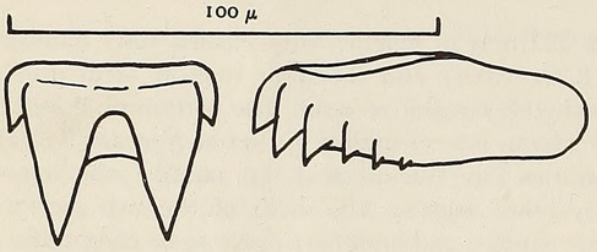


Figure 23

Half-Row of Radular Teeth of *Neocancilla emersoni* (PILSBRY)

2 massive cusps which are flanked by a small accessory cusp. Laterals about 1½ times the width of rhachidians, with 5 to 6 moderately small cusps, ultimate third of lateral plate bare.

The radula does not differ from that of *Neocancilla clathrus,* and the shells are similar too. I should not hesitate to place this species in the synonymy of *N. clathrus* (GMELIN).

Charitodoron TOMLIN, 1932.

Charitodoron TOMLIN, 1932, Ann. South Afr. Mus., **30:** 167. – Type species by original designation *Charitodoron euphrosyne* TOMLIN, 1932 (Natal).

Shell: Shell fusiform and fragile, aperture shorter than spire, sculpture consisting of spiral grooves or striae, axial ribs on early whorls, columella straight and lacking plicae, labral wall smooth, periostracum thin, operculum absent.
Animal: Black or very dark brown, with short tentacles and no eyes (*fide* BARNARD, 1960).
Radula: Similar in pattern to *Mitra* s. str., with 60 to 65 rows, rhachidians with 5 main cusps and somewhat obsolete side-cusps; laterals about 2.6 times the width of rhachidians, with 10 prominent cusps distributed almost along the entire width of the plate.
Habitat: From 300 to 700 fathoms.
Geographical Distribution: Endemic to the South African region (Natal - East London).
Age: ? Recent.

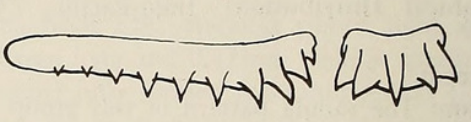


Figure 24

Half-Row of Radular Teeth of *Charitodoron bathybius* (BARNARD) [after BARNARD, 1959, figure 11 c – no magnification]

Discussion: TOMLIN (1932) established the genus *Charitodoron* for three South African deep water species and assigned the genus to the family Buccinidae on conchological grounds. BARNARD (1959) figured the radula of *Mitra (Dibaphus) bathybius* BARNARD, 1959, and commented on the great resemblance of his new species to the shells of *Charitodoron.* BARNARD (1960) was successful in obtaining specimens of *C. pasithea* TOMLIN, 1943, and *C. thalia* TOMLIN, 1932; an examination revealed the radula to be of the same pattern as *C. bathybius* (BARNARD), with 60 to 65 rows of teeth and a rhachidian with 6 cusps (i.e. no median cusp as in *C. bathybius*). The holotype of *Charitodoron,* however, did not contain an animal.

Although the radula is of the *Mitra* pattern, morphological characters of the shells of *Charitodoron* are unlike those of any other member of the Mitridae; the columellar plaits, a characteristic represented in all mitrid genera, are lacking in the South African genus. However, some volutid genera, i.e. *Fusivoluta* MARTENS, 1902, and *Neptuneopsis* SOWERBY, 1898, from East and South African waters equally lack columellar plaits.

The lack of columellar plicae, absence of eyes in the animal (?), benthic range and geographical distribution, favour a generic separation of this group of shells. *Charitodoron* has been tentatively retained in the Mitridae mainly on radula evidence supplied by BARNARD (1959, 1960). The genus includes the species *C. euphrosyne* TOMLIN, 1932, *C. agulhasensis* [(THIELE, 1925) – syn. *C. aglaia* TOMLIN, 1932], *C. thalia* TOMLIN, 1932, *C. pasithea* TOMLIN, 1943, and *C. bathybius* (BARNARD, 1959); the last two mentioned species appear to be synonyms of *C. thalia* TOMLIN.

Genus ? (Group 10 of Cooke, 1920 and Peile, 1936).

Mention must be made here of a group of species which possesses a radula consisting of rhachidians similar to those of *Vexillum,* but with numerous smaller denticles, and laterals similar to those of *Mitra* s. str. Cooke (1920, fig. 16) illustrated this type of radula under his group 10, and credited the radula to the species "*Mitra scabriuscula* L." Peile (1936) points out that Cooke's identification of *M. scabriuscula* L. was an error and that "L." should presumably be "Lamarck." The radula of *Pterygia scabricula* (Linnaeus) differs greatly from the radula figured by Cooke (*l. c.*), and Lamarck's "*M. scabriuscula*" is the species *Neocancilla papilio* (Link), with a radula also differing from that illustrated by Cooke. It is quite possible that Cooke's species was *Mitra granatina*

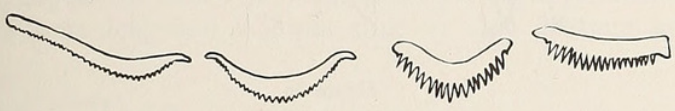


Figure 25

Half-Row of Radular Teeth of *Mitra* Species
[after Cooke, 1920, text figure 16 – no magnification]

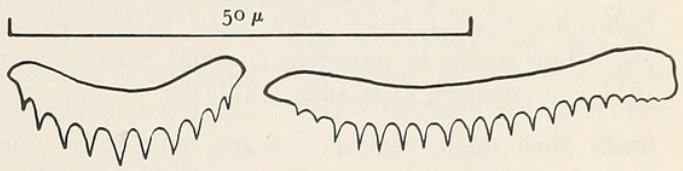


Figure 26

Half-Row of Radular Teeth of *Mitra* Species
[after Peile, 1936, figure 9 – x 300]

Lamarck, 1811, which is often found listed in literature as *Mitra scabriuscula* Lamarck.

A radula similar to that figured by Cooke was described and figured by Peile (1936, fig. 9) under the name *Cancilla circula* Kiener. This radula greatly resembles the radula of *Mitra filaris* (Linnaeus) figured here, except that the cusps of the rhachidians in Peile's specimens are more numerous.

Mitra filaris (Linnaeus, 1771); Cernohorsky, 1965, The Veliger **8** (2): 104; plt. 15, fig. 33.

Specimen from Le Goulet, Mauritius: Radular ribbon very thin, fragile and short, translucent white in colour, 0.9 mm long and 0.12 mm wide in shell 30 mm in length; fully formed rows number 73 (+ 2 nascentes) and no appreciable wear is evident in the front rows of the ribbon apart from some missing cusps. Rhachidians concavely depressed and with 10 small and weak cusps. Laterals about $1\frac{3}{4}$ times the width of rhachidians with 15 to 20 shallowly-rooted teeth which extend over the entire width of the plate and are very small or almost obsolete at both ends of the plate.

The above specimen was found on an egg-mass consisting of a cluster of 85 to 90 tightly packed brownish egg-capsules secured to a piece of seaweed. Capsules were on the average 3.5 to 4 mm in height, 1.0 to 1.2 mm in width and contained from 130 to 150 creamy-coloured undivided spherical eggs which measured from 110 μ to 180 μ in diameter; the whole egg-mass would therefore contain between 11000 and 13000 eggs.

Discussion: In view of the distinct radula pattern and other peculiarities of the radula, Peile's remarks (1936)

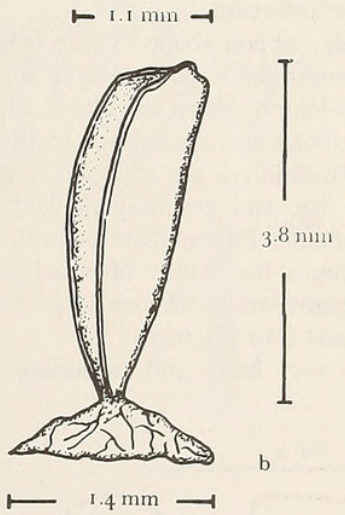


Figure 27

a: Half-Row of Radular Teeth of *Mitra filaris* (Linnaeus)
b: Egg-Capsule of *Mitra filaris* (Linnaeus)

that this group of shells is deserving of generic rank must be supported. No taxonomic unit name, however, can be applied to this group at this stage, as the radula of *Cancilla isabella* Swainson, the type species of *Cancilla,* is unknown. Should this species have a radula similar to that of group 10, then the group of shells comprising *C. philippinarum* (A. Adams) and "*C. circula*" (Kiener) would require a new name.

Imbricariinae Troschel, 1867
(nom. corr.)

The subfamily includes 4 genera, three of which are Recent Indo-Pacific developments, and one genus extends as far as the Caribbean region.

A poison gland is present, and the radula consists of a unicuspid, bicuspid or multicuspid rhachidian and variable laterals according to genus. Members of all genera contained within this subfamily are sand-dwellers.

