

# Calliostomatidae (Gastropoda: Trochoidea) from New Caledonia, the Loyalty Islands, and the northern Lord Howe Rise

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## ABSTRACT

Thirty species (27 new) of Calliostomatidae are recorded from the study region, all but two of which are new records. An additional new species is based on material from northern New Zealand. They are referred to *Fautor* Iredale, 1924, *Benthastelena* Iredale, 1936, *Ampullotrochus* Monterosato, 1890 (as subgenera of *Calliostoma* Swainson, 1840), *Bathyfautor* gen. nov., *Dactylastele* gen. nov., *Laetifautor* Iredale, 1929, *Selastele* gen. nov., *Fautrix* gen. nov., and *Thysanodonta* Marshall, 1988. A new tribe, Fautricini, is introduced for species with a radula that is evidently the most primitive (plesiomorphic) in the family, and Fautricini either represents the common basal stock or an early offshoot from it. Calliostomatidae is treated as a family within Trochoidea rather than a subfamily of Trochidae as has been traditional. Three calliostomatid genus group taxa are newly synonymised: *Tristichotrochus* Ikebe, 1942 (= *Benthastelena* Iredale, 1936), *Salsipotens* Iredale, 1924 (= *Astele* Swainson, 1840), *Spicator* Cotton & Godfrey, 1935 (= *Laetifautor* Iredale, 1929). Criteria used for taxonomic discrimination, evolutionary history, and some biogeographical observations are discussed. All calliostomatid genus group taxa and taxa removed (some newly) from the family are listed in appendices. A lectotype is designated for *Zizyphinus scobinatus* A. Adams, 1863.

## RÉSUMÉ

Les Calliostomatidae (Gastropoda: Trochoidea) de Nouvelle-Calédonie, des îles Loyauté et du Nord de la Ride de Lord Howe.

Trente espèces (dont 27 espèces nouvelles) de Calliostomatidae sont recensées dans la région considérée, et toutes sauf deux représentent des signalisations géographiques nouvelles. Une autre espèce nouvelle est décrite à partir de matériel du Nord de la Nouvelle-Zélande. Les espèces sont classées dans les genres *Fautor* Iredale, 1924, *Benthastelena* Iredale, 1936, *Ampullotrochus* Monterosato, 1890 (traités comme sous-genres de *Calliostoma* Swainson, 1840), *Bathyfautor* gen. nov.,

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*Dactylastele* gen. nov., *Laetifautor* Iredale, 1929, *Selastele* gen. nov., *Fautrix* gen. nov., et *Thysanodonta* Marshall, 1988. La nouvelle tribu Fautricini, créée pour les taxons dont la radula est apparemment la plus primitive (plésiomorphe), représente le stock ancestral de la famille ou une branche ancienne de celui-ci. Calliostomatidae est traité comme une famille de Trochoidea, et non simplement comme une sous-famille de Trochidae comme il est habituel de le faire. Trois noms du groupe-genre sont mis en synonymie: *Tristichotrochus* Ikebe, 1942 (= *Benthastelena* Iredale, 1936), *Salsipotens* Iredale, 1924 (= *Astele* Swainson, 1840) et *Spicator* Cotton & Godfrey, 1935 (= *Laetifautor* Iredale, 1929). Les caractères utilisés pour la systématique et l'histoire évolutive de la famille sont discutés, de même que diverses observations de biogéographie. Une liste complète des taxons du groupe-genre appartenant à la famille Calliostomatidae, ainsi qu'une liste de ceux qui en ont été exclus (certains pour la première fois dans ce travail), figurent en appendice. Un lectotype de *Zizyphinus scobinatus* A. Adams, 1863 est choisi.

## INTRODUCTION

During the last few decades French oceanographic expeditions have sampled benthic biota at over 600 dredge and trawl stations off New Caledonia, the Loyalty Islands and on the Lord Howe Seamount Chain (RICHER DE FORGES, 1990). The resulting material (MNHN) is by far the richest and most comprehensive collection of benthic tropical biota ever assembled from the Indo-Pacific, particularly from depths greater than 100 metres on rugged substrata. The molluscan material includes many hundreds of undescribed species and great numbers of new distributional records. These collections dramatically reveal how little is actually known of the biotas occurring on seamounts and off tropical islands in general, especially in the western Pacific, and they probably afford a mere hint of the species richness in this huge region. Through the generosity of Dr Philippe Bouchet (MNHN), I am privileged to be able to describe the rich calliostomatid material from these collections.

Calliostomatids are trochiform gastropods that range from about 8-100 mm in shell height. They are exclusively marine and occur in all oceans from the intertidal zone to about 3,000 metres depth, typically on rocky substrata. Related to trochids they are characterised by a distinctive protoconch sculpture and radular morphology. The group is richly speciated with more than 250 valid Recent species, including those named herein. About 300 fossil taxa have been named. While many of the fossils are doubtfully or categorically not calliostomatids or are synonyms, I have personally examined about 70 undescribed Tertiary species (mainly from Australia and New Zealand) as well as a similar number of undescribed Recent species. Whereas some species are commonly found associated with algae, gut contents and field observations reveal that all are carnivores when adult, feeding mostly upon Cnidaria and, to a lesser extent, sponges or carion.

## ABBREVIATIONS AND TEXT CONVENTIONS

### *Repositories*

AMS	: Australian Museum, Sydney
BMNH	: The Natural History Museum, London
LACM	: County Museum of Natural History, Los Angeles
MNHN	: Muséum national d'Histoire naturelle, Paris
NMNZ	: Museum of New Zealand, Wellington
NMP	: Natal Museum, Pietermaritzburg
NSMT	: National Science Museum, Tokyo
NZGS	: Institute of Geological and Nuclear Sciences, Lower Hutt
NZOI	: National Institute of Water and Atmospheric Sciences, Wellington
USNM	: National Museum of Natural History, Washington DC

*Other abbreviations*

- D : Diameter  
 H : Height  
 P : Primary spiral (Fig. 1)  
 S : Secondary spiral (Fig. 1)  
 TW : Teleoconch whorls (number)  
 dd : no live-taken specimens present in sample  
 lv : live-taken specimens present in sample  
 spm : specimen, condition unknown  
 OD : Original designation  
 SD : Subsequent designation.

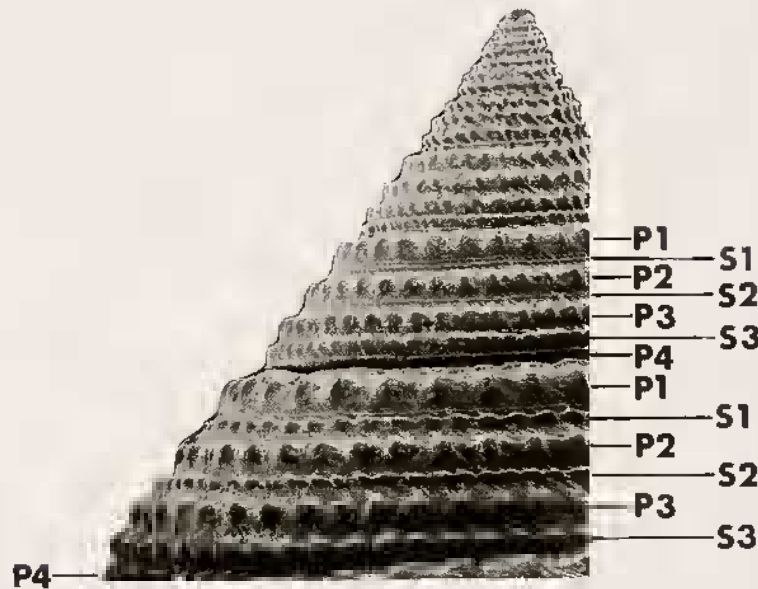


FIG. 1. — Key to standard calliostomatid spiral cord numbers on two whorls of *Calliostoma (Maurea) osbornei* Powell, 1926 (off Cape Maria van Diemen, New Zealand, 38-43 m. NMNZ M74665,  $\times 7$ ). P = primary spiral cord, S = secondary spiral cord.

Height precedes diameter in all given dimensions. All shell measurements were taken on the longitudinal axis or at right angles to it. Unless specified, all material is in Muséum National d'Histoire Naturelle, Paris.

## SYSTEMATIC ACCOUNT

Subclass PROSOBRANCHIA Milne Edwards, 1848

Order VETIGASTROPODA Salvini-Plawen, 1980

Superfamily TROCHOIDEA Rafinesque, 1815

Family CALLIOSTOMATIDAE THIELE, 1924

DIAGNOSIS. — *Shell* trochiform or turbiniform, 8-100 mm high, umbilicate or anomphalous, internally nacreous. Protoconch sculptured with network of threads that enclose roughly hexagonal spaces. First teleoconch whorl convex, subsequent whorls flat to convex or angulate; sculpture rarely absent, usually consisting of nodular spiral cords that multiply by intercalation (rarely by fission) and

axial riblets, the axials generally restricted to earliest whorls, though in some species persistent throughout. Operculum chitinous, thin, multispiral. *Radula* (adult) with the formula  $\infty + 1-17 + 1 + 17-1 + \infty$ , tooth morphology very diverse (see subfamily diagnoses); lateral teeth added incrementally by intercalation in the central field in Calliostomatinae, and by morphological transformation of marginal teeth in Fautricini. Jaw plates large, buccal musculature very strong. Cephalic tentacles elongate, tapered, papillate, well developed eyes on swellings at their outer bases in all species examined. Snout tip papillate, ventral lip split and rolled to form an incomplete tube (pseudoproboscis), dorsal lip with a cuticularised lining that extends into buccal cavity. Epipodium well developed with prominent neck lobes. Cephalic lappets large, small or absent. Up to five prominent epipodial tentacles on each side, side of foot papillate. Sexes separate. (See FRETTER & GRAHAM, 1962, 1977 for more detailed anatomical data).

REMARKS. — Interpretation of the relationships between calliostomatid species and thus resolution of actual or potential phylogenetic radiations within the family has proved to be extremely and unusually difficult. This is due primarily to the fact that radular morphology and external anatomy are in general highly conservative within the major groups. Many groups of species that seem to represent independent phylogenetic radiations on the basis of distinctive combinations of shell characters, cannot be neatly defined as genera or subgenera because, considered together with other species, there is a bewildering mosaic of intermediate character states. Shell shape and sculpture, though diverse, are generally variations on a very limited theme, and it is clear that many of the most pronounced differences are merely the result of accelerated or retarded development, often in apparently closely related species. In most calliostomatids (i.e. most Calliostomatinae), the first few teleoconch whorls are convex and sculptured with four strong primary spiral cords (P1-P4, see Fig. 1), P4 being peripheral and more or less covered by succeeding whorls. On the first whorl P1-P4 or P2-P4 typically commence simultaneously, and P1 is usually either weaker than P2 and P3 when commencing simultaneously, or it appears later. With subsequent growth the whorls typically become flatter-sided, P1-P3 remain similar, or P1 becomes larger than P2 and P3, and spiral cords are multiplied by intercalation of secondaries and sometimes tertiaries. In some species P2 and P3 become relatively stronger after the first whorl and may remain relatively strong throughout, any secondary spirals that intercalate between them typically remaining substantially weaker than the primaries (compare Figs 49 and 55). While there are exceptions, particularly large spiral cords tend to occur in species with convex whorls and in which P1 either is relatively weak throughout, appears very late, or entirely fails to develop. Adults of these species resemble their own juvenile stages to some extent, and it seems that they are paedomorphic, with retarded somatic development. Polarity for these character states, however, cannot be resolved without knowledge of the fossil record. Calliostomatids that are considered to have "juvenilized" adult shell morphology include species of *Laetifautor*, *Coralastele*, *Otukaia*, *Omphalotukaia*, and some species of *Benthastelena*. Since phylogenetic groups (e.g. genera) within the family naturally comprise species in which character states are accelerated or retarded to varying degrees, conspicuous differences in shell morphology such as whorl convexity alone may not necessarily be suitable for discrimination at generic or subgeneric level.

Major interspecific differences in radular morphology include the shape of the central tooth, the number and shape of the lateral teeth, and features of the marginal teeth, especially the innermost pair. As recently demonstrated by WARÉN (1990), calliostomatid radulae undergo pronounced changes with increasing shell size/age, which include a progressive change in shape and increase in number of lateral teeth (by intercalation) and a change in shape of the innermost pair of marginal teeth. As with the shell, differences in the radula, particularly the number of lateral teeth, cannot be utilised for genus group discrimination in isolation, since development of this organ structure is obviously accelerated or retarded to varying degrees in related species.

When viewed on a worldwide basis, a number of more or less nebulous natural (phylogenetic) groups are recognisable, though most of them have proved to be unusually difficult to quantify or

to define objectively with traditional methods, particularly with due consideration to heterochrony. Molecular cladistic techniques would seem to be a promising source of data for resolution of the phylogenetic structure of this family, and indeed for the whole of the Trochoidea.

Included genera and subgenera are listed in Appendix 1. For genus group taxa removed from the family see Appendix 2.

*PROTOCONCH.* — The calliostomatid protoconch is highly distinctive in having a sculptural network of crisp threads that enclose more or less hexagonal spaces, and in having a thickened apertural rim. Thread thickness, enclosed space size, overall protoconch size, and degree of exertion (tilting) are interspecifically variable and intraspecifically highly stable. The shape of the tip of the apical fold may be rounded or tightly pinched, an obese protoconch evidently reflecting a large yolk supply. BANDEL (1982) has shown that the surface sculpture is secreted after deformation (folding) of the protoconch, presumably via solute transmission through the semipermeable outer shell layer at an early stage of mineralisation. The fully mineralised shell is almost perfectly bilaterally symmetrical, and so far no species have been noted in which the tip of the apical fold bulges abapically as in some trochids (HADFIELD & STRATHMANN, 1990). Incidentally, these latter authors misinterpreted trochids with abapically bulging protoconch tips as having "heterostrophic" shells. This is incorrect, because the archaeogastropod protoconch is asymmetrically (in this case) or symmetrically folded about an axis, and there is no accretionary shell growth.