Imbricaria Schumacher, 1817.

Imbricaria Schumacher, 1817, Essai Nouv. Syst., p. 236 – Type species by monotypy *I. conica* Schumacher, 1817 = *I. conularis* (Lamarck, 1811).

Shell: Shell small, conical in shape, solid, spire short and often depressed and concave, whorls smooth or spirally grooved and pitted, aperture long, straight and narrow, outer lip thick and smooth, columella with numerous oblique plicae, anterior canal short; shell covered with a thin periostracum.

Radula: Radular ribbon about 13% in length in relation to total shell-length, and about 14% in width in relation to total ribbon-length; there are about 20 rows of teeth per 1 mm of ribbon and 26 rows of teeth per 10 mm of shell-length. Rhachidians are tricuspid, 2 cusps are large and equal in size, and generally flanked by small side cusps and a smaller intermediate central cusp. Laterals 1.4 to 1.75 times the width of rhachidians, humped towards the centre and with one large inward-pointing massive cusp and 0 to 12 cusps.

Animal: Foot very large and extending well past the apex of the shell during the crawling position; siphon, tentacles and eyes moderately large.

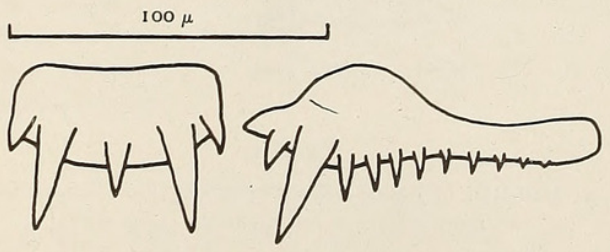


Figure 28
Half-Row of Radular Teeth of *Imbricaria conularis* (Lamarck)

Habitat: In sand only.

Geographical Distribution: Indo-Pacific.

Age: Recent.

Discussion: A description of the radula of *Imbricaria conularis* (Lamarck), *I. olivaeformis* (Swainson) and *I. punctata* (Swainson) can be found in Cooke, 1920 and Cernohorsky, 1966.

Imbricaria filum (Wood, 1828), Ind. Test., Suppl. plt. 3, fig. 30.

Specimen from Le Goulet, Mauritius: Radular ribbon dark amber in colour, 1.8 mm long and 0.44 mm wide in shell 18.0 mm in length; fully formed rows number 39 (+ 3 nascentes) and no appreciable wear was apparent on the front rows of teeth. Rhachidians slightly heart-shaped with 2 prominent main cusps and 4 slender accessory cusps, 2 on either side. Laterals about 1½ times the width of rhachidians, wide and short, equipped with a curved process projecting towards rhachidians, and one massive cusp which is flanked by a small denticle.

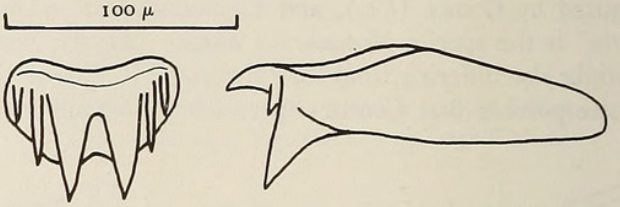


Figure 29
Half-Row of Radular Teeth of *Imbricaria filum* (Wood)

This species is generally assigned to the genus *Swainsonia*; however, its relationship lies with *Imbricaria olivaeformis* (Swainson).

Cancilla Swainson, 1840.

Cancilla Swainson, 1840, Treat. Malac., 127:320. – Type species by subsequent designation (Herrmannsen, 1846) *Tiara isabella* Swainson, 1831.

Shell: Shell slender and fusiform, sutures plain, whorls sculptured with elevated keel-like ridges, intervening grooves often axially striate; aperture narrow and fusiform, interior highly enamelled and smooth, columella plicate, anterior canal narrow and produced, outer lip generally long and crimped; shell covered with a thin epidermis.

Animal: In this group of species the sole of the animal's foot is almost always white or cream in colour; siphon variable, often variegated and lined with black and white, remainder of animal variable in colour.

Radula: Radular ribbon is fairly broad in relation to total ribbon-length, and the number of rows of teeth per 1 mm of ribbon-length is rather small (14 to 16 rows). Rhachidians variable, laterals with 1 massive long inward point-

ing cusp and resembling those of the genus *Imbricaria*.
Habitat: In clean and muddy sand, occasionally in sand pools of coral reefs, from the intertidal zone to deeper water.
Geographical Distribution: Indo-Pacific and Panamanian provinces, Caribbean?
Age: Eocene to Recent.
Discussion: The radula of the type species is unknown and should on examination the radula prove to be different, a new generic name would have to be provided for this group of shells. Species contained in this genus were placed in Cooke's group 6, which also included *Cancilla flammigera* (Reeve) and *C. interlirata* (Reeve) [*vide* Cooke, 1920].

Cancilla philippinarum (A. Adams, 1853); Cernohorsky, 1965, The Veliger 8 (2): 107; plt. 15, fig. 32.

Specimen from Fiji: Radular ribbon white in colour, 3.0 mm long and 0.58 mm wide in shell 23.0 mm in

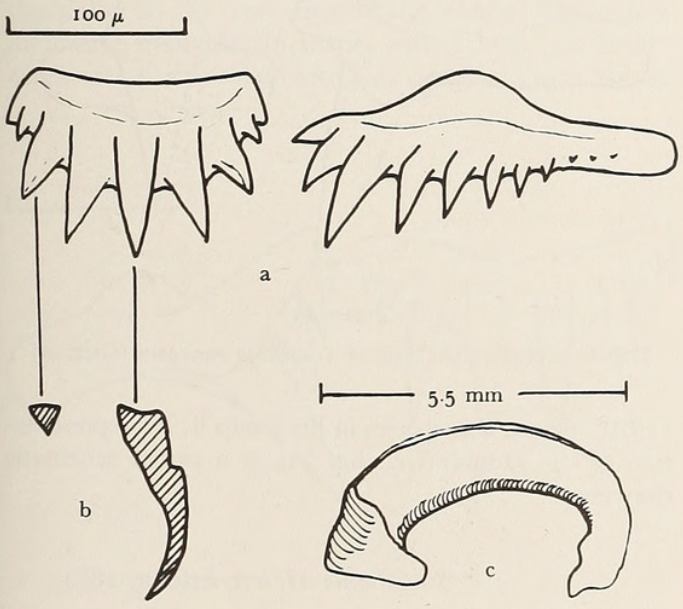


Figure 30

Cancilla philippinarum (A. Adams)
a: Half-Row of Radular Teeth of
b: Profile of Cusps
c: Lateral View of Penis

length; fully formed rows number 41 (+ 2 nascentes), and no appreciable wear was evident on the rhachidians of the front rows, although some of the laterals had cusps broken off. Rhachidians moderately broad with 7 fairly large and long cusps; the 3 central cusps are almost equal in size and the last side cusps are rather small. Laterals 1½ times the width of the rhachidians, with 11 to 13 cusps which are distributed almost along the entire width of the plate; one massive cusp is long and inward pointing and the ultimate 2 to 3 cusps appear only as small denticles.

Cancilla circula (Kiener, 1839); Cernohorsky, 1965, The Veliger 8 (2): 102; plt. 16, fig. 40.

Specimen from Fiji: Radular ribbon white, 3.0 mm long and 0.39 mm wide in shell 18 mm in length; fully formed rows number 47 (+ 2 nascentes) and rhachidians do not show any appreciable wear in the front rows of teeth, although some cusps are broken off in laterals. Rhachidians very short and broad, with 7 slender cusps of varying length; 2 cusps are rather long and the remaining 5 cusps are much shorter and of about equal size, although the size appears to fluctuate throughout the

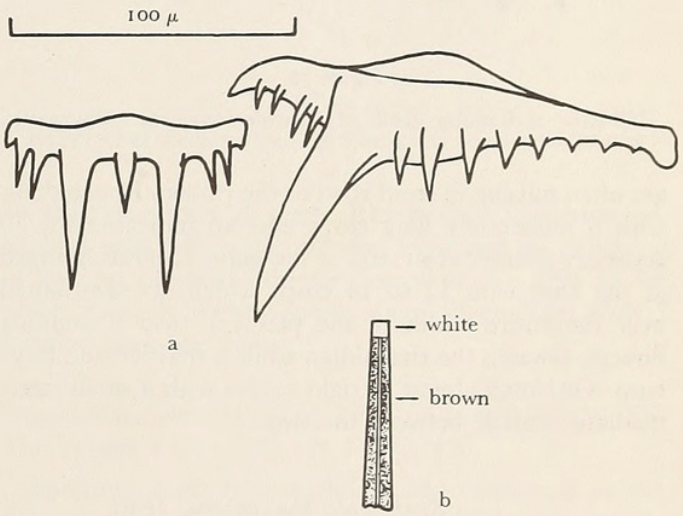


Figure 31

a: Half-Row of Radular Teeth of "*Cancilla circula*" (Kiener)
b: Distal End of Siphon Showing Pattern of Brown and White

rows of the same ribbon. Laterals about 1½ times the width of rhachidians with a curved inward-pointing beak and 11 to 14 cusps; 1 of the cusps is very long and massive and tends to be broken off in a good many rows of the ribbon.

The sole of the animal's foot is creamy-white; dorsum of foot is cream and heavily speckled and variegated with yellow. Siphon whitish underneath, brown on top with a white transverse zone at the distal end and a narrow longitudinal white central line; tentacles are short and brown, proboscis translucent white.
Discussion: The correct interpretation of Kiener's *Can-*

cilla circula is somewhat uncertain; however, the radula illustrated here came from a specimen of *C. circula* illustrated in CERNOHORSKY, 1965, and in shell characters approximating *C. sulcata* (SWAINSON).

Cancilla strigillata (SOWERBY, 1874); CERNOHORSKY, 1965, The Veliger 8 (2): 97; plt. 15, fig. 31.

Specimen from Fiji: Radular ribbon translucent white, 1.7 mm long and 0.32 mm wide in shell 16 mm in length; fully formed rows number 46 (+ 2 nascentes) and teeth

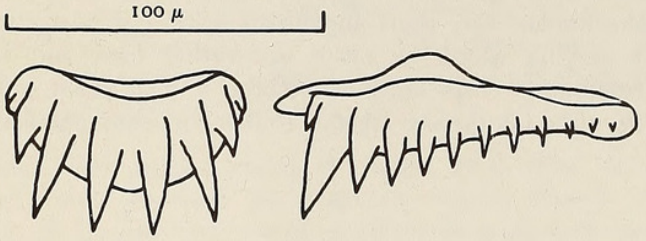


Figure 32
Half-Row of Radular Teeth of *Cancilla strigillata* (SOWERBY)

are often missing in front rows of the ribbon. Rhachidians with 6 moderately long cusps and an indication of an accessory denticle at the end of the plate. Laterals humped at the base with 12 to 14 cusps which are distributed over the entire width of the plate; 1 cusp is pointing directly towards the rhachidian while a massive and large cusp is oriented almost at right angles with a small intermediate denticle between the two.

Scabricola SWAINSON, 1840.

Scabricola SWAINSON, 1840, Treat. Malac., 127: 319 – Type species by subsequent designation (GRAY, 1847) *Mitra serpentina* LAMARCK, 1811 = *Scabricola variegata* (GMELIN, 1791).

Shell: Shell moderate in size, elongate-ovate to cylindrical in outline, moderately solid, sculpture consisting of from 5 to 8 convexly rounded whorls and fine moderately deep spiral grooves, grooves punctate or striate; resulting spiral ridges angulate on penultimate whorl but becoming broad and flat towards the base; columella calloused and with 5 to 6 prominent plicae, outer lip crenulate or crimped, rounded anteriorly; aperture longer than the spire, early whorls granulose.

Scabricola variegata (GMELIN, 1791); CERNOHORSKY, 1965, The Veliger 8 (2): 100; plt. 14, fig. 24 a.

Radula of specimen from Mauritius: The rhachidians and part of laterals (cusp included) rusty-brown, remainder thin and whitish; ribbon 3.2 mm long and 0.35 mm wide in shell 20.0 mm in length. Fully formed rows number 36 (+ 4 nascentes). Rhachidians triangular with one very strong and deeply-rooted central cusp. Laterals about $1\frac{1}{5}$ times the width of rhachidians, and equipped with a curious inward-facing rounded projection and a massive long inward-pointing cusp; other cusps or denticles are absent.

Habitat: In clean sand, occasionally in exposed sand pits.
Geographical Distribution: Indo-Pacific.
Age: Recent.
Discussion: This type of radula is unique among all other mitrid radula types; both the rhachidians and laterals are unicuspid, and cusps are very strong and long. COOKE

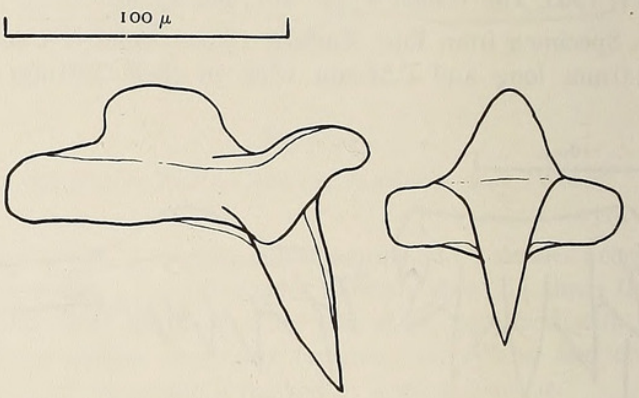


Figure 33
Half-Row of Radular Teeth of *Scabricola variegata* (GMELIN)

(1920) placed this species in his group 8; his representation of the radula (*l.c.*, fig. 14) is a rather schematic drawing.

Swainsonia H. & A. ADAMS, 1853.

Swainsonia H. & A. ADAMS, Gen. Rec. Moll. 1: 180 (*nom. nov. pro Mitrella* SWAINSON, 1832, *non* RISSO, 1826) – Type species by subsequent designation (COSSMANN, 1899) *Mitra fissurata* LAMARCK, 1811 = *Swainsonia fissurata* (LAMARCK, 1811).

Shell: Shell moderately small, oliviform, smooth and shiny, occasionally puncto-striate, spire short and pointed, aperture long and narrow, outer lip smooth and generally slightly longer than the anterior canal, columella plicate, labrum smooth; shell with a thin epidermis.
Radula: Rhachidians with 6 long cusps and 2 small side-cusps, plate concave, some cusps triangular in profile; laterals about the same width as rhachidians, with 3 to

5 massive beak-like cusps, first cusp the largest and gradually diminishing in size towards the base of the plate.

The radula of *Swainsonia* slightly resembles the radula of *Vasum* RÖDING, 1798, particularly the laterals.

Habitat: In clean or slightly muddy sand, in shallow and slightly deeper water.

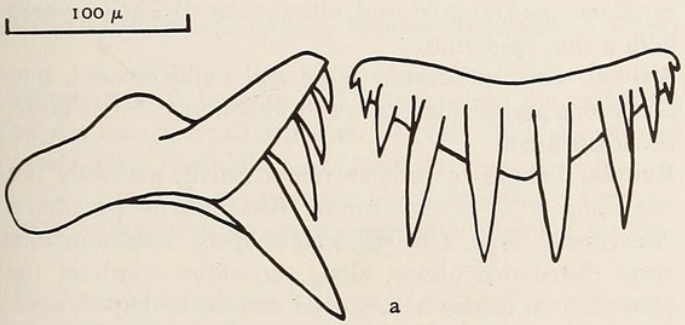
Geographical Distribution: Indo-Pacific.

Age: Recent.

Discussion: CERNOHORSKY (1965) erroneously listed *Mitra olivaeformis* SWAINSON as the type-species of *Swainsonia*; this species should be transferred to *Imbricaria* on radula evidence (COOKE, 1920, fig. 9 and PEILE, 1936, p. 142).

Swainsonia fissurata (LAMARCK, 1811); SHIKAMA, 1963, Shells world ill. col., plt. 75, fig. 7.

Specimen dredged from 17 fathoms at Rivière Noire, Mauritius: Radular ribbon rusty-brown in colour, 4.4 mm long and 0.68 mm wide in shell 27 mm in length; fully formed rows number 40 (+ 1 nascent) and wear was discernible in the front rows of the ribbon. Rhachidians somewhat triangular in shape, with 8 long and slender cusps and a very small accessory denticle; cusps are triangular in profile. Laterals about the same size as rhachidians with 4 strong and massive cusps which diminish in size towards the bottom of the plate.



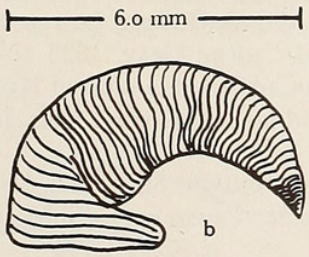


Figure 34

a: Half-Row of Radular Teeth of *Swainsonia fissurata* (LAMARCK)
b: Lateral View of Penis

Swainsonia newcombi PEASE, 1865; TINKER, 1958, Pacif. Seashells, plt. facing p. 144, centre figs.

Specimen from Kailua Bay, Oahu, Hawaii: Radular ribbon rusty-brown in colour, 3.2 mm long and 0.46 mm wide in shell 20 mm in length; fully formed rows number 47 + 1 nascent) and no appreciable wear was apparent on the front rows of teeth. Rhachidians somewhat triangular with 6 long and slender cusps and an indication of vestiges of small accessory cusps at the sides of the plate. Laterals slightly longer than rhachidians with 2 massive beak-like cusps.