*TELEOCONCH I.* — All known calliostomatines exhibit a pronounced growth scar on the first quarter teleoconch whorl, the position of which is interspecifically variable though intraspecifically rather stable (Figs 2-3). Sculpture before the scar comprises 4-6 fine, crisp, similar spiral threads, and usually 1, 2 or more varices. Sculpture immediately after the scar is usually discordant (Fig. 2), though a few species exhibit a rather fluid transition to succeeding teleoconch sculpture, usually accompanied by a sudden increase in the strength of the spiral sculpture (Fig. 3). From descriptions of calliostomatids reared in aquaria (LEBOUR, 1936; HOLYOAK, 1988; RAMON, 1990; K. BANDEL pers. comm.), teleoconch accretion commences immediately or soon after formation of the terminal varix of the protoconch (here interpreted as the point of settlement). During the period of initial teleoconch formation the young evidently subsists on residual yolk, the resorbed velum, and perhaps dissolved organic matter, probably increasingly supplemented by detritus ingested from the substratum. It seems clear that the postlarval scar represents a growth pause or a crisis period and I suggest that it may denote the transition to exclusive detritivory (later transitional to carnivory). It may actually mark the transition to carnivory, at least in some species, though the radula may be insufficient to deal with Cnidaria or sponges at such an early stage of development. This interpretation is at variance with that of HICKMAN (1992: fig. 5G) who identified the terminal protoconch varix and the varix following it as denoting the times of hatching and settlement respectively. Note that the postlarval scar in the species illustrated by HICKMAN is situated immediately on the adapertural side of the varix following that denoted as time of "settlement".

*TELEOCONCH II.* — With the exception of a few more or less smooth species, the majority of calliostomatids are sculptured with prominent (usually nodular) spiral cords and axial costae, the latter generally confined to the early spire whorls. There are usually four primary spiral cords (P1-P4, Fig. 1) on the early spire whorls, to which others are added by intercalation (rarely fission) of secondary spirals (S1-S3) and sometimes one or more tertiary spirals that may enlarge to resemble the primaries or secondaries. The number, spacing, relative size, rate of enlargement, position, point of origin, and cross-sectional shape of spiral cords are primary criteria for discrimination of species group taxa. Sculpture tends to be intraspecifically highly stable on the early spire whorls, and increasingly variable on later whorls, due primarily to intercalation of varying numbers of tertiary spirals at varying positions with varying rates of enlargement. Accordingly, for descriptions and discrimination of taxa, careful attention must be paid to the origin and development of individual

elements of the spiral sculpture by tracing them from the beginning of the teleoconch — mere counting of the number of spiral cords on particular whorls is virtually useless. Unequivocal objectivity can only be achieved through rigorous application of the excellent spiral designation system initiated by IKEBE (1942), which is reproduced here for convenience (Fig. 1).

Sculptural features combine to produce an infinite variety of distinctive, intraspecifically stable gross shell facies, particularly on the early teleoconch. Natural (phylogenetic) groups segregated on the basis of highly distinctive radular morphology (e.g. *Astele*, *Laetifautor*, *Fautrix* gen. nov. and *Thysanodonta*) tend also to have distinctive early teleoconch facies. Nevertheless, even highly distinctive shell facies are typically impossible to quantify and very difficult to describe objectively (especially with verbal economy), so illustrations (SEM) are an integral component of my genus group diagnoses.

*RADULA*. — As recently shown by WARÉN (1990), the calliostomatine radula is distinctive among trochoideans in that the innermost pair of marginals become greatly enlarged at an extremely early stage of ontogenesis, after which the central and lateral teeth arise by intercalation in the central field. In other trochoideans (and apparently in the new calliostomatid tribe Fautricini — see below) the lateral teeth arise through progressive in-column morphological transformation of marginal teeth, and any additional laterals are added pair by pair through transformation of successive columns of marginals. For comparative purposes, therefore, it is clearly essential to compare radulae from individuals at equivalent stages of development, ideally maturity since related species will naturally differ in rates of somatic development.

Calliostomatine radular morphology is on the whole exceedingly conservative, and species with highly divergent shell morphologies commonly have fundamentally similar radulae. Nevertheless there is interspecific variation and intraspecific stability in the relative size, shape, and number of teeth and cusps in adult radulae. The overall shape of the central and lateral teeth and the sizes of their basal plates cannot be determined from standard SEM views of artificially protracted radulae because these teeth are longer than broad, crowded, strongly curved and typically flexible. Tooth outline can be accurately determined only by flattening excised individual teeth, while the relative sizes of the basal plates are best determined by light microscopy of stained preparations using substage lighting. While experimental use of these techniques on various species revealed many taxonomically significant features, they are omitted from the present study not only because of time constraints, but also because shell and gross radular characters are considered to be adequate for discrimination of species and most supraspecific groups. Most natural (phylogenetic) groups that can be discriminated on shell morphology tend also to have characteristic numbers of lateral teeth, for example species of *Laetifautor* have only one pair of laterals, while the type species of *Venustatrochus* has as many as 17 pairs per transverse row. The majority of calliostomatines have 5-9 pairs of laterals at maturity and interspecific variation by 1 or 2 pairs is common within groups of closely related species. The low number of lateral teeth in *Laetifautor* species and the exceptionally small size of the lateral and central teeth with respect to the innermost marginals strongly suggests that development of the radula is retarded (Figs 136-137). Unlike juvenile calliostomatids (WARÉN, 1990: fig. 6B), teeth in the central field in *Laetifautor* are slender with serrated edges, which suggests that the condition is the result of a paedomorphic process rather than a primary one. By contrast, the adult radula in species of *Selastele* gen. nov. (Figs 138-139) have exceptionally high numbers of lateral teeth relative to body size, yet few marginal teeth (as in juveniles), while all of the teeth are weakly solidified and semigelatinous. The number of marginal teeth has evidently been reduced by a paedomorphic process that has differentially failed to retard multiplication of the lateral teeth during ontogenesis. For *Selastele* the large number of lateral teeth and dissimilarity between young and adult teleoconch suggests that small size is the result of dwarfism rather than a paedomorphic process.

*DIET AND FEEDING MODE*. — Although shallow water calliostomatines are frequently observed in association with algae, careful field observations and examination of gut contents reveals that all are

obligate carnivores (MARSHALL, 1988; FERRO & CRETILLA, 1993). The majority of species feed on Cnidaria (commonly hydroids), and a few feed exclusively on sponges. From examination of many radulae from about 100 species of calliostomatids from throughout the world belonging to a variety of genera and subgenera, the only teeth that exhibit any significant degree of wear are the enlarged innermost pair of marginals. Evidently, therefore, all of the other teeth are involved primarily in food retention and clasp for transportation into the mouth.

When an excised calliostomatine radula is stretched apart and bent as if it were being pulled around the tip of the odontophore, the innermost pair of marginal teeth stand vertically and rigid with their laterally compressed vertical cutting areas aligned on the longitudinal axis. Thus the columns of innermost marginals function like a pair of chainsaws as the radula is worked back and forth around the odontophore tip by the massively developed buccal muscles. The tips of the (flexible) immediately adjacent laterals are commonly observed to be cleanly broken or entirely missing at the anterior end of the radula, and this damage is clearly incurred through accidental emplacement between the slashing innermost marginals and the prey/substratum. Several species are known in which the "cutting" areas are naturally absent from the outermost 1-3 pairs of laterals throughout the entire adult radula. It is possible that these "cutting" areas are progressively reduced during ontogenesis or they may simply never develop (juvenile radulae not seen).

In the new tribe Fautricini (see below), all of the innermost 9 pairs of marginal teeth are greatly enlarged and strengthened during ontogenesis, and clearly all of them are directly involved in food preparation (Figs 144-145). MARSHALL (1988) hypothesised that the bizarre radula in Thysanodontinae (Figs 148-149) may be somehow involved in suctorial feeding.

#### Subfamily CALLIOSTOMATINAE Thiele, 1924

DIAGNOSIS. — *Shell* as for Calliostomatidae. *Radula* with the formula  $\infty + 1-17 + 1 + 17-1 + \infty$ . Central and lateral teeth typically thin or very thin in section, with angulate, finely serrate tips. Innermost pair of marginal teeth typically shorter and stouter than other marginals, and modified to some degree. Outer marginals slender with narrow, finely serrate tips; outermost few marginals usually with blunt, cusplless tips and often fused.

Included genera and subgenera: see appendix 1.

#### Genus *CALLIOSTOMA* Swainson, 1840

*Calliostoma* Swainson, 1840: 218, 351. Type species (SD by HERRMANNSEN, 1846: 154): *Trochus conulus* Linnaeus, 1758; Recent, north eastern Atlantic and Mediterranean.

#### Synonyms:

*Ziziphinus* Gray, 1840: 151 = *Nomen nudum*.

*Conulus* Nardo, 1841: 244. Type species (OD): *Trochus conulus* Linnaeus, 1758 (not *Conulus* Leske, 1778, not Fitzinger, 1833).

*Ziziphinus* Gray, 1842: 57. Type species (SD by GRAY 1847: 145 and by tautonomy): "*Trochus ziziphinus*" = *Trochus ziziphinus* Linnaeus, 1758; Recent, north eastern Atlantic and Mediterranean.

*Zizyphinus* Gray, 1847: 237. Incorrect subsequent spelling of *Ziziphinus* Gray, 1842.

*Callistoma*/*Callistomus* Herrmannsen, 1846: 154, 1852: 22. Unnecessary emendations of *Calliostoma* Swainson.

*Jacinthinus* Monterosato, 1889: 79. Type species (SD by CLENCH & TURNER, 1960: 11): *Trochus conulus* Linnaeus, 1758.

REMARKS. — SWAINSON (1840: 218) first introduced *Calliostoma* as a subgenus of *Trochus* Linnaeus, 1758 with the entry "... forming our subgenus *Calliostoma* ... *Trochus zizyphinus* of British writers will give a very good idea of these shells ...". This does not constitute original designation of a type species (ICZN Art. 67c). Contrary to the opinion of some authors (e.g. CLENCH & TURNER, 1960; ABBOTT, 1974), *T. zizyphinus* is not type species by monotypy either (Art. 68d), since SWAINSON (1840: 351) included eight taxa in the formal diagnosis of *Calliostoma*, including *T. zizyphinus* and *T. conulus* (as *zizyphina* and *conula*). Since no type species was designated, the type species is *T. conulus* through subsequent designation by HERRMANNSEN (1846: 154) (Art. 69a).

At its earliest introduction by GRAY (1840: 151), *Ziziphimus* appears in a list without associated species, description or comment and is thus a *nomen nudum* (IREDALE, 1913). At the second introduction the name is again without associated species, GRAY (1842: 57) stating (under *Thalotia*) "in *Ziziphimus*, *Cantharidus*, and *Thalotia* the mouth is oblong and simple and the axis is covered by the inner lip; the former is top-shaped, the *Cantharidi* arc ovate and green within". The first use of *Zizyphims* (note spelling) in connection with nominate species was by GRAY (1843: 237) who included four New Zealand species and two mislocalised North American species. GRAY (1847: 145) subsequently designated the European species *T. ziziplinus* (i.e. *Trochus zizyphinus* Linnaeus, 1758) as type species of *Ziziplinus* Gray, 1840, while REHDER (1937: 115) selected the North American species *Trochus canaliculatus* "Martyn" Lightfoot as type species of *Zizyphimus* Gray, 1843. On the face of it, therefore, *Ziziphimus* and *Zizyphimus* would seem to be distinct genus group taxa with separate type species, and they were so interpreted by KEEN (1960). It seems preferable, however, to treat *Ziziplinus* in the spirit with which it was intended (tautonomy), and interpret *T. zizyphimus* as type species of *Ziziphimus* Gray, 1842 by subsequent designation of GRAY 1847. Gray's *Zizyphimus* is eliminated as an uncorrected subsequent spelling since it is neither a mandatory change nor a demonstrably intentional emendation (ICZN Art.33). Consequently REHDER's (1937: 115) selection of *T. canaliculatus* as type species of *Zizyphimus* was unnecessary.

#### Subgenus *CALLIOSTOMA* (*s. str.*) Swainson, 1840

DIAGNOSIS. — *Shell* up to about 35 mm high, stout, narrowly to broadly conical, periphery rounded or angulate, anomphalous. P1-P4 commencing immediately or P1 later, strong to very strong, persisting or becoming obsolete; axial sculpture very weak or absent. nodules absent or large and bluntly rounded. *Animal* with large left and right neck lobes, and 3 or 4 small epipodial tentacles on each side. Cephalic tentacles tapered, extending little beyond tip of snout. Central and lateral teeth broad-based, thin in section and flexible, laterals with very slender tips. Jaw plates with short elements at anterior margins.

REMARKS. — The concept of *Calliostoma* (*s. str.*) is here restricted to the following taxa: *C. combus* (Linnaeus, 1758), *C. zizyphinum* (Linnaeus, 1758), *C. langieri* (Payraudeau, 1826), *C. occidentale* (Mighels, 1842), *C. gualtierianum* (Philippi, 1848), *C. hirondellei* Dautzenberg & Fischer, 1896, *C. grimaldii* Dautzenberg & Fischer, 1896, *C. cleopatra* (Fischer, 1898), *C. laqueatum* (Locard, 1897) and *C. oppansum* (Locard, 1897). All of these occur in the north eastern Atlantic and/or Mediterranean, with the exception of *C. occidentale*, which occurs in the north eastern and north western Atlantic. The limits of morphological expression within the subgenus are uncertain, and I have only included species that seem most likely to represent a tight phylogenetic radiation. Inclusion of *C. occidentale*, perhaps the most divergent in shell morphology, provides both morphological and geographical links between eastern and western Atlantic species groups.

Three groups of western Pacific species with rather distinctive shell facies are here referred to subgenera *Ampullotrochus*, *Fautor*, and *Benthastelena*. Despite the extreme conservatism of *Calliostoma* (*s. lat.*) world wide, these groups all seem to represent separate phylogenetic radiations. Indeed one or more of them may eventually prove to be worth recognising as genera, but until the family is better known I prefer a conservative approach. As stated above these groups are difficult to objectively define in that the combinations of character states are difficult to quantify or verbalise.

Judging from illustrations, the following Recent European species may not belong in *Calliostoma* (*s. str.*) and their precise relationships within Calliostomatidae are uncertain: *Calliostoma caroli* Dautzenberg, 1927, *C. leptophyma* Dautzenberg & Fischer, 1896, *Z. milneedwardsi* Locard, 1897, *C. normani* Dautzenberg & Fischer, 1897, *Z. triporcatus* Fischer in Filhol, 1886.



Subgenus *FAUTOR* Iredale, 1924

*Fautor* Iredale, 1924: 230. Type species (OD): *Zizyphinus comptus* A. Adams, 1855; Recent, southern Australia.