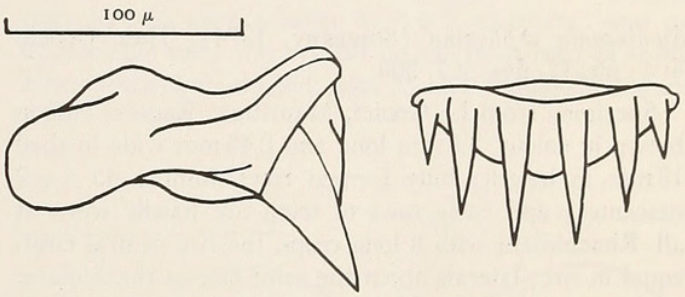


Figure 35

Half-Row of Radular Teeth of *Swainsonia newcombi* (PEASE)

Swainsonia casta (GMELIN, 1791); CERNOHORSKY, 1965 The Veliger 8 (2): 153; plt. 23, fig. 130.

Specimen from Fiji: Radular ribbon brown in colour, 5.0 mm long and 0.62 mm wide in shell 27.0 mm in length; rhachidians are hardly worn at all while only a few

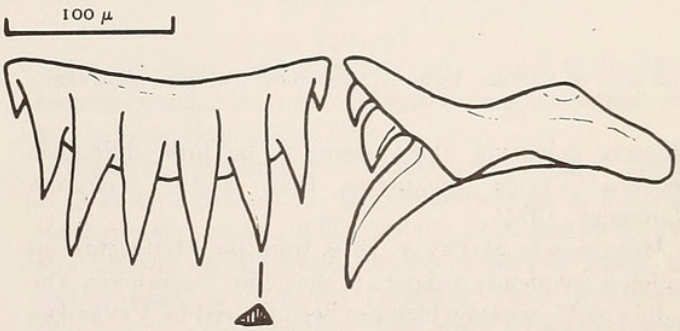


Figure 36

Half-Row of Radular Teeth of *Swainsonia casta* (GMELIN)

cusps are missing in laterals. Fully formed rows number 54 (+ 2 nascentes). Rhachidians concave at base becoming somewhat arched towards the roots of the teeth, and equipped with 6 main cu ps and 2 smaller but solid accessory cusps towards the base; the 2 central cusps are equal sized and in profile have a triangular cutting edge. Laterals about the same size as rhachidians, massive, unusual in shape, the plate consisting of a knuckled base and 3 prominent curved cusps which diminish in size towards the base; the main cusp is very large, solid and triangular in profile.

Swainsonia zephyrina (Sowerby, 1874), Thes. Conch. 4: 4; plt. 17, figs. 307, 308.

Specimen from Le Goulet, Mauritius: Radular ribbon brown in colour, 3.8 mm long and 0.45 mm wide in shell 18 mm in length; fully formed rows number 45 (+ 2 nascentes) and early rows of teeth are hardly worn at all. Rhachidians with 8 long cusps, the two central cusps equal in size; laterals about the same size as rhachidians, with 5 massive cusps which point towards the rhachidian, and which diminish in size towards the base; the fifth cusp is often very small and hardly visible in some rows of the same ribbon.

Discussion: Peile (1936, fig. 7) illustrated the radula of *Mitra mariae* A. Adams, 1853, which appears very similar to that of *Swainsonia zephyrina*. Apart from a slightly

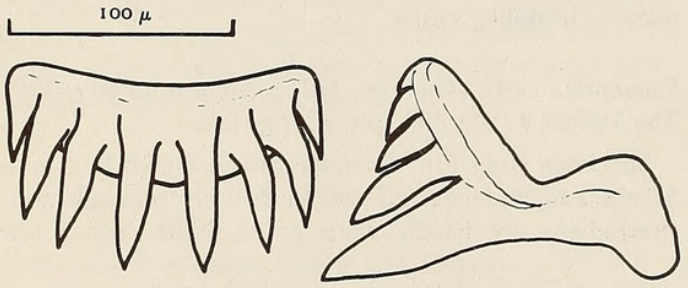


Figure 37

Half-Row of Radular Teeth of *Swainsonia zephyrina* (Sowerby)

different colouring, there seems to be little difference between *S. fusca* (Swainson, 1832) and *S. zephyrina* (Sowerby, 1874).

Mitra zonata Marryat, 1819, from the Mediterranean region is frequently assigned to the genus *Swainsonia*. The radula of *M. zonata* which has been figured by Vayssière (1901), has rhachidians with 7 moderately long cusps and laterals with 20 to 21 cusps; the radula is in fact very similar to that of *M. cardinalis* (Gmelin), and belongs to *Mitra* s. str.

Vexillinae Thiele, 1929.

The subfamily comprises 2 genera and 3 subgenera, with *Vexillum* representing the oldest genus of the subfamily, and *Pusia* its latest offshoot. Species are numerous, mainly tropical and subtropical in distribution. A poison gland is absent in members of the subfamily; the foot, tentacles and eyes are generally larger than those of the Mitrinae, and species of Vexillinae primarily inhabit sand substrata.

The radula of the Vexillinae consists of a wide and multicuspid or narrow and tricuspid rhachidian and sickle-shaped curved laterals which are in the process of reduction.

Vexillum Röding, 1798.

Vexillum Röding, 1798, Mus. Bolten., p. 138 - Type species by subsequent designation (Woodring, 1928) *Vexillum plicatum* Röding, 1798 = *Vexillum plicarium* (Linnaeus, 1758).

Shell: Shell 10 mm to 80 mm in size, fusiform or elongate-ovate, sutures plain or tuberculate, sculptured with axial plicae or striae and transverse grooves or ridges; aperture narrow or moderately wide and elongate, often constricted basally, labrum lirate, columella plicate; anterior canal narrow and produced, often recurved; shell covered with a thin epidermis.

Animal: Foot moderately large and multicoloured, tentacles long and slender; eyes and siphon moderately large, proboscis small.

Radula: Length of radular ribbon small, generally not exceeding 10% of shell-length. Rhachidians are of the "rastriform" type, bow- or wing-shaped, with numerous cusps distributed almost along the entire width of the plate; lateral teeth small, curved and sickle-shaped, overlapping the rhachidians for a short distance. The radula of *Vexillum* is rather similar to the radula of the genus *Nux* Barnard, 1960; the rhachidians bear a certain resemblance to those of *Cyllene* Gray, 1833 (Nassidae).

Habitat: In clean and muddy sand of lagoons and sandbanks and in sand-pockets of coral reefs, from shallow to deeper water.

Geographical Distribution: Since Late Miocene confined to the Indo-Pacific, Panamic, Caribbean and Atlantic regions.

Age: Eocene to Recent.

Discussion: The radula of *Vexillum sanguisugum* (Linnaeus), the type species of *Pulchritima* Iredale, was figured by Peile (1936, fig. 11) and it is that of *Vexillum* s. str.; this genus is superfluous and should be placed in its proper synonymy. The radula of *Mitropifex quasillus*

IREDALE, the type species of *Mitropifex* IREDALE, 1929, is unknown to me; however, the radula of *Mitropifex collinsoni* (A. ADAMS) as figured by HABE (1943, plt. 3, fig. 13) does not differ from *Vexillum* in any way.

Vexillum exasperatum (GMELIN, 1791); CERNOHORSKY, 1965, The Veliger 8 (2): 124; plt. 19, fig. 77.

Specimen from Fiji: Radular ribbon translucent-white in colour, 1.1 mm long and 0.09 mm wide in shell 21 mm in length; fully formed rows number 45 (+ 3 nascentes), and no apparent wear in the front rows of teeth was discernible apart from some missing laterals. Rhachidians broad and bow-shaped, 2½ times the width of laterals, with 19 to 21 slender and moderately long cusps; the central cusp is broader and longer while the end-cusps appear only as small denticles. Laterals sickle-shaped and overlapping rhachidians to about the sixth cusp.

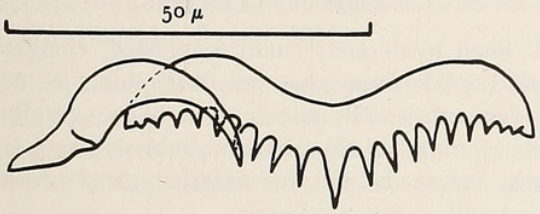


Figure 38

Half-Row of Radular Teeth of *Vexillum exasperatum* (GMELIN)

This species is the type species of *Arenimitra* IREDALE, 1929, which becomes synonymous with *Vexillum* RÖDING.

Vexillum cadaverosum (REEVE, 1844); CERNOHORSKY, 1965, The Veliger 8 (2): 118; plt. 18, fig. 71.

Specimen from Fiji: Radular ribbon translucent-white in colour, 1.27 mm long and 0.19 mm wide in shell 17 mm in length; fully formed rows number 46 (+ 2 nascentes), and appreciable wear was evident in the front rows. Rhachidians bow-shaped with 21 rather slender cusps, central of which is broader and longer than the rest. Laterals smaller than rhachidians, unicuspid and with a knuckle-like hump at the base of the tooth.

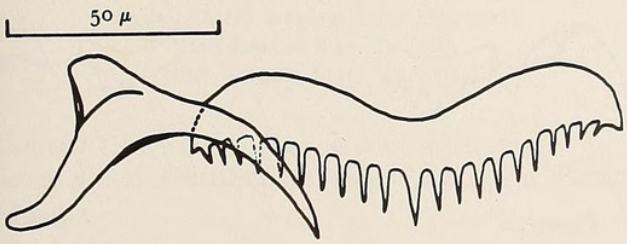


Figure 39

Half-Row of Radular Teeth of *Vexillum cadaverosum* (REEVE)

Vexillum semifasciatum (LAMARCK, 1811); CERNOHORSKY, 1965, The Veliger 8 (2): 135; plt. 22, fig. 112.

Specimen from Fiji: Radular ribbon yellowish in colour, 0.72 mm long and 0.13 mm wide in shell 19 mm in length; fully formed rows number 67 (+ 2 nascentes) and no appreciable wear was evident on the front rows of teeth. Rhachidians bow-shaped, with 15 to 17 equal-sized cusps which are distributed along the entire width of the plate. Laterals smaller than rhachidians, unicuspid, slender and overlapping rhachidians.

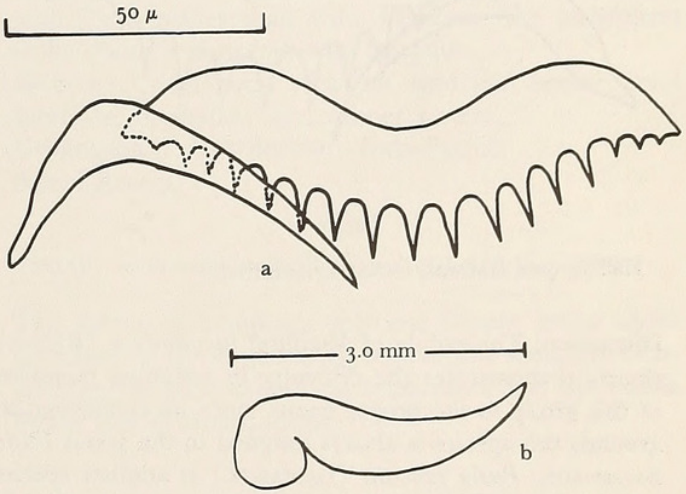


Figure 40

Vexillum semifasciatum (LAMARCK)
a: Half-Row of Radular Teeth
b: Lateral View of Penis

Vexillum semifasciatum (LAMARCK) is the type species of *Costellaria* SWAINSON, 1840 by monotypy (as *Costellaria rigida* SWAINSON, 1822). For the latter species SWAINSON offered an illustration which is beyond doubt the species *Mitra semifasciata* LAMARCK (*vide* SWAINSON, 1822, plt. 29, centre figures). The *Mitra rigida* SWAINSON of 1840, however (text fig. 84 d), is the species *Vexillum deshayesi* (REEVE, 1844). The genus *Costellaria* should be placed in the synonymy of *Vexillum* s. str.

Vexillum luculentum (Reeve, 1845); Cernohorsky, 1965, The Veliger **8** (2): 147; plt. 22, fig. 122.

Specimen from Fiji: Radular ribbon translucent-white, 0.9 mm long and 0.12 mm wide in shell 13 mm in length; fully formed rows number 58 (+ 2 nascentes), and the two front rows of teeth show appreciable wear on the rhachidians. Rhachidians bow-shaped with 9 moderately large cusps of about equal length with the exception of the last cusp which is appreciably smaller; the ends of the plate are bare. Laterals smaller than rhachidians, unicuspid, slender and overlapping rhachidians.

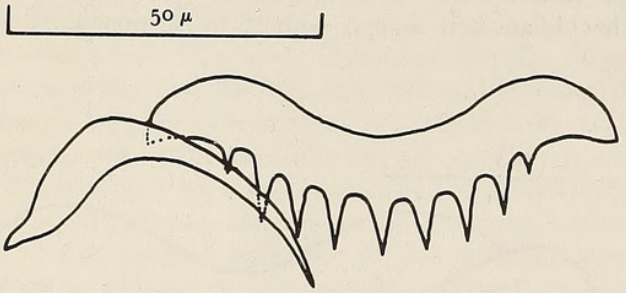


Figure 41

Half-Row of Radular Teeth of *Vexillum luculentum* (Reeve)

Discussion: The radula of *Vexillum luculentum* (Reeve) clearly demonstrates the difficulty in assigning members of this group to the proper genus, since on conchological grounds this species is always assigned to the genus *Pusia* Swainson. *Pusia crocata* (Lamarck) is another species which must be removed to *Vexillum*, as the radula is similar to that of *V. costellaris* (Lamarck) (*fide* Peile, 1936). Cooke (1920) examined the radula of *Pusia cancellarioides* (Anton) [reported as *Vexillum nodosum* (Swainson)] from Hawaii, and found the rhachidians to possess 7 to 8 cusps and to belong to *Vexillum*.

It is highly probable that the radula of the type species of *Pusia*, i.e. *P. microzonias* (Lamarck), will have a radula of the *Vexillum* pattern. In that case the genus *Pusiolina* (type species *Voluta tricolor* Gmelin, 1791) would have to be used for species possessing a radula consisting of a tricuspid rhachidian.

(Zierliana) Gray, 1847.

Zierliana Gray, 1847, Proc. Zool. Soc. London, p. 141 – Type species by original designation *Voluta ziervoyelii* Gmelin, 1791 = *Vexillum (Zierliana) ziervogelii* (Gmelin) [emended Dillwyn, 1817].

Shell: Shell moderately small, oviform, spire shorter than the aperture, whorls coarsely axially plicate; columella with 4 oblique folds, posteriorly calloused, outer lip thickened and dentate on inner margin.
Radula: Thiele (1931) places the subgenus as a section of *Vexillum*, and remarks that the rhachidian tooth of *Zierliana* is multicuspid.
Habitat: Generally inhabits sand substrate under basalt or coral rocks towards the high tide region.
Geographical Distribution: Indo-Pacific.
Age: Recent.

Pusia Swainson, 1840.

Pusia Swainson, 1840, Treat. Malac. **127**: 320 – Type species by monotypy *Mitra microzonis* [*sic*] Lamarck. 1811 = *Pusia microzonias* (Lamarck, 1811).

Shell: Shell moderately small, depressed, elongate-ovate to ovate, solid, sutures smooth, tuberculate or coronate, whorls smooth, axially plicate or nodulose, spirally striate or ridged, outer lip thick or thin, labrum lirate or rarely smooth, columella plicate, anterior canal short; shell covered with a thin epidermis.
Radula: Radula consists of tricuspid rhachidians, base of plate concave, length of cusps variable, central cusp generally slightly larger; lateral teeth about equal in size to rhachidian or only slightly smaller, and in the form of simple hook-like teeth. The radula of *Pusia* resembles the radulae of some species of *Metzgeria* Norman, 1879 (Vasidae), *Rapana* Schumacher, 1817 and *Columbarium* von Martens, 1881 (Muricidae), and somewhat less those of *Oliva* Bruguière, 1789. The rhachidian on its own is rather similar to that of *Volutocorbis* Dall, 1890 (Volutidae).

Radulae of *Pusia* have been figured by Peile (1922), Thiele (1931), Habe (1943) and Barnard (1959).

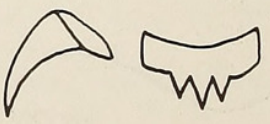


Figure 42

Half-Row of Radular Teeth of *Pusia hizenensis* (Pilsbry) [after Habe, 1943, plate 3; figure 10]

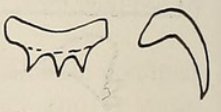


Figure 43

Half-Row of Radular Teeth of *Pusia tricolor* (Gmelin) [after Peile, 1922, figure 5]

Habitat: In sand-pockets of coral reefs and cracks and crevices of coral reef flats and underside of coral rocks, from the intertidal zone to deeper water.
Geographical Distribution: Indo-Pacific, Panamic, Caribbean and Mediterranean regions.
Age: Late Miocene to Recent.
Discussion: The true *Pusia* may have developed independently in the Indo-Pacific from *Vexillum* and re-entered the European-Mediterranean region prior to the disappearance of the Tethys sea. Radulae of *Pusia* pattern formed group 12 in Cooke's arrangement.

(Thala) H. & A. Adams, 1853.

Thala H. & A. Adams, 1853, Gen. Rec. Moll. 1: 178 – Type species by subsequent designation (Cossmann, 1899) *Mitra mirifica* Reeve, 1845.