REMARKS. — *Fautor* is here utilised as a subgenus of *Calliostoma* for a group of predominantly Indo-western Pacific taxa that differ from species of *Calliostoma* (*s. str.*) (Fig. 20) in having narrower, more finely beaded spiral cords. I am unable to detect any constant differences between the two groups in the radula, jaws or external anatomy. Although relative size of the spiral cords and nodules admittedly seems rather trivial, viewed as a whole the two groups exhibit a distinctive mosaic combination of character states that is difficult to objectively quantify or describe. Moreover, I am strongly disinclined to treat them as synonyms because *Fautor*, as here limited, is almost certainly polyphyletic.

In addition to the species described herein, the following species are considered to belong in *Fautor*: *Calliostoma admirandum* Smith, 1906 (off Tranvancore), *Zizyphinus allporti* Tenison Woods, 1875 (southern Australia), *Calliostoma funiculare* Melvill, 1906 (Persian Gulf), *Zizyphinus scobinatus* A. Adams, 1863 (Bombay), *Calliostoma takujii* Kosuge, 1986 (Bonin Islands), and perhaps the eastern Atlantic species *C. lithocolletum* Dautzenberg, 1925.

The type species of *Fautor* (*Z. comptus*, Figs 4-6, lectotype Fig. 4) was based on specimens reputedly from New Caledonia, although nothing strictly similar to it has ever been obtained in the New Caledonia region. As correctly concluded by BRAZIER (1895), the type material is in fact indistinguishable from the New South Wales form of a common indigenous southern Australian species. *C. (F.) comptus* has at times been confused with *Trochus poupineli* Montrouzier, 1875 (e.g. FISCHER, 1879; IKEBE, 1942; KOSUGE, 1984) although in fact MONTROUZIER'S species differs widely and is herein referred to *Dactylastele* gen. nov.

*Calliostoma (Fautor) boucheti* sp. nov.

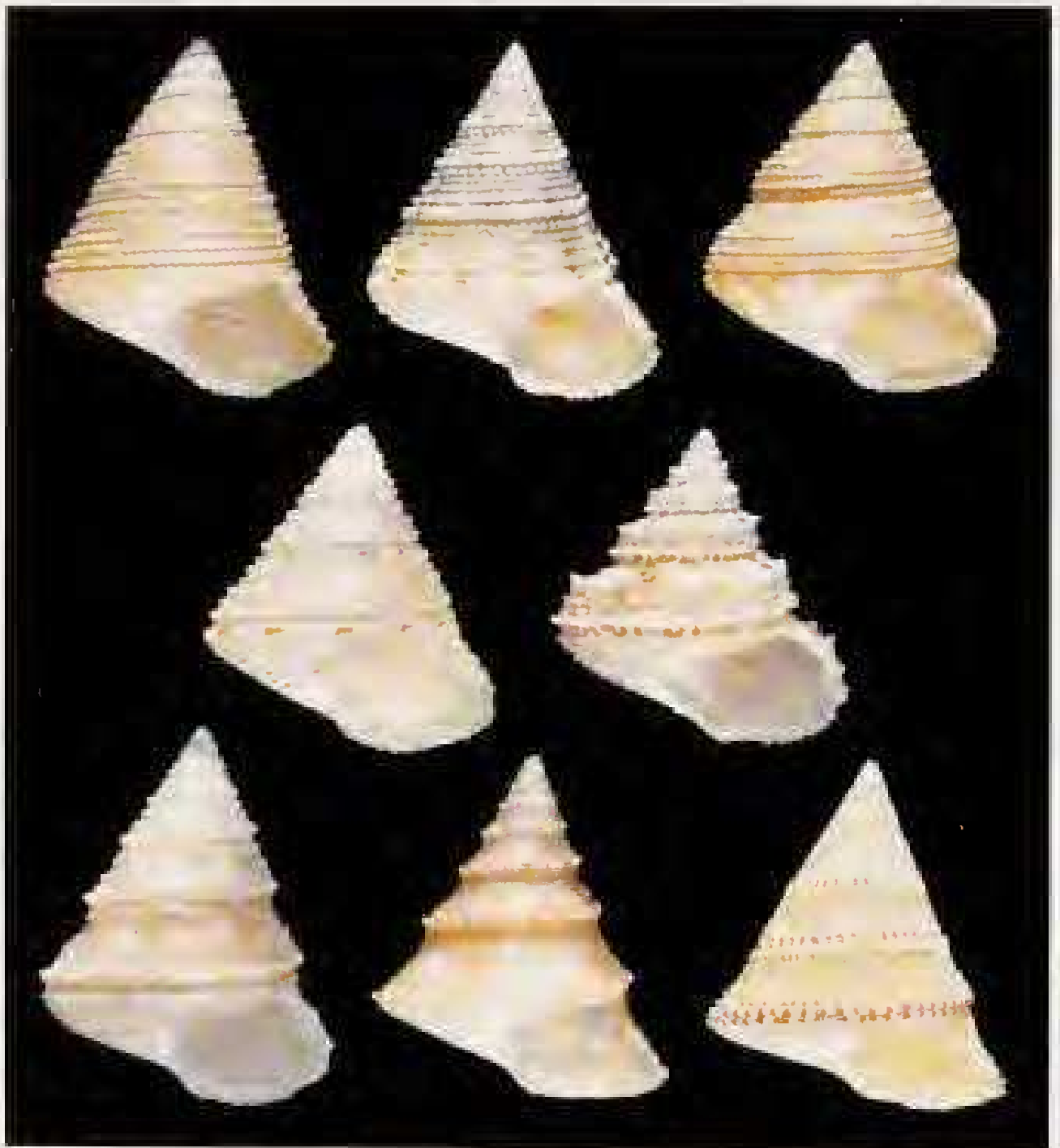
Colour Plate; Figs 3, 7-9, 117, 150, 155; Table 1

TYPE MATERIAL. — Holotype (13.0 × 10.6 mm, 7.30 TW) MNHN. Paratypes: 90 MNHN, 1 AMS C201701, 1 BMNH 1995.013, 1 NMP, 1 USNM, 2 NMNZ M262476.

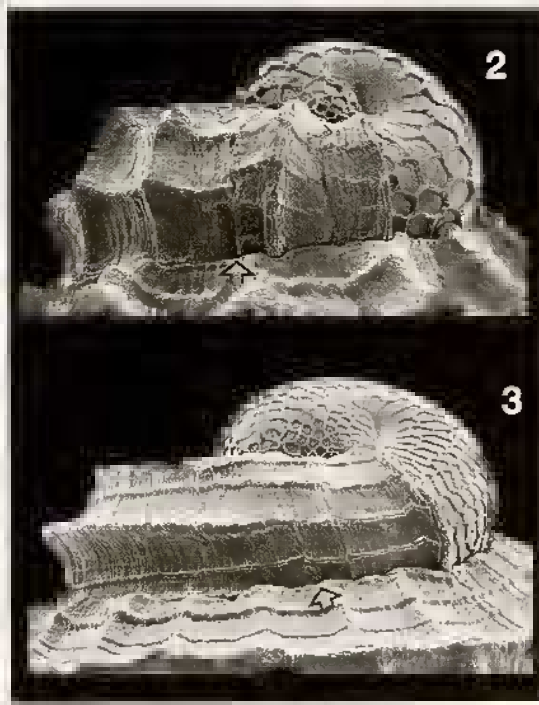
TYPE LOCALITY. — Off S. New Caledonia, CHALCAL 2, stn DW 75, 24°39' S, 168°40' E, 600 m.

MATERIAL EXAMINED. — All type material. **New Caledonia**. BIOCAL: stn DW 66, 24°55' S, 168°22' E, 505-515 m, 5 dd (paratypes). CHALCAL 2: stn DW 72, 24°55' S, 168°22' E, 527 m, 33 lv (31 MNHN, 2 NMNZ). — Stn DW 73, 24°40' S, 168°38' E, 573 m, 8 lv (1 AMS, 1 BMNH, 4 MNHN, 1 NMP, 1 USNM). — Stn DW 74, 24°40' S, 168°38' E, 650 m, 13 lv (paratypes). — Stn DW 75, 24°39' S, 168°40' E, 600 m, 4 lv (holotype and 3 paratypes). SMIB 3: stn DW 1, 24°56' S, 168°22' E, 520 m, 2 lv (paratypes). — Stn DW 2, 24°53' S, 168°22' E, 530-537 m, 8 lv (paratypes). — Stn DW 3, 24°55' S, 168°22' E, 513 m, 7 lv (paratypes). — Stn DW 5, 24°55' S, 168°22' E, 502-512 m, 4 lv (paratypes). — Stn DW 6, 24°56' S, 168°21' E, 505 m, 5 lv (paratypes). — Stn DW 7, 24°55' S, 168°21' E, 505 m, 5 lv (paratypes). — Stn DW 8, 24°45' S, 168°08' E, 233 m, 1 dd (paratype). — Stn DW 22, 23°03' S, 167°19' E, 503 m, 2 lv (paratypes).

DISTRIBUTION (Fig. 155). — South of Ile des Pins, southern New Caledonia and northern Norfolk Ridge, 233-650 m, living at 502-650 m.



COLOUR PLATE. — Holotypes of *Calliostoma* species. Top row (left to right): *Calliostoma (Fautor) boucheti*, 13.0 × 10.6 mm; *C. (F.) houbricki*, 12.8 × 10.8 mm; *C. (F.) metivieri*, 11.5 × 9.40 mm. Centre row (left to right): *C. (F.) chesterfieldense*, 7.60 × 6.90 mm; *C. (Benthastelena) diademutum*, 11.0 × 10.5 mm. Bottom row (left to right): *C. (F.) periglyptum*, 10.2 × 8.30 mm; *C. (Ampullotrochus) heros*, 11.6 × 10.2 mm; *C. (A.) xanthos*, 8.00 × 6.90 mm.



FIGS 2-3. — Side views of tip of spire showing postlarval growth scar denoted by arrows. — 2, *Laetifactor rubropunctatus* (A. Adams), off Swain's Reef, Queensland, 100 m, AMS C153215,  $\times 147$ . — 3, *Calliostoma (Fautor) boucheti*, paratype, BIOCAL: stn DW 66,  $\times 123$ .

**DESCRIPTION.** — *Shell* up to 13 mm high, rather lightly built, glossy, spire narrowly conical, very weakly cyrt-conoid, 1.92-2.05x as high as aperture, mean spire angle 57-62°, anomphalous.

*Colour* of protoconch reddish brown. Teleoconch grading from reddish to yellowish brown over 1st 2 whorls, subsequent whorls bright orange to yellowish brown, pale green nacreous layer showing through translucent outer layer in spiral interspaces, inner and outer lip margins white.

*Protoconch* 400-430  $\mu\text{m}$  wide, sculptured with network of fine threads that enclose roughly hexagonal spaces. Apical fold tip rounded, terminal varix rounded.

*Teleoconch* of up to 7.30 whorls; 1st tenth whorl with 4 crisp spiral threads, delineated by growth scar. First 2 whorls strongly convex, angulated at P3, 3rd whorl becoming flat, subsequent whorls flat; periphery angulate, becoming tightly rounded late on last adult whorl, S3 and P3 peripheral; base weakly convex. Spire and basal spirals prominent, rounded, multiplying by intercalation, their rounded conical nodules stronger on spire; axial riblets strong on 1st 3 whorls, becoming obsolete on 4th whorl. P2-P4 commencing immediately after post-larval growth scar: P2 and P3 strong, similar, flange-like and weakly undulant on 1st whorl, becoming nodular on 2nd whorl (P2) and 3rd whorl (P3). P1 a fine thread on 1st whorl, enlarging over 2nd whorl to become as large as P2 and P3 on 3rd whorl, thereafter slightly larger than others. P4 partly covered by succeeding whorls.

Secondary spirals enlarging to resemble primaries; S1 commencing late 3rd - mid 4th whorl, S2 commencing end 2nd - late 3rd whorl, S3 commencing mid - end 4th whorl.

Tertiary spirals numbering 1 or more, usually commencing on last adult whorl, remain weaker than primaries and secondaries. Base with 12-17 spiral cords, stronger and more strongly nodular on inner half, nodular on outer half on last adult whorl only. Microsculpture of fine crisp spiral threads on 1st 2 whorls; fine collabral growth lines throughout, crisply defined between P3 and P4 before appearance of S3. Aperture subquadrate. Outer lip thin at rim, slightly thickened within. Inner lip of moderate thickness. No parietal inductura.

*Animal* creamy white, snout tip laterally expanded, set with slender papillae. Cephalic tentacles long, tapered, finely papillate, prominent eyes at outer bases. Neck lobes thin, left considerably larger and more convoluted, 3 right and 4 left epipodial tentacles. Operculum typical.

*Radula* (Fig. 117). Central and lateral teeth thin in section with broad, laterally expanded bases. Tip of central tooth narrowly tapered, finely serrate. Lateral teeth similar. 6 pairs in adults; tips very long, slender, finely serrate. Innermost marginal teeth stout, broad-based, with 3 or 4 strong cusps. Outer marginals numerous, tips finely serrate, outermost 5 marginals on each side fused, tips spatulate.

*Jaw plate* (Fig. 150) with broadly rounded anterior margins, fringing elements short.

TABLE 1. — *Calliostoma (Fautor) boucheti*. Shell measurements (mm) and countings (CHALCAL 2; stns DW 73, DW 74, DW 75).

Character	n	Range	Mean	SD
H	15	9.20-13.00	11.39	1.17
D	15	8.30-11.20	09.88	0.91
H/D	15	1.11-01.28	01.15	0.04
TW	15	6.25-07.30	06.85	0.29

REMARKS. — Compared with the superficially similar Australian species *C. (F.) comptum*, *C. (F.) boucheti* differs in numerous details of shell, colour, shape and sculpture. These differences include much finer protoconch sculpture, flange-like cords on the first teleoconch whorl, the later development of P1, and the more evenly conical spire.

ETYMOLOGY. — Named after Philippe BOUCHET (MNHN).

*Calliostoma (Fautor) richeri* sp. nov.

Figs 10-12, 118, 153; Table 2

TYPE MATERIAL. — Holotype (12.3 × 9.30 mm, 8.10 TW) MNHN. Paratypes: 34 MNHN, 1 AMS C201702, 1 BMNH 1995.014, 2 NMNZ M262470, 1 NMP, 1 USNM.

TYPE LOCALITY. — S. New Caledonia, LAGON, stn 400, 22°34' S, 167°14' E, 64 m.