Shell: Shell small, fusiform, apex produced and smooth, sculpture consisting of spiral rows of nodules, body whorl produced anteriorly, columella plicate, aperture narrow, outer lip thick and denticulate, anterior canal produced and recurved.
Radula: Radula pattern very similar to that of *Pusia;* the rhachidians are bow-shaped with the ends bent slightly backwards, and equipped with 3 prominent cusps which on rare occasions are flanked by very small side-denticles; laterals as in *Pusia.*

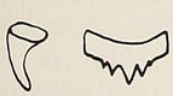


Figure 44

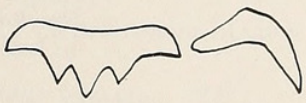


Figure 45

Pusia (Thala) ogasawarana (Pilsbry)
Half-Row of Radular Teeth
[after Habe, 1943, plate 3, figure 11]

Pusia (Thala) simulans (von Martens)
Half-Row of Radular Teeth
[after Thiele, 1931, figure 394]

Habitat: Under coral rocks on sand substratum.
Geographical Distribution: Indo-Pacific and Panamic regions.
Age: Recent.
Discussion: This subgenus comprises only a very few species. The species *Thala ogasawarana* var. Pilsbry, 1904, figured by Habe (1961, plt. 34, fig. 1) appears to be conspecific with *Mitra secalina* Gould, 1860, from the Ryukyu Islands.

(Idiochila) Pilsbry, 1921.

Idiochila Pilsbry, 1921, Proc. Acad. Nat. Sci. Philad. **72:** 315. – Type species by original designation *Mitra turben* Reeve, 1844.

Shell: Shell small, solid, oviform and obese, axially closely plicate, interstices striate, sutures prominently deep; spirally ridged towards the base, aperture narrow, outer lip contracted anteriorly, labrum lirate, parietal wall calloused, columella with 5 to 6 prominent folds, anterior canal somewhat produced.
Radula: The radula of the type species is unknown; however, most conchological characters suggest a relationship with *Pusia* rather than with *Vexillum*; the assignment under *Pusia* is therefore only tentative.
Habitat: Under coral rocks on sand and broken coral substrate, in shallow and deeper water.
Geographical Distribution: Indo-Pacific.
Age: ? Recent.

Cylindromitrinae Cossmann, 1899.

This subfamily comprises only one Recent genus which developed in the Indo-Pacific region. The shells are characterized by their cylindrical appearance and the radula by the lack of lateral teeth.

Pterygia Röding, 1798.

Pterygia Röding, 1798, Mus. Bolten., p. 51. – Type species by subsequent designation (Dall, 1915) *Pterygia nucella* Röding, 1798 = *P. dactylus* (Linnaeus, 1767).

Shell: Shell moderate in size, cylindrically-ovate, solid, thick, spire short, body whorl smooth or sculptured with spiral ridges or striae; outer lip long and thick, smooth or crenulate, columella with numerous oblique plicae; shell covered with a thin epidermis.
Animal: Foot generally large, tentacles short, proboscis very slender and extremely long (occasionally 3 to 4 times the length of the shell).
Radula: The radular teeth differ from all other mitrid radulae in the absence of lateral teeth; rhachidians are slightly similar in form to those of the genus *Swainsonia* and are equipped with 5 to 9 cusps. The radular ribbon is fragile and very small in relation to shell-length.
Habitat: In clean sand, from shallow to deeper water.

Geographical Distribution: Indo-Pacific.
Age: Recent.

Pterygia nucea (Gmelin, 1791); Cernohorsky, 1965, The Veliger **8** (2): 153; plt. 23, fig. 128.

Specimen from Fiji: Radular ribbon white in colour, 1.2 mm long and 0.06 mm wide in shell 40 mm in length; fully formed rows number 75 (+ 2 nascentes). Rhachidians roughly elliptical, prominently curved inward, with 2 knob-like protrusions at either end, and 9 moderately small cusps; the central cusp is the longest and remainder of cusps protrude only slightly past the edge of the plate. The teeth are so prominently curved that if too much pressure is applied to the cover slide, the rhachidians will tend to split centrally. Lateral teeth absent.

The proboscis is very long and slender, 85 mm long and 0.9 mm wide in fully extended position in a shell 40 mm in length.

Discussion: Peile (1922) remarked that the radula of *Pterygia dactylus* (Linnaeus) preserved in the British Museum (Natural History) collection also lacks laterals.

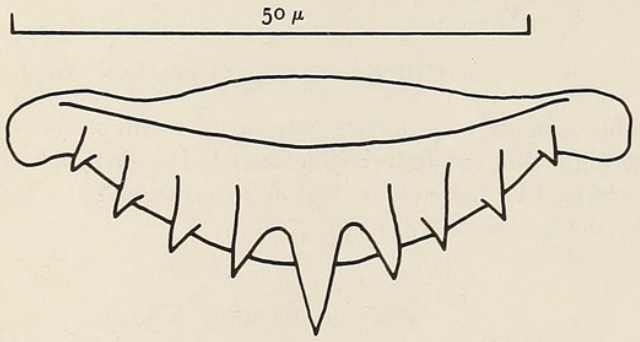


Figure 46
One Row of Radular Teeth of *Pterygia nucea* (Gmelin)

Thiele (1931) figures the radula of *P. crenulata* (Gmelin) which lacks laterals; the rhachidian in this species has 5 cusps, with the central cusp the longest.

Pterygia nucea (Gmelin) is the type species of *Acuticylindra* Iredale, 1929; the species, however, is obviously congeneric with *P. dactylus* (Linnaeus), the type species of *Pterygia*.

Pterygia scabricula (Linnaeus, 1758); Cernohorsky, 1965, The Veliger **8** (2): 153; plt. 13, fig. 6.

Specimen from Fiji: Radular ribbon translucent white in colour, 1.5 mm long and 0.09 mm wide in shell 20 mm in length; fully formed rows number 88 (+ 4 nascentes) and no wear was evident on the front rows of teeth. Rhachidians concave, with 7 sharp cusps, central cusp the largest, remainder diminishing in size towards the end of the plate. Lateral teeth absent.

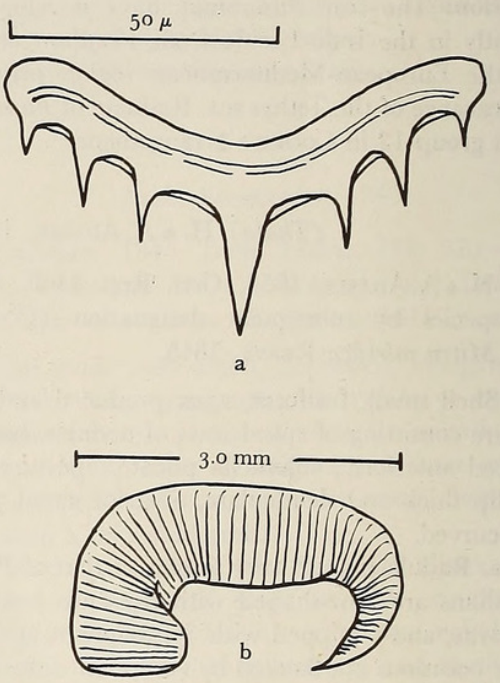


Figure 47
Pterygia scabricula (Linnaeus)
a: One Row of Radular Teeth
b: Lateral View of Penis

The proboscis measured 17 mm in a shell 20 mm in length. This species is generally placed in either *Mitra* s. str. or *Scabricola*. It should be removed from Mitrinae and assigned to Cylindromitrinae.

SYNONYMIC LIST
OF THE PROPOSED ARRANGEMENT OF THE FAMILY MITRIDAE

(Type species are shown in brackets; genera based on a fossil type species are indicated with †)

Mitrinae Swainson, 1831.

Genus
Mitra Röding, 1798 – Type species *Mitra mitra* (Linnaeus, 1758)

Mitra MARTYN, 1784 [(non binomial) – *M. tessellata* MARTYN, 1784 = *Voluta incompta* SOLANDER in LIGHTFOOT, 1786]
Mitra RÖDING, 1798 [*Voluta episcopalis* LINNAEUS, 1758 = *Voluta mitra* LINNAEUS, 1758]
Mitraria RAFINESQUE, 1815 [*Voluta episcopalis* LINNAEUS, 1758 = *V. mitra* LINNAEUS, 1758]
Thiarella SWAINSON, 1840 (in err. pro *Tiarella*, first reviser HERRMANNSEN, 1847)
Tiarella SWAINSON, 1840 (no type designated; synonymous with *Mitra* RÖDING, 1798)
Tiara SWAINSON, 1840 (pars) [non *Tiara* SWAINSON, 1831]
Nebularia SWAINSON, 1840 [*Mitra contracta* SWAINSON, 1820]
Chrysame H. & A. ADAMS, 1853 [*Mitra coronata* LAMARCK 1811]
Isara H. & A. ADAMS, 1853 [*Mitra bulimoides* REEVE, 1845]
Ziba H. & A. ADAMS, 1853 [*Mitra carinata* SWAINSON, 1824]
Phaeomitra VON MARTENS, 1880 (no type designated; *Mitra fulva* SWAINSON, 1829 = *M. coffea* SCHUBERT & WAGNER, 1829 is the first species listed)
Cucurbita SCUDDER, 1882 (*nom. nud.*)
† *Eumitra* TATE, 1889 [*Mitra alokiza* TENISON-WOODS, 1889]
Fuscomitra PALLARY, 1900 [*Mitrella fusca* SWAINSON, 1824]
Papalaria DALL, 1915 [(no type designated; applies to the group of "the smooth red-spotted Mitras regarded hitherto as typical" (DALL, 1915)]
Episcomitra MONTEROSATO, 1917 [*Mitra zonata* MARRYAT, 1819]
Atrimitra DALL, 1918 [*Mitra idae* MELVILL, 1893]
† *Diplomitra* FINLAY, 1927 [*Cymbiola nitens*, MARSHALL, 1918]
Vicimitra IREDALE, 1929 [*V. prosphora* IREDALE, 1929]

Subgenus
(Dibaphus) PHILIPPI, 1847 – Type species *Conohelix edentula* SWAINSON = *Conus edentulus* REEVE, 1844
Mutyca H. & A. ADAMS, 1853 [*Mitra ancillides* BRODERIP, 1836]
Mitroidea PEASE, 1865 [*M. multiplicata* PEASE, 1865]
Mauritia H. ADAMS, 1869 (non TROSCHEL, 1863) [*M. barclayi* H. ADAMS, 1869]

Genus
Strigatella SWAINSON, 1840 – Type species *Mitra zebra* LAMARCK, 1811 = *Voluta paupercula* LINNAEUS, 1758
† [?] *Mitreola* SWAINSON, 1832 [*M. monodonta* LAMARCK, 1803]

Genus
Neocancilla CERNOHORSKY, 1966 – Type species *Voluta papilio* LINK, 1807

Genus
?: Group 10 of COOKE, 1920 – ? *Mitra scabriuscula* LAMARCK = ? *M. granatina* LAMARCK, 1811

Genus
Charitodoron TOMLIN, 1932 – Type species *C. euphrosyne* TOMLIN, 1932 [originally established as genus in Buccinidae].

Imbricariinae TROSCHEL, 1867

Genus
Imbricaria SCHUMACHER, 1817 – Type species *I. conica* SCHUMACHER, 1817 = *I. conularis* (LAMARCK, 1811)
Conoelix SWAINSON, 1821 [*C. lineatus* SWAINSON, 1821 = *Mitra conularis* LAMARCK, 1811]
Conohelix SOWERBY, 1825 [in err. pro *Conoelix* SWAINSON, 1821]
Conoehelix SWAINSON, 1840 [in err. pro *Conoelix* SWAINSON, 1821]
Mitricaria YATES, 1885 [? in err. pro *Imbricaria* SCHUMACHER, 1817]

Genus
Cancilla SWAINSON, 1840 – Type species *Tiara isabella* SWAINSON, 1831 [?] *Tiara* SWAINSON, 1831 (pars)

Genus
Scabricola SWAINSON, 1840 – Type species *Mitra serpentina* LAMARCK, 1811 = *Scabricola variegata* (GMELIN, 1791)
Scabricula SOWERBY, 1842 (in err. pro *Scabricola* SWAINSON, 1840)
Scabicola GRAY, 1847 (in err. pro *Scabricola* SWAINSON, 1840)

Genus
Swainsonia H. & A. ADAMS, 1853 – Type species *Mitra fissurata* LAMARCK = *Swainsonia fissurata* (LAMARCK, 1811)
Mitrella SWAINSON, 1831 (*non* RISSO, 1826) – [*M. fissurella* LAMARCK = *Mitra fissurata* LAMARCK, 1811]
Swainsonia H. & A. ADAMS, 1853 (*nom. nov. pro Mitrella* SWAINSON, 1831)

Vexillinae Thiele, 1929

Genus

Vexillum Röding, 1798 – Type species *V. plicatum* Röding, 1798 = *V. plicarium* (Linnaeus, 1758)

Turricula Klein, 1753 (pre-Linnaean)

Vexillum Röding, 1798 [*V. plicatum* Röding, 1798 = *Voluta plicaria* Linnaeus, 1758]

Turris Montfort, 1810 (*non* Röding, 1798) – *Voluta vulpecula* Linnaeus, 1758]

Vulpecula Blainville, 1824 [*Voluta vulpecula* Linnaeus, 1758]

Tiara Swainson, 1831 [*Mitra corrugata* Lamarck, 1811 = *Voluta rugosa* Gmelin, 1791]

Thiara Swainson, 1840 (non Röding, 1798) (in err. pro *Tiara* Swainson)

Callithea Swainson, 1840 (non Boisduval, 1835) [*Voluta sanguisuga* Linnaeus, 1758]

Costellaria Swainson, 1840 [*Mitra rigida* Swainson, 1821 = *M. semifasciata* Lamarck, 1811]

Turricula auctt. (non Schumacher, 1817)

† *Mesorhytis* Meek, 1876 [*Fasciolaria (M.) gracilenta* Meek, 1876]

Latiromitra Locard, 1897 [*L. specialis* Locard, 1897 – originally introduced as a genus in Pisaniidae]

† *Waimatea* Finlay, 1927 [*Mitra inconspicua* Hutton, 1885]

Pulchritima Iredale, 1929 (nom. nov. pro *Callithea* Swainson, 1840)

Arenimitra Iredale, 1929 [*Mitra arenosa* Lamarck, 1811 = *Voluta exasperata* Gmelin, 1791]

Mitropifex Iredale, 1929 [*M. quasillus* Iredale, 1929]

† *Parvimitra* Finlay, 1930 [*P. pukeuriensis* Finlay, 1930]

Subgenus

(Zierliana) Gray, 1847 – Type species *Voluta ziervoyelii* Gmelin, 1791 = *Zierliana ziervogelii* (Gmelin, 1791) – emend. Dillwyn, 1817

† *Conomitra* Conrad, 1865 [*Mitra fusoides* Lea, 1833]

Ziervogelia P. Fischer, 1884 (emend. van. pro *Zierliana* Gray, 1847)

Genus

Pusia Swainson, 1840 – Type species *Tiara (Pusia) microzonis (sic)* Lamarck, 1811 = *Mitra microzonias* Lamarck, 1811

Pusiola Monterosato, 1917 (*non* Wallengren, 1863) [*Voluta tricolor* Gmelin, 1791]

Pusiolina Cossmann, 1921 (nom. nov. pro *Pusiola* Monterosato, 1917)

Peculator Iredale, 1924 [*P. verconis* Iredale, 1924]

Austromitra Finlay, 1927 [*Columbella rubiginosa* Hutton, 1873 = *Mitra analogica* Reeve, 1845]

† *Balcomitra* Finlay, 1927 [*Mitra paucicostata* Tate, 1889]

† *Proximitra* Finlay, 1927 [*Vexillum rutidolomum* Suter, 1885]

Subgenus

(Thala) H. & A. Adams, 1853 – Type species *Mitra mirifica* Reeve, 1845

Subgenus

(Idiochila) Pilsbry, 1921 – Type species *Mitra turben* Reeve, 1844

Cylindromitrinae Cossmann, 1899

Genus

Pterygia Röding, 1798 – Type species *P. nucella* Röding, 1798 = *P. dactylus* (Linnaeus, 1767)

Cylindra Schumacher, 1817 (*non* Illiger, 1802) [*C. coronata* Schumacher, 1817 = *Voluta crenulata* Gmelin, 1791]

Cylindromitra P. Fischer, 1884 [*Voluta crenulata* Gmelin, 1791]

Cylinder Melvill & Standen, 1895 (*non* Montfort, 1810) (in err. pro *Cylindra* Schumacher, 1817)

Acuticylindra Iredale, 1929 [*Voluta nucea* Gmelin, 1791]

Pterigia Dautzenberg, 1935 (in err. pro *Pterygia* Röding, 1798)

Genera Established in or Occasionally Assigned to The Family Mitridae

Aidone H. & A. Adams, 1853 [*Mitra insignis* A. Adams, 1853] – Fam. Columbellidae

Volutomitra H. & A. Adams, 1853 [*Mitra groenlandica* Beck in Möller, 1842] – Fam. Volutidae

Mitropsis Pease, 1867 [*M. fusiformis* Pease, 1867 =*Columbella paumotensis* Tryon, 1883] – Fam. Columbellidae

Microvoluta Angas, 1877 [*M. australis* Angas, 1877] – Fam.Volutidae

Mitrolumna Bucquoy, Dautzenberg & Dollfuss, 1883 [*Mitra olivoidea* Cantraine, 1835] – *Mitromorpha* A. Adams, 1865; Fam. Turridae

Clinomitra Bellardi, 1889 [*C. rovasendae* Bellardi, 1889] – Fam. Turridae

Diptychomitra Bellardi, 1889 [*D. eximia* Bellardi, 1889] – Fam. Columbellidae

The genera *Volutomitra* H. & A. Adams and *Microvoluta* Angas, are assigned to the family Mitridae by Cotton (1957). Both these genera belong to the subfamily Volutomitrinae within the family Volutidae. The rhachidians of *Volutomitra typica* Strebel, 1908 (= *fragillima* Watson, 1882) and *V. groenlandica* (Beck in Möller, 1842) resemble that of *Amoria turneri* (Gray in Griffith & Pidgeon, 1834) very closely; the rhachidian plate is wishbone or "Y"-shaped, with one single pointed cusp, while laterals are small and obliquely rhomboidal. Members of Volutomitrinae inhabit temperate and subarctic waters.