MATERIAL EXAMINED. — **New Caledonia**. LAGON: stn 113, 22°23' S, 166°48' E, 32 m, 2 dd (paratypes). — Stn 146, 22°24' S, 166°55' E, 40-52 m, 3 dd (paratypes). — Stn 234, 22°33' S, 166°51' E, 56 m, 1 dd (paratype). — Stn 240, 22°23' S, 166°59' E, 42 m, 1 dd (paratype). — Stn 297, 22°39' S, 166°46' E, 30 m, 1 dd (paratype). — Stn 301, 22°35' S, 166°52' E, 46 m, 1 dd (paratype). — Stn 303, 22°38' S, 166°49' E, 35 m, 1 dd. — Stn 314, 22°39' S, 166°51' E, 46 m, 1 dd (paratype). — Stn 315, 22°37' S, 166°53' E, 50 m, 1 lv (paratype). — Stn 317, 22°33' S, 166°53' E, 66 m, 1 dd (paratype). — Stn 327, 22°26' S, 167°04' E, 60 m, 2 dd (paratypes). — Stn 328, 22°27' S, 167°03' E, 72 m, 1 dd (paratype). — Stn 332, 22°34' S, 166°57' E, 80 m, 2 dd (paratypes). — Stn 350, 22°39' S, 166°57' E, 67 m, 2 dd (paratypes). — Stn 352, 22°35' S, 166°59' E, 82 m, 1 lv (paratype). — Stn 359, 22°33' S, 167°04' E, 74 m, 3 dd (paratypes). — Stn 376, 22°34' S, 167°06' E, 75-76 m, 2 dd (paratypes). — Stn 386, 22°37' S, 167°09' E, 128 m, 1 dd (paratype). — Stn 400, 22°34' S, 167°14' E, 64 m, 11 dd (holotype and paratypes: 4 MNHN, 1 AMS, 1 BMNH, 2 NMNZ, 1 NMP, 1 USNM). — Stn 401, 22°32' S, 167°15' E, 49 m, 2 dd (paratypes). — Stn 557, 22°47' S, 166°54' E, 44 m, 1 dd. — Stn 565, 22°49' S, 166°55' E, 52 m, 1 dd (paratype). — Stn 569, 22°49' S, 166°59' E, 62 m, 1 dd (paratype). MUSORSTOM 4: stn DW 204, 22°37' S, 167°06' E, 120 m, 1 dd.

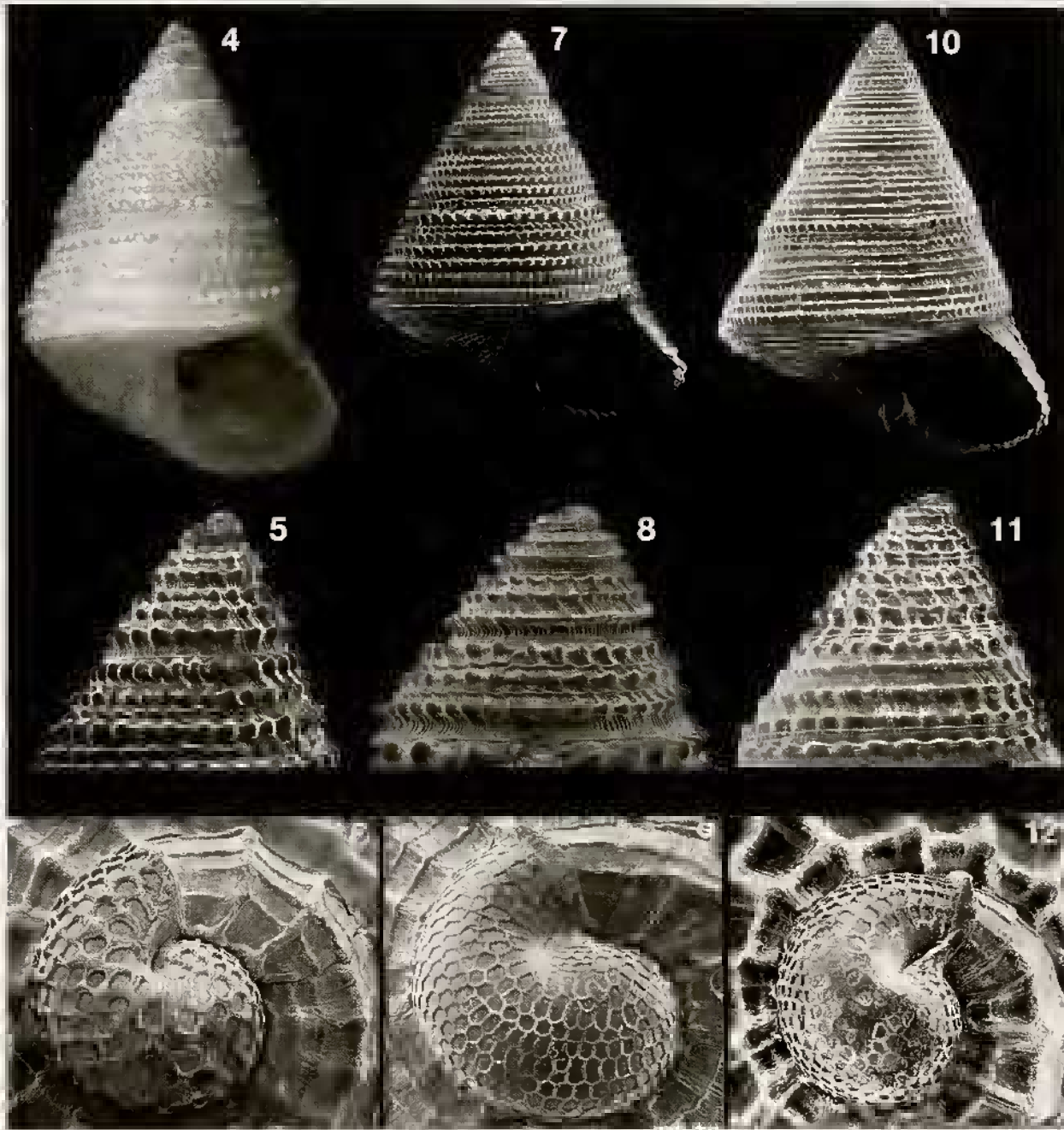
DISTRIBUTION (Fig. 154). — Lagoons of southern New Caledonia, 30-128 m, living at 50-82 m.

DESCRIPTION. — Shell up to 17.3 mm high, glossy, of moderate thickness; spire narrowly and rather evenly conical, 2.26-3.02x higher than aperture; mean spire angle 45-55°, anomphalous.

Colour of protoconch apical fold tip yellowish brown, elsewhere white. Teleoconch white or pale buff, pale green nacreous layer showing through translucent outer layer. After 3rd or 4th whorl spire with narrow, pale yellowish brown axial maculations, spiral cords on spire and base spotted with pale yellowish brown between nodules.

Protoconch 330-370 μm wide, sculptured with network of fine threads that enclose roughly hexagonal spaces. Apical fold tip tapered, terminal varix strong, rounded.

Teleoconch of up to 9.75 whorls; conspicuous growth scar immediately after protoconch. First whorl convex, next whorl becoming almost flat, subsequent whorls very weakly convex with almost flush suture; periphery angulate, becoming tightly rounded on last adult whorl, S3 and P4 peripheral; base weakly convex. Spire and base with prominent, rounded spiral cords that multiply by intercalation; axial riblets strong



FIGS 4-12. — Genus *Calliostoma*, subgenus *Fautor*. — 4. *Calliostoma (Fautor) comptum*, lectotype BMNH, 11.  $1 \times 7$ , 90 mm. — 5-6, *C. (Fautor) comptum*, off Twofold Bay, New South Wales, 15 m, NMNZ M262482, 5  $\times$  14, 6  $\times$  92. — 7, *C. (F.) boucheti*, holotype, 13.0  $\times$  10.6 mm. — 8-9, *C. (F.) boucheti*, paratype, BIOCAL: stn DW 66, 8  $\times$  21, 9  $\times$  108. — 10-11, *C. (F.) richeri*, holotype, 12.3  $\times$  9.30 mm, 11  $\times$  20. — 12, *C. (F.) richeri*, paratype, LAGON: stn 315,  $\times$  120.

on 1st 2 or 3 whorls, becoming obsolete on 3rd or 4th whorls, rounded nodules at intersections. P1-P3 commencing immediately; P1 commencing much weaker than P2 and P3, gradually enlarging to resemble them by end of 1st whorl; P4 almost entirely exposed on spire after 2nd whorl. Secondary spirals enlarging to resemble primaries, S1 commencing at start of 4th - mid 5th whorl, S2 commencing on early 3rd - early 5th whorl; S3 commencing on mid 2nd - start of 3rd whorl, becoming stronger than P4. Tertiary spire spirals

commencing after 5th or 6th whorl generally 1 in each interspace, resembling primaries and secondaries on last adult whorl. Following disappearance of axial riblets, P1, S3 and P4 with rounded nodules, other spire spirals become more weakly nodular, mostly gently undulant; S3-P4 interspace about as wide as each spiral, other interspaces considerably wider than each spiral. Basal spirals numbering 11-17, weakly nodular, interspaces wider than each spiral. Fine collabral growth lines throughout, most prominent on base. Aperture

subquadrate. Outer lip thin at rim, thickened within, large adults with 4 or 5 low, rounded spiral ridges within. Inner lip thick. Parietal inductura deposited only in large adults, of moderate thickness.

*Radula* (Fig. 118—poor preparation from decayed animal) with 3 pairs of lateral teeth, innermost marginals with 5 or 6 cusps, otherwise similar to those of *C. (F.) comptum* and *C. (F.) bouchei*.

TABLE 2. — *Calliostoma (Fautor) richeri*. Shell measurements (mm) and countings (LAGON: stns 297, 359, 376, 400, 401).

Character	<i>n</i>	Range	Mean	SD
H	13	09.10-17.30	11.80	2.05
D	13	07.20-11.40	09.19	1.12
H/D	13	01.14-01.52	01.28	0.08
TW	13	07.30-09.75	08.07	0.63

REMARKS. — *Calliostoma (Fautor) richeri* differs from *C. (F.) comptum* and other species of subgenus *Fautor* from the New Caledonia area in having only 3 pairs of lateral teeth. The species is particularly distinctive in the combination of colour pattern, very narrowly conical spire, flattened teleoconch whorls, and the virtual obsolescence of nodules on spire spirals other than P1, S3 and P4 after the disappearance of the axial costae. *C. (F.) richeri* is the dominant calliostomatid in the lagoons of southern New Caledonia.

ETYMOLOGY. — Named after Bertrand RICHER DE FORGES, ORSTOM, New Caledonia.

*Calliostoma (Fautor) necopinatum* sp. nov.

Figs 31-33, 121, 155; Table 3

TYPE MATERIAL. — Holotype (10.2 × 8.00 mm, 6.75 TW) MNHN. Paratypes: 12 MNHN, 1 AMS C201703, 1 BMNH 1995.015, 1 NMNZ M262468, 1 NMP, 1 USNM.

TYPE LOCALITY. — N. New Caledonia, MUSORSTOM 4, stn DW 164, 18°33' S, 163°13' E, 255 m.

MATERIAL EXAMINED. — All type material. New Caledonia, MUSORSTOM 4: stn DW 164, 18°33' S, 163°13' E, 255 m, 7 lv (holotype and 6 paratypes).

LAGON: stn 444, 18°15' S, 162°59' E, 300-350 m, 11 lv (paratypes: 1 AMS, 1 BMNH, 6 MNHN, 1 NMNZ, 1 NMP, 1 USNM).

DISTRIBUTION (Fig. 155). — Off d'Entrecasteaux Reefs, northern New Caledonia, 255-350 m, living at 300-350 m.

DESCRIPTION. — *Shell* up to 12.6 mm high, stout, glossy; spire narrowly conical, very weakly cyrtconoid, 1.92-2.06x higher than aperture; mean spire angle 57-61°, anomphalous.

*Colour* of apical fold tip yellowish brown, rest of protoconch and 1st 1 or 2 teleoconch whorls white. Subsequent spiral whorls buff white, yellowish brown axial maculations or small scattered spots on 2nd - 4th or 3rd and 4th whorls, peripheral spots only on 1 or more later whorls in heavily pigmented specimens. Base white.

*Protoconch* 400-420 μm wide, sculptured with network of fine threads that enclose roughly hexagonal spaces. Apical fold tip tightly rounded, terminal varix rounded.

*Teleoconch* of up to 7.20 whorls; 1st quarter whorl with 4 crisp spiral threads, delineated by growth scar. First 2 whorls convex, subsequent whorls very weakly convex with weakly impressed suture; periphery angulate, becoming rounded at

maturity; base weakly convex. Spire and basal spirals prominent, rounded, multiplying by intercalation, with rounded conical nodules, interspaces about as wide as each spiral; axial riblets strong on 1st 2 whorls, becoming obsolete on 3rd whorl. P1-P4 commencing immediately after post larval growth scar. P1 weak at first, gradually enlarging to resemble similar P2 and P3 by end of 2nd whorl; P4 partly covered by succeeding whorls. Secondary spirals enlarging to resemble primaries, S1 commencing early 3rd - early 4th whorl; S2 commencing late 2nd - mid 3rd whorl, S3 commencing early - late 4th whorl. Earliest tertiary spiral commencing between P1 and S1 on or near 6th whorl, enlarging to resemble interspaces on last adult whorl. Base with 12-15 spiral cords, stronger and more strongly nodular over inner half. Numerous fine spiral threads on 1st 2 whorls; raised collabral

growth lines throughout, prominent in P3-P4 interspace before appearance of S3. Aperture subquadrate. Outer lip thin at rim, thickened within, strongly so on abapical side. Inner lip thick. Parietal lip extremely thin.

*Radula* (Fig. 121 - from dried animal) with 5 pairs of lateral teeth, innermost marginal with 5 or 6 stout cusps. *Radula* and jaws otherwise as in *C. (F.) bouchei*.

TABLE 3. — *Calliostoma (Fautor) necopinatum*. Shell measurements (mm) and countings (LAGON: stn 444, MUSORSTOM 4; stn DW 164).

Character	n	Range	Mean	SD
H	10	9.80-12.60	10.76	0.91
D	10	8.00-10.00	08.55	0.65
H/D	10	1.16-01.31	01.25	0.04
TW	10	6.40-07.20	06.78	0.28

REMARKS. — *Calliostoma (Fautor) necopinatum* is superficially similar to broad forms of the southern Australian species *C. (F.) comptum* in gross facies but in fact it differs in numerous details, most notably the smaller, more finely sculptured protoconch (diameter 400-420  $\mu\text{m}$  instead of 500-530  $\mu\text{m}$ ) and finer nodules. Among previously described species, *C. (F.) necopinatum* seems to be most closely related to *C. simplex* Schepman, 1908 (Banda Sea, 304 m - holotype ZMA), differing in having a colour pattern on the early teleoconch, in the earlier appearance of S1 (early 3rd - 4th whorl instead of late 5th whorl), in having somewhat finer spiral cords and nodules on the spire, and, in having 12-14 instead of 10 more closely spaced spiral cords on the base. The largest mature specimens of *C. (F.) necopinatum* are smaller than the holotype of *C. simplex* (height 12.6 vs. 14.3), and their peripheries become rounded about one full whorl earlier.

ETYMOLOGY. — Unexpected (Latin).

*Calliostoma (Fautor) paradigmatum* sp. nov.

Figs 13-15, 119, 155; Table 4

TYPE MATERIAL. — Holotype (11.4  $\times$  10.0 mm, 6.75 TW) MNHN. Paratypes: 11 MNHN, 1 AMS C201704, 1 NMNZ M262465, 1 NMP, 1 USNM.

TYPE LOCALITY. — S. New Caledonia, MUSORSTOM 4, DW 220, 22°58' S, 167°38' E, 505-550 m.

MATERIAL EXAMINED. — **New Caledonia.** MUSORSTOM 4: stn DW 159, 18°46' S, 163°16' E, 585 m, 1 lv. — Stn DW 220, 22°58' S, 167°38' E, 505-550 m, 5 lv (holotype and paratypes: 2 MNHN, 1 AMS, 1 NMNZ).

CHALCAL 2: stn DW 76, 23°41' S, 167°45' E, 470 m, 2 dd (paratypes).

BIOCAL: stn DW 33, 23°10' S, 167°10' E, 675-680 m, 1 dd (paratype). — Stn DW 36, 23°09' S, 167°11' E, 650-680 m, 2 dd (paratypes). — Stn CP 40, 22°55' S, 167°24' E, 650 m, 1 dd (paratype).

— Stn DW 51, 23°05' S, 167°45' E, 680-700 m, 5 lv (paratypes: 3 MNHN, 1 NMP, 1 USNM).

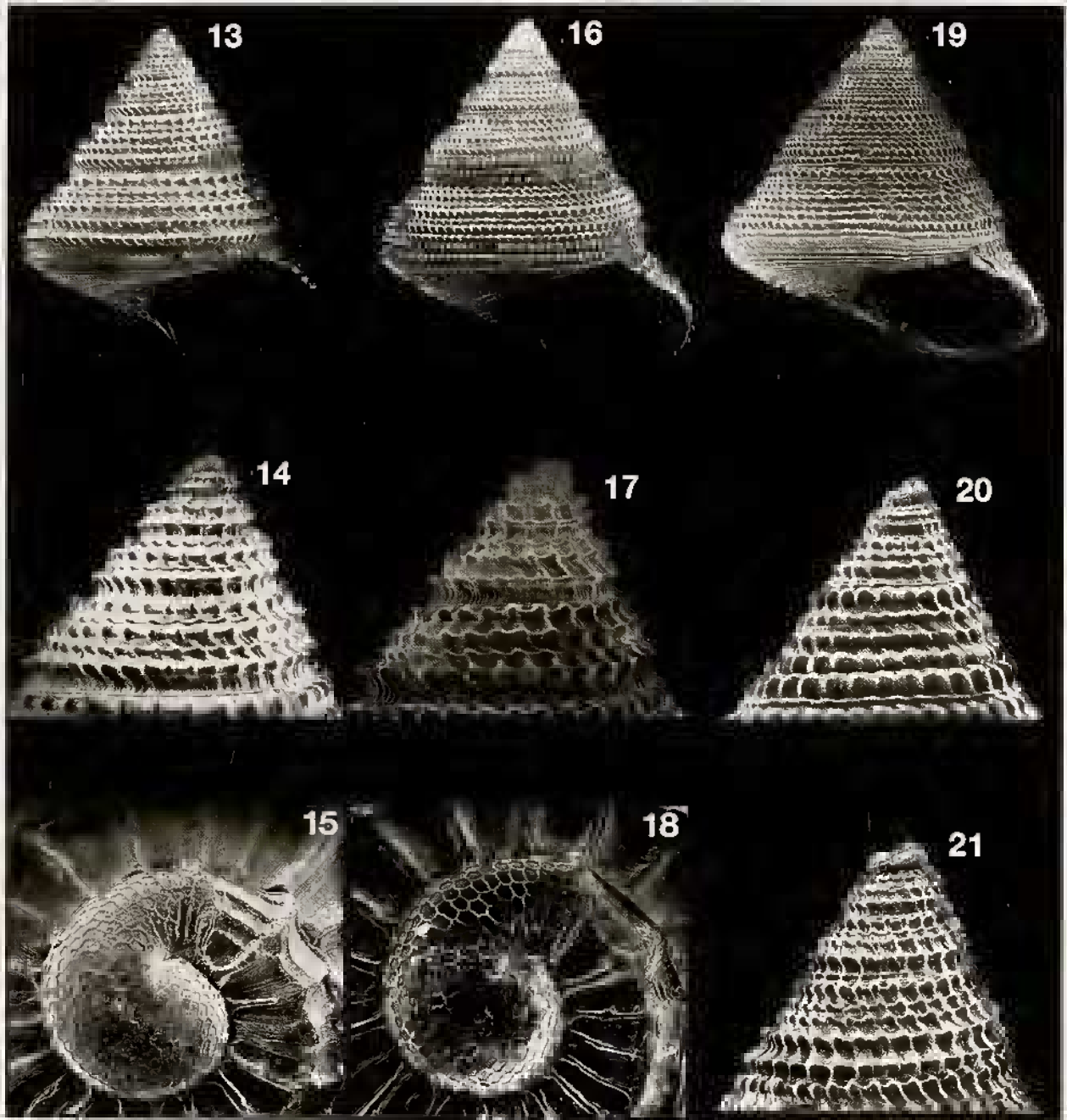
DISTRIBUTION (Fig. 155). — Off Ile Surprise, northern New Caledonia (alive at 585 m), and south of Ile des Pins, southern New Caledonia, 470-775 m, living at 505-700 m.

DESCRIPTION. — *Shell* up to 13.9 mm high, glossy, of moderate thickness; spire rather broadly and evenly conical, 1.55-1.65x higher than aperture, mean spire angle 31-35°, anomphalous.

*Colour*: Uniform white, pale pink and green nacreous

layer showing through translucent outer layer in spiral interspaces.

*Protoconch* 400-430  $\mu\text{m}$  wide, sculptured with network of fine threads that enclose roughly hexagonal spaces. Apical fold tip rounded, terminal varix strong, rounded.



Figs 13-21. — Genus *Calliostoma*, subgenera *Fautor*, *Calliostoma* and *Ampullotrochus*. — 13-14, *Calliostoma (Fautor) paradigmatum*, holotype, 11.4 × 10.0 mm, 14 × 13. — 15, *C. (F.) paradigmatum*, paratype, BIOCAL: stn DW 51, × 96. — 16-17, *C. (F.) metivieri*, holotype, 11.5 × 9.40 mm, 17 × 20. — 18, *C. (F.) metivieri*, paratype, CHALCAL 2: stn DW 76, × 116. — 19, *C. (F.)* sp. cf. *metivieri*, CHALCAL 2: stn DW 74. — 20, *C. (C.) zizyphinum*, Calvi, Corsica (Swedish Museum of Natural History, Stockholm), × 16. — 21, *C. (Ampullotrochus) granulatum*, Benicarlo, Spain. MNMZ M237686, × 18.

*Teleoconch* of up to 7.60 whorls; 1st eighth whorl with crisp spiral threads, delineated by growth scar. First 3 whorls convex, subsequent whorls weakly convex, suture well impressed; periphery angulate, becoming rounded at maturity, P3 peripheral; base weakly convex. Spire and basal spirals rounded, multiplying by intercalation; nodules roundly conical on spire, bluntly rounded on base; axial costae strong on

1st 3 whorls, weakening on 4th whorl, obsolete on subsequent whorls. P2-P4 commencing immediately, P2 and P3 strong and similar throughout, P4 partly covered by succeeding whorls, P1 commencing mid 2nd - early 3rd whorl, as large as P2 and P3 on 4th and later whorls. S1 and S2 becoming as large as primaries, S1 commencing early - late 4th whorl, S2 commencing early 3rd - early 4th whorl; S3 commencing



mid 6th - mid 7th whorl, remaining weaker than others, occasionally absent. Tertiary spirals commencing on last adult whorl, 1 per interspace. Base with 12-17 spiral cords, inner 3 nodular, others becoming nodular on last adult whorl. Fine collabral growth lines throughout. Aperture subquadrate. Outer lip thin at rim, modestly thickened within. Inner lip of moderate thickness. Parietal glaze very thin, translucent.

*Animal* (MUSORSTOM 4: stn DW 159) creamy white. Snout tip

laterally expanded, fringed with slender papillae. Cephalic tentacles tapered, finely papillate, prominent eye stalks at bases. Neck lobes well developed, thin, left considerably larger, 3 right and 4 left tapered epipodial tentacles.

*Jaw* plates with broadly rounded anterior edges, fringing elements short.

*Radula* (Fig. 119) of adult with 6 pairs of similar lateral teeth, innermost pair of marginals with 5 or 6 stout cusps, otherwise as in *C. (F.) boucheti*.

TABLE 4. — *Calliostoma (Fautor) paradigmatum*. Shell measurements (mm) and countings (BIOCAL: stns DW 36, DW 51, CHALCAL 2: stn DW 76, MUSORSTOM 4: stn DW 220).

Character	<i>n</i>	Range	Mean	SD
H	9	8.90-13.90	10.72	1.52
D	9	8.10-11.40	09.53	1.00
H/D	9	1.06-01.22	01.12	0.05
TW	9	6.00-07.60	06.48	0.51

REMARKS. — *Calliostoma (Fautor) paradigmatum* is readily separable from the somewhat similar *C. (F.) necopinatum* sp. nov. by the lack of a colour pattern and the broader spire angle. It differs further from this and from other calliostomatids in numerous details of shell morphology. The single specimen from northern New Caledonia (MUSORSTOM 4: stn DW 159) differs from southern specimens in the earlier appearance (early 5th instead of 6th - mid 7th whorl) and stronger development of S3. Although they appear to be otherwise indistinguishable, in the absence of material from geographically intermediate localities it is impossible to ascertain the status of the northern form, the characters of which were therefore excluded from the shell description.

ETYMOLOGY. — The name alludes to the rather generalised shell morphology of the species (Latin).

*Calliostoma (Fautor) metivieri* sp. nov.

Colour Plate; Figs 16-18, 120, 153; Table 5

TYPE MATERIAL. — Holotype (11.5 × 9.40 mm, 7.00 TW) MNHN. Paratypes: 23 MNHN, 1 AMS 201705, 1 BMNH 1995.016, 2 NMNZ M262464, M262469, 1 NMP, 1 USNM.

TYPE LOCALITY. — S. New Caledonia, SMIB 4. stn DW 65, 22°55' S, 167°15' E, S, 400-420 m.

MATERIAL EXAMINED. — All type material. **New Caledonia**. SMIB 1: stn DW 2, 22°52' S, 167°13' E, 415 m, 4 lv (paratypes: 1 AMS, 1 BMNH, 2 MNHN).

SMIB 2: stn DW 3, 22°56' S, 167°15' E, alive, 412-428 m, 4 lv (paratypes: 3 MNHN, 1 NMP). — Stn DW 5, 22°56' S, 167°14' E, 398-410 m, 2 dd (paratypes). — Stn DW 8, 22°54' S, 167°13' E, 435-447 m, 1 lv (paratype). — Stn DW 16, 22°51' S, 167°12' E, 390 m, 1 dd (paratype).

SMIB 3: stn DW 12, 23°38' S, 167°42' E, 470 m, 2 lv (paratypes). — Stn DW 13, 23°38' S, 167°42' E, 448 m, 1 lv (paratype). — Stn DW 24, 22°59' S, 167°21' E, 535 m, 2 lv (paratypes).

SMIB 4: stn DW 65, 22°55' S, 167°15' E, 400-420 m, 1 lv (holotype).

MUSORSTOM 4: stn DW 222, 22°58' S, 167°33' E, 410-440 m, 3 dd (paratypes).

CHALCAL 2: stn DW 76, 23°41' S, 167°45' E, 470 m, 5 lv (paratypes: 3 MNHN, 1 NMNZ, 1 USNM). — Stn DW 77, 23°38' S, 167°43' E, 435 m, 1 lv (paratype).

BIOCAL: stn DW 44, 22°47' S, 167°14' E, 440-450 m, 3 lv (paratypes: 2 MNHN, 1 NMNZ).

DISTRIBUTION (Fig. 154). — South of Ile des Pins, southern New Caledonia, 390-535 m, living at 400-535 m.

DESCRIPTION. — *Shell* up to 12.3 mm high, of moderate thickness, stout, glossy; spire narrowly and rather evenly conical, 1.68-2.05 × higher than aperture, mean spire angle 62-66°, anomphalous.

*Colour* of protoconch and 1st teleoconch whorl yellowish brown, next 2 whorls translucent white; subsequent spire whorls with irregular yellowish brown maculations, or yellowish brown with scattered white patches, pale green nacreous layer showing through translucent outer shell layer in spiral interspaces; irregular, wavy, yellowish brown axial bands extending from S3 onto outer two thirds or occasionally all of base, elsewhere white base.

*Protoconch* 400-420 μm wide, sculptured with network of fine threads that enclose roughly hexagonal spaces. Apical fold tip rounded, terminal varix rounded.

*Teleoconch* of up to 7.75 whorls; 1st eighth whorl with crisp spiral threads, delineated by growth scar and strong, rounded varix. First 2 whorls strongly convex, subsequent whorls weakly convex, periphery rounded, base weakly convex, suture well impressed. Spire and basal spirals prominent, rounded, multiplying by intercalation, rounded conical no-

dules on spire, rounded nodules on base; interspaces about as wide as each spiral; axial riblets strong on 1st 3 whorls, becoming obsolete over next 2 whorls. P2-P4 commencing immediately after post larval growth scar; P2 and P3 similar throughout, P4 weaker; P1 commencing late 2nd or early 3rd whorl, enlarging to resemble P2 and P3; P4 partly covered by succeeding whorls. Secondary spirals enlarging to resemble primaries, S1 commencing early 4th - early 5th whorl, S2 commencing mid 3rd - mid 4th whorl, S3 commencing late 4th - late 5th whorl. Tertiary spirals commencing on last 1 or 2 whorls in adults, 1 in each of most interspaces. Base with 12-15 spiral cords, inner 3 or 4 spirals becoming nodular only on last whorl in adults. Fine collabral growth lines throughout. Aperture subquadrate. Outer lip thin at rim, thickened within, strongly so at base, inner lip thick. Parietal inductura extremely thin or absent.