SUMMARY

In view of the group's geologic history, zoogeography, diversity in radula pattern, differences in animal structure and variability of ecological requirement, it would be malacologically unsound to combine the 500-odd Recent species under one genus *Mitra*. The single genus theory advocated by some writers would in addition create taxonomic problems because of secondary homonymy.

The proposed subdivision may appear rather orthodox with 45 to 50 species per genus. It is expected, however, that with more attention being devoted to the soft parts by future investigators, the taxonomic value of several old-established genera may be either confirmed or rejected; it may also be necessary to establish new genera for the reception of well-defined natural groups of mitrids. In conclusion it may be said that sufficient evidence has been advanced to realize that the present generic assignment of species whose radulae remain unknown will at times prove to be erroneous.

ACKNOWLEDGMENTS

I would like to thank Dr. D. McMichael, Australian Museum, Sydney, and Drs. H. Rehder and J. Rosewater, Smithsonian Institution, Washington, for the often time-consuming compilation of reference material.

I wish to acknowledge with thanks Dr. Myra Keen's interest in this project and express my gratitude to Mr. E. Coan for his co-operation in this proposed revision of the family, and for information on references unavailable to me.

I wish to thank the following collectors for preserved mitrid material: Mr. and Mrs. R. F. Browne, Nausori; Mrs. J. Cate, Los Angeles; Mrs. E. Couacaud, Mauritius; Mr. W. Eyerdam, Seattle; Mr. and Mrs. F. Freitag, Suva; Mr. G. Griffen, Suva; Mr. and Mrs. N. Hunter, Avoca Beach; Mr. A. Jennings, Nadi Airport; and Mr. C. Weaver, Hawaii.

LITERATURE CITED

Allan, Joyce

1959. Australian shells; rev. ed. Melbourne, i - xxi; 1 to 487; plts. 1 - 44; text figs.

Barnard, Keppel Harcourt

1959. Contributions to the knowledge of South African marine Mollusca, Part II : Gastropoda: Prosobranchiata: Rhachiglossa. Ann. South Afric. Mus. 45 (1): 1 - 237; 52 figs. (June)

1960. The genus *Charitodoron* Tomlin, 1932. Journ. Conch. 24 (11): 402 (16 June 1960)

1960 a. New species of South African marine gastropods. Journ. Conch. 24 (12): 438 - 442; 3 text figs. (16 Dec. 1960)

Cate, Jean M.

1962. Revision of some Hawaiian mitrid species (Mollusca: Gastropoda) The Veliger 4 (3): 140 - 149; plts. 33 - 35 (1 January 1962)

Cernohorsky, Walter Oliver

1965. The Mitridae of Fiji. The Veliger 8 (2): 70 - 160; plts. 13 - 23; 11 text figs.; 1 map (1 October 1965)

1966. Radulae of four species of Mitridae (Mollusca: Gastropoda). Journ. Conch. 26: 15 - 18; 4 text figs.

Cooke, Alfred Hands

1920. The radulae of the Mitridae. Proc. Zool. Soc. London for 1919, 29: 405 - 422; 18 text figs. (25 Febr. 1920)

Cossmann, Alexandre Édouard Maurice

1899. Essais de paléoconchologie comparée 3: 1 - 201; 8 plts.

Cotton, Bernard Charles

1957. Family Mitridae; publication No. 12. Roy. Soc. So. Austral., Malac. Sect., Adelaide; 6 pp., 1 plt. (unpagin.)

Dall, William Healey

1915: A monograph of the molluscan fauna of the *Orthaulax pugnax* zone of the Oligocene of Tampa, Fla. U. S. Nat. Mus. Bull. 90: i - xv; 1 - 173; plts. 1 - 26

Gray, John Edward

1847. A list of the genera of Recent Mollusca, their synonyma and types. Proc. Zool. Soc. London 15 (178): 129 - 219 (10 November 1847)

1853. On the teeth of the genus *Mitra*, Lamarck. Ann. Mag. Nat. Hist.; ser 2, 12: 129 - 130

Habe, Tadashige

1943. On the radulae of Japanese marine gastropods (I). Japan. Journ. Malac. 13 (1 - 4): 68 - 76; plts. 3 - 4

Herrmannsen, A. N.

1846 - 1852. Indices generum malacozoorum primordia. 1: i - xvii; 1 - 637 (Sept. 1846 - July 1847); 2: xxix - xlii; 1 to

717 (July 1847 - March 1849); Suppl. et Corrig. i - v; 1 - 140 (December 1852)

PACE, S.

1902. Contributions to the study of the Columbellidae. Proc. Malac. Soc. London 5 (1 - 2): 36 - 154 (no. 1 - 23 April 1902, no. 2 - 1 July 1902)

PEILE, A. J.

1922. The radula in some Mitridae. Proc. Malac. Soc. London 15 (2 - 3): 93 - 94; text figs. (Dec. 1922)

1936. Radula notes. Proc. Malacol. Soc. London 22 (3): 139 - 144; 12 text figs.

1937. Radula notes. — II. Proc. Malacol. Soc. London 22 (4): 181 - 186; text figs. 13 - 24; 2 tables (13 March 1937)

REEVE, LOVELL AUGUSTUS

1844 - 1845. Conchologia Iconica. Monograph of the genus *Mitra*. 10: plts. 1 - 39

SHIKAMA, TOKIO

1963. Selected shells of the world illustrated in colours. Tokyo, 1: 1 - 154; 102 col. plts.; 192 text figs.

1964. Selected shells of the world illustrated in colours. Tokyo, 2: 1 - 212; 70 col. plts.; 245 text figs.

SOWERBY, GEORGE BRETTINGHAM

1874. Thesaurus Conchyliorum. Monograph of the genus *Mitra*. 4: 1 - 46; plts. 1 - 28.

STOLL, N. R., *et al.*

1961. International Code of Zoological Nomenclature adopted by the XV International Congress of Zoology. London; xvii + 176 pp.

SWAINSON, WILLIAM

1820 - 1833. Zoological illustrations or original figures and descriptions of new, rare, or interesting animals, selected chiefly from the classes of ornithology, entomology, and conchology, and arranged according to their natural affinities. London (Balwin & Cradock), 6 vols. [series 1: 1 - 3; series 2: 1 - 3]

1840. A treatise on malacology, or the natural classification of shells and shellfish. London, pp. 1 - 419; text figs.

THIELE, JOHANNES

1931 - 1935. Handbuch der systematischen Weichtierkunde. Jena, pp. 1 - 1154; 893 text figs.

TINKER, SPENCER WILKIE

1958. Pacific sea shells (2nd. ed.) 240 pp.; 99 plts.

TOMLIN, JOHN READ LE BROCKTON

1932. Reports of the marine Mollusca in the collection of the South African Museum. VI - VIII. Ann. South Afr. Mus. 30: 157 - 169; text figs.

TROSCHEL, FRANZ HERMANN

1868 - 1869. Das Gebiss der Schnecken zur Begründung einer natürlichen Classification. Berlin, Vol. 2, prts. 2, 3

VAYSSIÈRE, ALBERT JEAN BAPTISTE MARIE

1901. Étude zoologique et anatomique de la *Mitra zonata* MARRYATT. Journ. de Conchyl. 49: 77 - 95; plt. 3

WENZ, WILHELM

1940-1943. Handbuch der Paläozoologie; Gastropoda, Prosobranchia 6 (1): 1 - 1639; 4211 text figs.

WINCKWORTH, RONALD

1945. The types of the Boltenian genera. Proc. Malacol. Soc. London 26: 136 - 148

WOODRING, WENDELL PHILLIPS

1928. Miocene mollusks from Bowden, Jamaica. Part 2: Gastropods and discussion of results. Carnegie Inst. Washington, Publ. 385: i - vii + 1 - 564; 3 text figs.; plts. 1 - 40 (28 Nov.)