*Animal* unknown (material dried).

*Radula* (Fig. 120) and jaws similar to that of *C. (F.) boucheii* sp. nov., 6 pairs of lateral teeth, innermost marginal teeth with 4 or 5 stout cusps.

TABLE 5. — *Calliostoma (Fautor) metivieri*. Shell measurements (mm) and countings (BIOCAL: stn DW 44, CHALCAL 2: stn DW 76, SMIB 1: stn DW 2, SMIB 2: stns DW 5, DW 16, SMIB 3: stns DW 13, SMIB 4: stn DW 65).

Character	n	Range	Mean	SD
H	14	9.10-12.30	10.73	0.98
D	14	7.70-10.20	09.00	0.80
H/D	14	1.14-01.34	01.19	0.05
TW	14	6.60-07.75	07.01	0.31

REMARKS. — *Calliostoma (Fautor) metivieri* superficially resembles *C. (F.) necopinatum* sp. nov. but differs in numerous details of shell morphology, more conspicuously the colour and colour pattern, and in being more finely sculptured. It differs from *C. (F.) paradigmaticum* in having a colour pattern, finer nodules on the spire, and in that S3 appears earlier and enlarges to resemble the other primary spirals.

A single specimen taken alive from a seamount to the south east of New Caledonia (CHALCAL 2: stn DW 74, 24°40' S, 168°38' E, 650 m; Fig. 19) differs from the type (described) material in being uniform pale yellowish brown and in that S3 commences early on the 3rd teleoconch whorl instead of on the late 4th or 5th whorl. Additional material will be required to ascertain whether it represents a phenotypic variant, a local form of *C. (F.) metivieri*, or a distinct species.

The gut of the holotype contained much indeterminate detrital material and a few monaxonic and tetraxonic sponge spicules.

ETYMOLOGY. — Named after Bernard MÉTIVIER (MNHN).

*Calliostoma (Fautor) houbricki* sp. nov.

Colour Plate; Figs 22-24, 122, 156; Table 6

TYPE MATERIAL. — Holotype (12.8 × 10.8 mm, 8.30 TW) MNHN. Paratypes: 12 MNHN, 1 NMNZ M262466.

TYPE LOCALITY. — S. New Caledonia, SMIB 5, stn DW 81, 22°38' S, 167°35' E, 110 m.

MATERIAL EXAMINED. — All type material. **New Caledonia**. LAGON: stn 598, 22°19' S, 167°06' E, 73-75 m, 1 dd (paratype). — Stn 603, 22°16' S, 167°05' E, 78-80 m, 1 dd (paratype). — Stn 830, 20°49' S, 165°19' E, 105-110 m, 2 dd (paratypes). — Stn 933, 20°45' S, 164°15' E, 90-100 m, 2 dd (paratypes).

MUSORSTOM 4: stn DW 203, 22°36' S, 167°05' E, 105-110 m, 1 dd (paratype). — Stn DW 204, 22°37' S, 167°06' E, 120 m, 1 dd (paratype).

CHALCAL 2: stn DW 84, 23°24' S, 168°07' E, 170 m, 1 dd (paratype).

SMIB 5: stn DW 81, 22°38' S, 167°35' E, 110 m, 4 lv (holotype and paratypes: 2 MNHN, 1 NMNZ). — Stn DW 82, 22°32' S, 167°32' E, 155 m, 1 dd (paratype).

DISTRIBUTION (Fig. 156). — Off northern and southern New Caledonia, 73-170 m, living at 110 m.

DESCRIPTION. — *Shell* up to 12.8 mm high, glossy, stout, spire narrowly and rather evenly conical, 1.90-2.00x as high as aperture, mean spire angle 53-57°, omphalous.

*Colour*: Protoconch and 1st teleoconch whorl white, subsequent whorls white or pale buff with irregular yellowish brown axial maculations; all or most spiral interspaces on spire and base other than S3-P4 interspace each with narrow yellowish brown line that is either continuous or paler or locally absent between maculations on spire.

*Protoconch* 350-370 µm wide, sculptured with network of fine crisp threads that enclose roughly hexagonal spaces, apical fold tip rounded, terminal varix strong.

*Teleoconch* of up to 8.30 whorls, a conspicuous growth scar immediately following protoconch. First whorl convex, subsequent whorls almost flat, suture essentially flush, periphery angulated at S3, base weakly convex. Spiral cords on spire and base prominent, multiplying by intercalation; axial

costae strong on 1st 3 whorls, obsolete on subsequent whorls though persisting rather strongly on base. P1-P4 commencing immediately after post larval growth scar; P1 weak on 1st half whorl, rapidly enlarging to resemble P2 and P3, which are strong and similar throughout; P4 weaker, partly covered by succeeding whorls. Secondary spirals enlarging to resemble primaries; S1 commencing mid 5th - late 6th whorl; S2 absent; S3 commencing late 2nd - very early 3rd whorl, becoming stronger than primaries. Tertiary spirals commencing on last adult whorl, 1 per interspace. Nodules roundly conical on spire; smaller, low and rounded on base. Base with 8-11 rounded, similar spiral cords. Aperture subquadrate. Outer lip thin at rim, thickened within. Inner lip thick. Parietal inductura very thin.

*Radula* (Fig. 122) with 4 pairs of lateral teeth, similar to that of *C. (F.) bouchetti*.

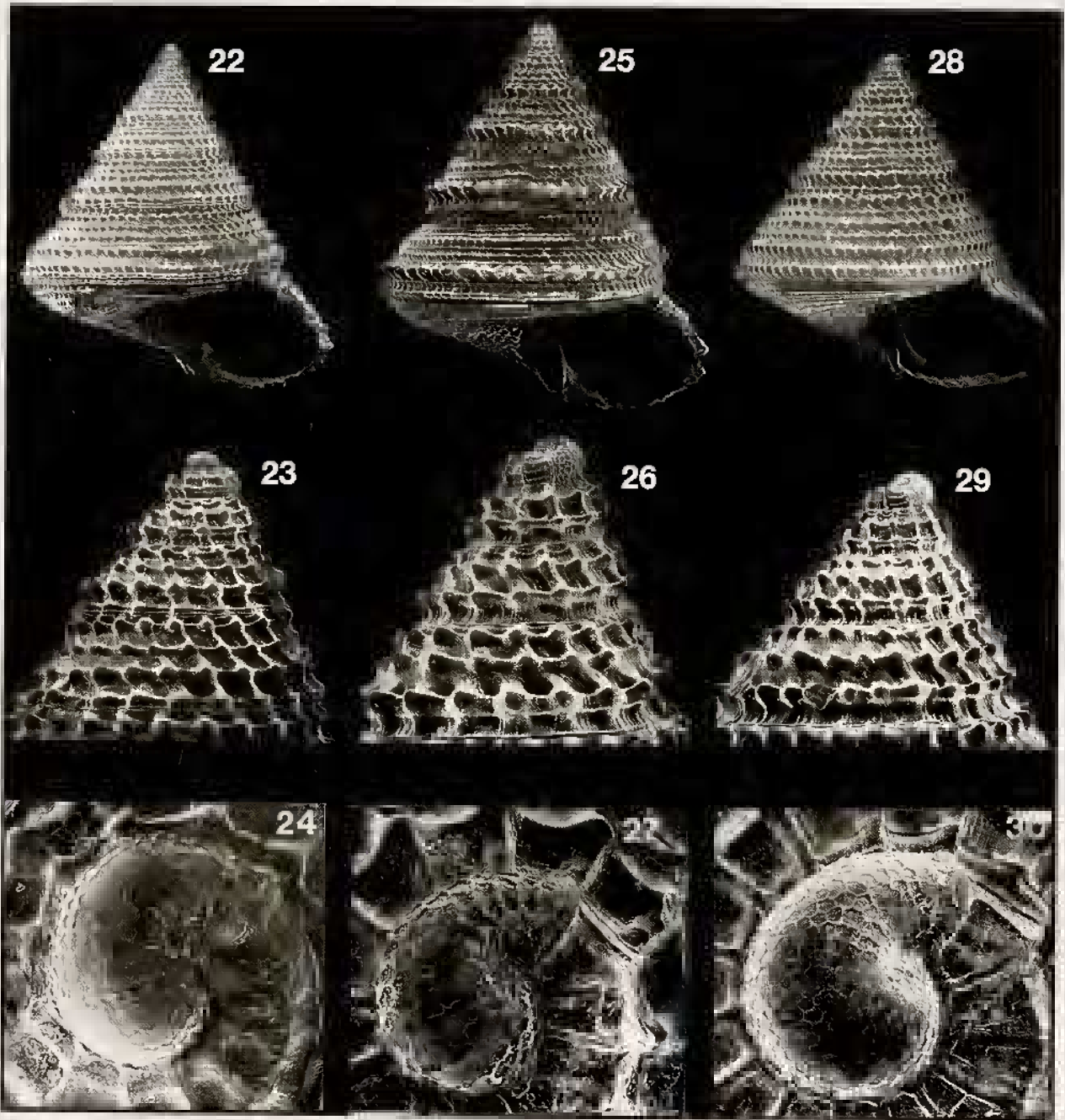
*Jaws* typical of subgenus *Fautor*.

TABLE 6. — *Calliostoma (Fautor) houbricki*. Shell measurements (mm) and counting (CHALCAL 2: stn DW 84, MUSORSTOM 4: stns DW 203, DW 204, SMIB 5: stn DW 81).

	<i>n</i>	Range	Mean	SD
H	7	8.50-12.80	9.71	1.60
D	7	7.30-10.80	8.28	1.24
H/D	7	1.11-01.23	1.17	0.03
TW	7	7.25-08.30	7.69	0.38

REMARKS. — *Calliostoma (Fautor) houbricki* closely resembles *C. (F.) scobinatum* (A. Adams in REEVE, 1863) from Bombay, India, in shape, sculpture, size relative to the number of whorls, colour, and colour pattern. The New Caledonian species differs in having a slightly broader protoconch (width 350-370 µm instead of 300 µm), stronger nodules on the spire with S3 more prominent, and in lacking the strong spiral ridges within the aperture at maturity.

The two syntype lots of *C. (F.) scobinatum* (BMNH 1968827, 1968828) together comprise three



Figs 22-30. — Genus *Calliostoma*, subgenus *Fautor*. — 22-24, *Calliostoma (Fautor) houbricki*, holotype, 12.8 × 10.8 mm, 23 × 24, 24 × 136. — 25, *C. (F.) periglyptum*, holotype, 10.2 × 8.30 mm. — 26-27, *C. (F.) periglyptum*, paratype, CHALCAL 2: sin CP 18, 26 × 32, 27 × 112. — 28-30, *C. (F.) chesterfieldense*, holotype, 7.60 × 6.90 mm, 29 × 24, 30 × 108.

specimens of *C. scobinatum* and four specimens of *C. duplicatum* (A. Adams, 1851). The specimen here chosen as lectotype (BMNH 1968827/1, 15.5 × 11.8 mm, 9.00 TW) agrees most closely with the original description and illustration (ADAMS in REEVE 1863: pl. 5, Fig. 29). An example of *C. duplicatum* from the same lot was interpreted as a "rounded form of *Z. scobinatus*" by REEVE (1863: pl. 5, Fig. 34). Compared with *C. scobinatum*, *C. duplicatum* differs in having stronger sculpture on

the spire, in having a rounded periphery at maturity and in lacking S3, among other differences. *C. duplicatum* is herein referred to *Dactylastele* gen. nov. A single syntype of *C. quadricolor* Schepman, 1908 (ZMA, "Siboga" stn 49a, Sape Strait, Lesser Sunda Is, Indonesia, 69 m) is extremely similar to *C. scobinatum* in shell morphology and, although leached due to prolonged storage in acidic alcohol, clearly shows fine yellowish brown spiral lines in the spiral interspaces as in *C. scobinatum* and *C. houbrieki*. It differs from both of the latter species, however, in that the prosocline axial costae on the early teleoconch are more crisply defined and persistent, and distinctly opisthocyrt instead of almost straight. SCHEPMAN'S (1908: 65) statement that the spire is "purplish at the top" is discordant also, although this colour is not evident in the bleached syntype. The syntype is clearly not the specimen illustrated or measured by SCHEPMAN (1908: 65, pl. 5, fig. 7; "alt 8 1/2, diam. maj. 7" mm, vs. 6.65 × 6.05 mm), which must therefore have been based upon the second specimen from "Siboga" stn 257. It is highly likely that the extant syntype is a distinct species. Unfortunately the originally illustrated specimen cannot be traced at ZMA (MOOLENBEEK pers. comm.). Although *C. scobinatum*, *C. houbrieki*, and the extant syntype of *C. quadricolor* are undoubtedly closely related, it will be impossible to ascertain their precise status with respect to one another until better, preferably topotypic, specimens of *C. quadricolor* are available for comparison.

Among other calliostomatids from the region presently under study, *C. houbrieki* is well characterised by its highly distinctive colour pattern. "*Calliostoma*" *poupineli* (see below) has a somewhat similar colour pattern but differs widely in shell and radular morphology.

ETYMOLOGY. — Named after Richard ('Joe') HOUBRICK (USNM).

*Calliostoma (Fautor) periglyptum* sp. nov.

Figs 25-27, 123, 157; Table 7

TYPE MATERIAL. — Holotype (10.2 × 8.30 mm, 7.50 TW) MNHN. Paratypes: 13 MNHN, 1 AMS C201706, 1 NMNZ M262472.

TYPE LOCALITY. — S. New Caledonia, CHALCAL 2, stn DW 71, 24°42' S, 168°10' E, S, 230 m.

MATERIAL EXAMINED. — All type material. **New Caledonia.** BIOCAL: stn DW 64, 24°48' S, 168°09' E, 250 m, 3 dd (paratypes).

CHALCAL 2: stn CP 18, 24°47' S, 168°09' E, 274 m, 2 dd (paratypes: 1 AMS, 1 MNHN). — Stn CP 20, 24°45' S, 168°09' E, 230 m, 1 lv (paratype). — Stn DW 71, 24°42' S, 168°10' E, 230 m, 4 lv (holotype and paratypes).

**Loyalty Islands.** MUSORSTOM 6: stn DW 399, 20°42' S, 167°00' E, 282 m, 2 dd (paratypes). — Stn DC 402, 20°30' S, 166°49' E, 520 m, 1 dd (paratype). — Stn DW 417, 20°42' S, 167°04' E, 283 m, 1 dd (paratype). — Stn DW 423, 20°26' S, 166°41' E, 280 m, 2 dd (paratypes: 1 MNHN, 1 NMNZ).

DISTRIBUTION (Fig. 157). — Off Lifou, Loyalty Islands, and south of New Caledonia, 230-520 m, living at 230 m.

DESCRIPTION. — *Shell* up to 10.2 mm high, glossy, stout, spire narrowly and rather evenly conical, 2.13-2.44x as high as aperture, mean spire angle 43-53°, anomphalous.

*Colour* of apical fold tip and suture on 1st teleoconch whorl brown, protoconch elsewhere white. Teleoconch pale yellowish brown with small, scattered, irregular, yellowish brown and white patches, P4 usually alternately streaked yellowish brown and white. Base either translucent white, or pale yellowish brown with yellowish brown streaks on some or all major spiral cords.

*Protoconch* 330-380 µm wide, sculptured with network of

fine, crisp threads that enclose roughly hexagonal spaces, apical fold tip tightly rounded, terminal varix strong.

*Teleoconch* of up to 7.60 whorls: 1st quarter whorl with crisp spiral threads, delineated by strong, rounded varix and growth scar. First 2.5 whorls convex, subsequent whorls weakly convex, angulated at peripheral P3, suture weakly impressed; base sharply contracted below P4, weakly convex, periphery tightly rounded on last adult whorl. Spiral cords on spire and base prominent, multiplying by intercalation; axial costae strong on 1st 4 whorls, weakening on 5th whorl, almost obsolete on subsequent whorls though persisting

rather strongly between P3 and P4, traversing base in adults. P2-P4 commencing immediately after post larval scar; P2 and P3 strong throughout, similar on 1st 2 whorls. P3 considerably stronger after 3rd whorl; P1 commencing at start of 2nd whorl, enlarging to resemble P2; P4 partly covered by succeeding whorls. Secondary spirals remaining weaker than primaries, S1 commencing mid 5th - mid 7th whorl, S2 commencing early - mid 4th whorl, S3 (when present) commencing end 5th - start of 8th whorl. Tertiary spirals commencing about mid 6th whorl, 1 per interspace. Nodules on spire roundly conical, strongest and sharpest on P3, basal

nodules low, rounded. Base with 10-14 similar, rounded spiral cords, inner 3 nodular and others smooth in immaturity, all nodular on last whorl in adults. Fine collabral growth lines throughout. Aperture subcircular. Outer lip thin at rim, thickened within, strongly so abapically. Inner lip thick. Parietal inductura extremely thin, translucent.

*Animal* unknown (material dried).

*Radula* (Fig. 123) and jaws similar to those in *C. (F.) bouchetti* sp. nov., 5 pairs of lateral teeth, innermost marginals with 4 or 5 stout cusps.

TABLE 7. — *Calliostoma (Fautor) periglyptum*. Shell measurements (mm) and countings (CHALCAL 2: stns CP 18, CP 20, DW 71, MUSORSTOM 6: stns DW 399, DW 423).

Character	n	Range	Mean	SD
H	10	6.90-10.20	8.24	0.95
D	10	5.90-08.30	6.73	0.66
H/D	10	1.12-01.35	1.22	0.06
TW	10	6.50-07.60	7.06	0.37

REMARKS. — *Calliostoma (Fautor) periglyptum* is rendered highly distinctive by the combination of small size, narrowly conical spire, and very prominent nodules on P3. *C. (F.) scobinatum* (Adams in REEVE, 1863) is similar in shape but differs markedly in having narrow spiral colour bands between the spiral cords, and in numerous details of teleoconch sculpture. The gut contents are white and comprise many very fine irregular particles and foram tests.

ETYMOLOGY. — Carved around (Greek).

*Calliostoma (Fautor) chesterfieldense* sp. nov.

Colour Plate: Figs 28-30, 124, 154; Table 8

TYPE MATERIAL. — Holotype MNHN. Paratypes: 5 MNHN, 1 NMNZ M262471.

TYPE LOCALITY. — Off Chesterfield Islands, MUSORSTOM 5, stn 379, 19°53' S, 158°40' E, 370-400 m.

MATERIAL EXAMINED. — All type material. **Chesterfield Islands**, MUSORSTOM 5: stn 339, 19°53' S, 158°38' E, 380-395 m, 1 lv (paratype). — Stn 362, 19°53' S, 158°40' E, 410 m, 1 lv (paratype). — Stn 378, 19°54' S, 158°38' E, 355 m, 1 dd (paratype). — Stn 379, 19°53' S, 158°40' E, 370-400 m, 4 lv (holotype and paratypes: 2 MNHN, 1 NMNZ).

DISTRIBUTION (Fig. 153). — Off Chesterfield Islands, 355-410 m, living at 370-410 m.

DESCRIPTION. — *Shell* up to 9.30 mm high, glossy, stout. Spire evenly conical, 1.50-1.69x as high as aperture, mean spire angle 60-64°, anomphalous.

*Colour* of apical fold tip yellowish brown, rest of protoconch and 1st teleoconch whorl pale yellowish brown; subsequent whorls buff white or pale yellowish brown; P2 with small, widely spaced yellowish brown spots, white after each spot then grading to ground colour before next spot; S3 and P4 white, with small yellowish brown spots; basal spirals spotted yellowish brown.

*Protoconch* 430-450 µm wide sculptured with network of

fine crisp threads that enclose roughly hexagonal spaces, apical fold tip rounded, terminal varix strong.

*Teleoconch* of up to 6.30 whorls. 1st eighth whorl with fine spiral threads, delineated by pronounced growth scar. First 2 whorls convex, next whorl becoming weakly convex, subsequent whorls almost flat, suture essentially flush; periphery angulated at S2 and P4, end of last adult whorl becoming tightly rounded; base weakly convex. Spiral cords on spire and base prominent, multiplying by intercalation; axial costae strong on 1st 3 whorls, weaker or almost obsolete on subsequent whorls. P2-P4 commencing immediately after

post larval scar; P2 and P3 strong and similar in size throughout; P1 commencing late on 1st whorl, rapidly enlarging to resemble P2 and P3 in size; P4 weaker, partly covered by succeeding whorls. Secondary spirals enlarging to resemble adjacent primaries; S1 commencing mid 4th - mid 5th whorl; S2 commencing early 4th whorl; S3 commencing late 3rd - early 4th whorl close beside P4, usually becoming almost or entirely fused with P4. Tertiary spirals commencing on last adult whorl, 1 or more, 1 per interspace. Nodules bluntly roundly conical on spire. After 3rd whorl, 1st (white) nodule after each yellowish brown spot on P2 distinctly enlarged, following nodules decreasing in size towards next white nodule. Base with 11-13 similar, rounded spiral cords, inner 2 or 3 with low, rounded nodules; outer spirals more or

less smooth, becoming nodular on last adult whorl. Fine collabral growth lines throughout. Aperture subquadrate. Outer lip thin at rim, thickened within, strongly so on abapical side. Inner lip thick. Parietal inductura extremely thin.

*Animal* creamy white. Tip of snout fringed with long narrow papillae. Cephalic tentacles long, narrow, tapered, finely papillate, large eyes at outer bases. Neck lobes well developed, left considerably larger. Epipodial tentacles slender, tapered, 4 on each side.

*Radula* (Fig. 124) and *jaws* similar to those of *C. (F.) boucheti*, 6 pairs of lateral teeth, innermost marginals with 3 or 4 stout cusps.

TABLE 8. — *Calliostoma (Fautor) chesterfieldense*. Shell measurements (mm) and countings.

H	D	H/D	TW	
4.20	4.00	1.05	4.30	MUSORSTOM 5: stn 362
7.10	6.60	1.07	5.60	MUSORSTOM 5: stn 379
7.60	6.90	1.10	5.90	Holotype
8.30	7.20	1.15	6.20	MUSORSTOM 5: stn 379
9.30	8.25	1.13	6.30	MUSORSTOM 5: stn 378

REMARKS. — *Calliostoma (Fautor) chesterfieldense* is similar to *C. (F.) metivieri* in size relative to the number of whorls and in shape, but differs, however, in numerous details, including colour and colour pattern, close proximity of S3 and P4, and the irregular-shaped nodules on P2.

ETYMOLOGY. — From Chesterfield Islands.

*Calliostoma (Fautor) vanbani* sp. nov.

Figs 34-36, 151, 153

TYPE MATERIAL. — Holotype (7.60 × 6.95 mm, 6.10 TW) MNHN. Paratypes: 4 MNHN, 1 NMNZ M262467.

TYPE LOCALITY. — N. New Caledonia, MUSORSTOM 4, stn DW 197, 18°51' S, 163°21' E, 550 m.

MATERIAL EXAMINED. — All type material. **New Caledonia**. LAGON: stn 444, 18°15' S, 162°59' E, 300-350 m, 1 dd (paratype). — Stn 475, 18°36' S, 163°11' E, 415-460 m, 1 dd (paratype). MUSORSTOM 4: stn DW 162, 18°35' S, 163°10' E, 525 m, 1 dd (paratype). — Stn DW 181, 18°57' S, 163°22' E, 350 m, 2 lv (paratypes: 1 MNHN, 1 NMNZ). — Stn DW 197, 18°51' S, 163°21' E, 550 m, 1 dd (holotype).

DISTRIBUTION (Fig. 154). — Off northern New Caledonia, 300-550 m, living at 350 m.

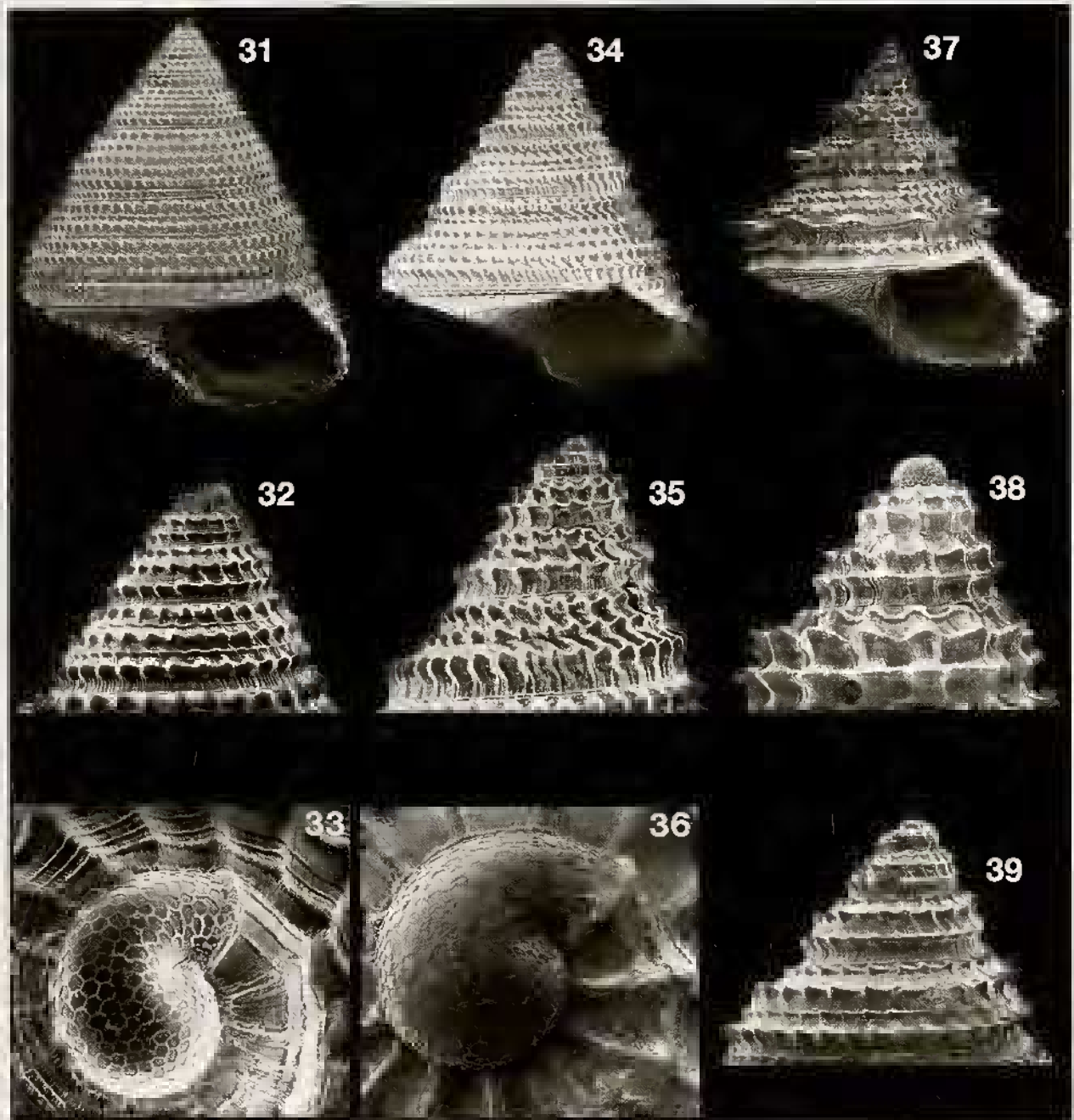
DESCRIPTION. — *Shell* up to 11.5 mm high, glossy, of moderate thickness; spire rather evenly conical, 2.25-2.38x higher than aperture; mean spire angle 55-56°, anomphalous.

*Colour* of protoconch yellowish brown. Teleoconch golden yellow, spirals and nodules predominantly translucent white; inner 3 basal spirals, their interspaces, and columella white.

*Protoconch* 400-430 μm wide, sculptured with network of fine threads that enclose roughly hexagonal spaces. Apical

fold tip rounded, terminal varix of moderate strength, rounded.

*Teleoconch* of up to 7.50 whorls; 1st eighth whorl with 4 similar spiral threads, delineated by growth, scar. First 2 spire whorls convex, subsequent whorls angulated at P3 and distinctly concave between P1 and P3, last whorl flattened; suture essentially flush after 3rd whorl; periphery tightly rounded, S3 peripheral, base weakly convex. Spire and basal



Figs 31-39. — Genus *Calliostoma*, subgenera *Fautor* and *Benthastelena*. — 31, *Calliostoma (Fautor) necopinatum*, holotype, 10.2 × 8.00 mm. 32-33, *C. (F.) necopinatum*, paratype, MUSORSTOM 4; stn DW 164, 32 × 18, 33 × 104. — 34-36, *C. (F.) vaubani*, holotype, 7.60 × 6.95 mm, 35 × 19, 36 × 120. 37-38, *C. (Benthastelena) katherina*, off Sydney, New South Wales, AMS C152388, 9.00 × 9.00 mm, 38 × 26. — 39, *C. (B.) aculeatum*, off Mikawa, Japan, NMNZ M242243, × 18.

spirals prominent, rounded, multiplying by intercalation, with rounded conical nodules; axial riblets strong on 1st 3 whorls, weakening and becoming obsolete on 4th whorl, though persisting between P3 and P4. P2 and P3 commencing immediately after post larval growth scar, similar on 1st whorl, P3 stronger thereafter; P1 commencing early on 2nd whorl, rapidly enlarging, as large as P2 on 3rd and 4th

whorls, after 4th whorl becoming as large as P3 or larger and substantially stronger than P2; P4 weakest, almost entirely covered by succeeding whorls. S1 commencing early 5th or 6th whorl, enlarging to resemble P2; S2 commencing early - mid 4th whorl, enlarging to resemble P2; S3 commencing mid 4th - early 5th whorl, becoming as large as P3. 1 or 2 tertiary spirals occasionally appear after 6th whorl. Basal spirals



numbering 11-14, inner 3 strongest, interspaces about as wide as each spiral, on 5th whorl outer 2 and inner 3 spirals nodular, others smooth until after 6th whorl. Collabral growth lines throughout, more prominent on base, on last adult whorl resolving as long, rounded axial riblets that interconnect nodules. Aperture subquadrate. Outer lip thin at rim, thicker within. Inner lip thick. Parietal inductura deposited only in large adults, very thin.

Animal white, snout lip fringed with slender papillae. Cephalic tentacles slender, tapered, finely papillate, large eyes at outer bases. Neck lobes well-developed thin, left considerably larger. Epipodial tentacles numbering 3 right and 4 left. Radula and jaws (Fig. 151) similar to those of *C. (F.) boucheti*, 5 pairs of lateral teeth, innermost marginals with 2-4 stout cusps.

TABLE 9. — *Calliostoma (Fautor) vaubani*. Shell measurements (mm) and countings.

H	D	H/D	TW	
05.85	5.65	1.03	5.75	MUSORSTOM 4: stn DW 181
07.10	6.60	1.07	6.25	LAGON: stn 444
07.60	6.95	1.09	6.10	Holotype
08.80	7.60	1.16	7.00	MUSORSTOM 4: stn DW 181
11.50	9.60	1.20	7.50	LAGON: stn 475

REMARKS. — *Calliostoma (Fautor) vaubani* is rendered highly distinctive by being concave between P2 and P3 and angulate at P3 on all but the earliest and last teleoconch whorls, and in that P1 enlarges to a greater size than P2 after the 4th whorl.

ETYMOLOGY. — After N.O. "Vauban".

#### Subgenus *BENTHASTELENA* Iredale, 1936

*Benthastelena* Iredale, 1936: 285. Type species (OD): *Benthastelena katherina* Iredale, 1936; Recent, Queensland.

Synonym:

*Tristichotrochus* Ikebe, 1942: 258. Type species (OD): *Calliostoma aculeatum* Sowerby, 1912; Recent, Japan (Syn. nov.).

REMARKS. — The type species of *Benthastelena* (Figs 37-38) and *Tristichotrochus* (Fig. 39) are essentially similar in gross shell facies, sharing convex whorls, umbilicus, thin shell, exsert protoconch, late-developing P1, relatively strong P2 and P3, high, narrow sharply angulate spiral cords, and sharply pointed nodules. Unfortunately, well preserved animals of *T. aculeatus* were unavailable to me, though isolated teeth from a decayed dry animal are very similar to those in *B. katherina*, the external anatomy, radula (Fig. 125) and jaws of which are similar to those in *Calliostoma (s. str.)* and subgenus *Fautor*. Since I am unable to find a single character or combination of character states that would justify placement of *B. katherina* and *T. aculeatus* in discrete genera or subgenera, *Tristichotrochus* is synonymised with the prior *Benthastelena*.

*Benthastelena* appears to be restricted to the tropical and subtropical western Pacific. Apart from the species recorded herein, typical members include the Japanese species *C. (T.) soyoae* Ikebe, 1942, as well as several undescribed species from off the Philippine Islands (NMNZ, MNHN). *Benthastelena* also seems to be an appropriate position for a second group with similar sculpture but in which P2 is not significantly enlarged, the spire is more narrowly conical with flatter whorls, and with or without a narrow umbilicus. This group includes such species as *T. tosaensis* Kuroda & Habe, 1961 (western Pacific), *C. (T.) gendalli* Marshall, 1979 (Kermadec Islands), and *C. (T.) paucicostatum* Kosuge, 1984 (Philippine Islands). As already discussed herein, adults of such typical *Benthastelena* species as *B. katherina* resemble their own juvenile stages in whorl convexity and in the relatively large size of P2 and P3.

*Benthastelena* is thus separated from *Calliostoma (s. str.)* (and other genus-group taxa) primarily on the basis of the high narrow, widely spaced, angulate spiral cords and the (generally)

prickly nodules on the spire whorls. In the apparent absence of other significant differences, it seems appropriate to interpret *Benthastelena* as a subgenus of *Calliostoma*.

Most species that have been referred to *Tristichotrochus* other than those already mentioned fall into three groups on the basis of distinctive shell morphology. These groups, typified by *Trochus unicus* Dunker, 1860 (Japan), *Ziziphinus haliarchus* Melvill, 1889 (Japan), and *Calliostoma formosense* E.A. Smith, 1907 (South China Sea) are each probably worthy of at least subgeneric status within *Calliostoma*, though resolution of these problems is beyond the scope of the present contribution.

*Calliostoma (Benthastelena) diadematum* sp. nov.

Colour Plate; Figs 40-42, 126, 154; Table 10

TYPE MATERIAL. — Holotype (11.0 × 10.5 mm, 7.25 TW) MNHN. Paratypes: 7 MNHN, 1 AMS C201707, 1 NMNZ M262463.

TYPE LOCALITY. — Chesterfield Islands, Capel Bank, MUSORSTOM 5, stn 255, 25°15' S, 159°55' E, 280-295 m.

MATERIAL EXAMINED. — **Chesterfield Islands**. MUSORSTOM 5: stn 255, Capel Bank, 25°15' S, 159°55' E, 280-295 m, 3 lv (holotype and paratypes: 1 AMS, 1 MNHN). — Stn 258, Capel Bank, 25°33' S, 159°46' E, 300 m, 2 dd (paratypes). — Stn 270, Capel Bank, 24°49' S, 159°34' E, 223 m, 1 dd (paratype). — Stn 276, Capel Bank, 24°49' S, 159°41' E, 269-258 m, 2 lv (paratypes: 1 MNHN, 1 NMNZ). — Stn 295, Argo Bank, 23°13' S, 159°32' E, 279 m, 1 dd (paratype). — Stn 298, Nova Bank, 22°44' S, 159°22' E, 320 m, 1 lv (paratype). — Stn DC 382, 19°37' S, 158°43' E, 580 m, 1 dd.  
**New Caledonia**. MUSORSTOM 4: stn DW 204, 22°37' S, 167°06' E, 120 m, 1 dd.

DISTRIBUTION (Fig. 153). — Capel Bank (type loc.), Argo Bank, Chesterfield Islands, and off southern New Caledonia. 120-580 m, living at 258-320 m.

DESCRIPTION. — *Shell* up to 12.7 mm high, glossy, stout, spire rather broadly conical. 1.43-2.05x as high as aperture, mean spire angle 59-71°, narrowly umbilicate.

*Colour* of protoconch and 1st teleoconch whorl pale buff white or white; subsequent whorls pale buff white or white, irregular yellowish, brown patches on shoulder and on outer part of base extending from below P3; smaller, mostly paler spots elsewhere on spire and base; last part of last adult whorl occasionally locally flushed pale pink.

*Protoconch* 370-400 µm wide, sculptured with network of fine, crisp threads that enclose roughly hexagonal spaces.

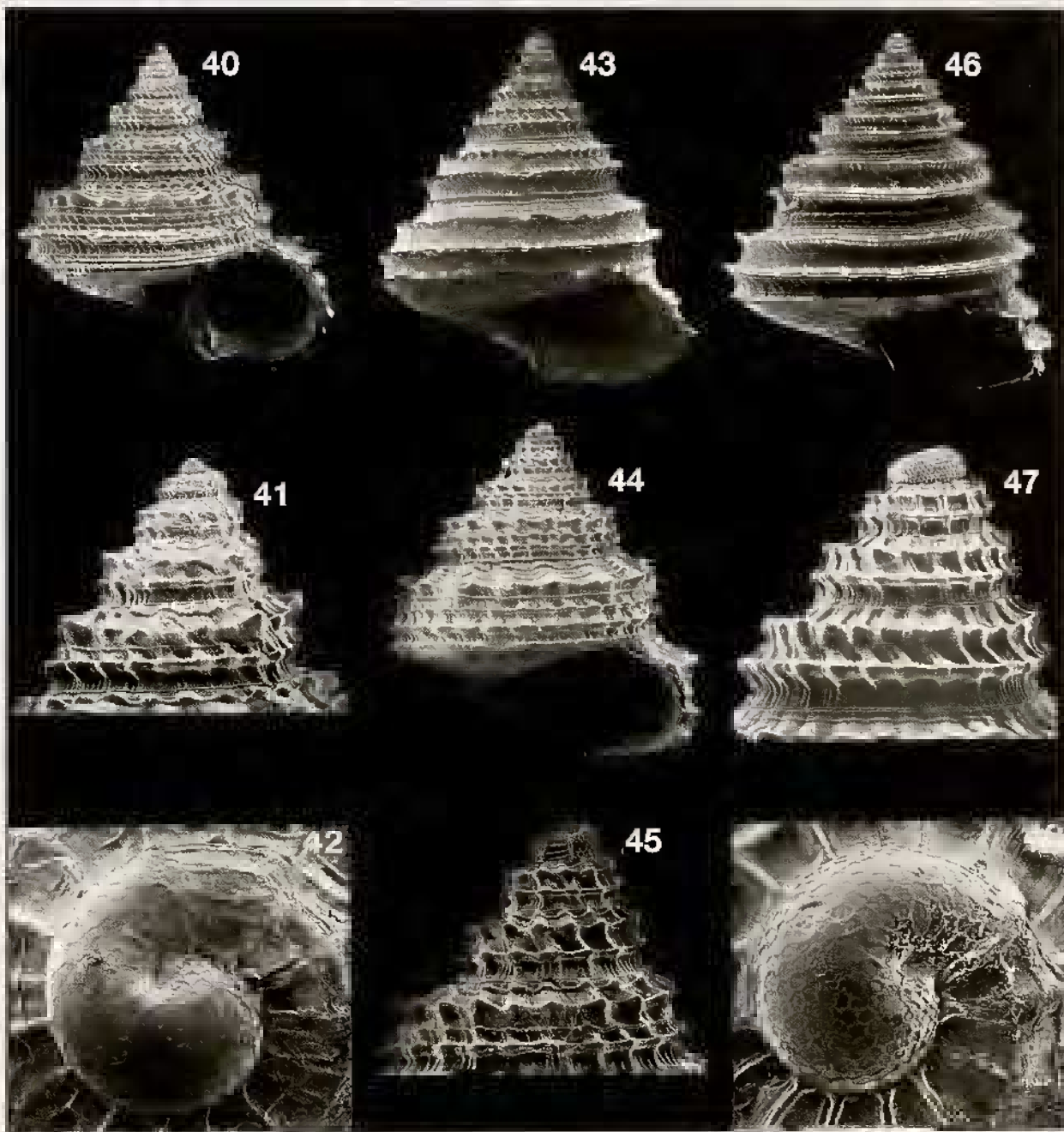
*Teleoconch* of up to 7.70 whorl; 1st eighth whorl with crisp spiral threads, delineated by strong, rounded varix and growth scar. First 2 whorls convex, subsequent whorls strongly angulated at P2, P3 peripheral, periphery evenly rounded at maturity, base convex, umbilical rim angulate. Spire and base with prominent spiral cords that multiply by intercalation; axial costae strong on 1st 4 or 5 whorls, considerably weaker or almost obsolete thereafter. P2-P4 commencing immediately after post larval scar, strong throughout; P1 a fine thread on 1st 2 whorls then gradually enlarging though remaining weaker than P2-P4; P4 partly covered by succeeding whorls. Secondary spirals remaining weaker than primaries, S1 commencing mid 4th - mid 5th whorl. S2 commencing mid 3rd - mid 5th whorl; S3 absent, positionally represented by fine tertiary spiral on last adult whorl. Tertiary spirals commencing after 5th whorl at varying stages and positions, enlarging to resemble secondaries, 1 per interspace. Nodules on spire roundly conical,

axially compressed; strong and uneven-sized on P2 and P3 after 2nd whorl, those on P2 upturned and approximately each 3rd - 4th nodule extremely large; P1 more weakly nodular, secondary and tertiary yet more weakly nodular. Base with 10 or 11 similar rounded spiral cords with low, rounded nodules. Fine collabral growth lines throughout. Umbilicus deep, wall almost vertical, smooth apart from obscure spiral lines, diameter 14.0-25.2% of shell diameter. Aperture subcircular. Outer lip thin at rim, thickened within. Inner lip thick. Parietal inductura extremely thin.

*Animal* (MUSORSTOM 5: stn 298) creamy white. Snout dorsoventrally flattened, slender, about twice as long as broad, tip laterally expanded and set with large slender papillae. Cephalic tentacles similar, slender, narrowly tapered, large eyes in prominent outer basal eyestalks. No right neck lobe. Left neck lobe large, about as long as cephalic tentacle, folded, thin in section. Epipodial tentacles slender, enlarging anteriorly, 4 on each side. Foot large, long and narrow, tip blunt, prominently anterolaterally cared, sides irregularly pustulate. Operculum typical, reddish brown.

*Radula* (Fig. 126) with the formula ∞ + 5 + 1 + 5 + ∞. Central and lateral teeth thin in section, flexible, tips finely serrate. Tip of central tooth narrowly angulate, tips of lateral teeth extremely slender. Innermost pair of marginal teeth stout, with 5 or 6 stout cusps. Next marginal narrower and longer, tip smaller and with 5 or 6 stout cusps. Outer marginals slender, tips with small slender cusps.

*Jaw* plates with elongate elements at leading edges.



FIGS 40-48. — Genus *Calliostoma*, subgenus *Benthastelena*. — 40-42. *Calliostoma (Benthastelena) diadematum*, holotype, 11.0 × 10.5 mm, 41 × 18, 42 × 128. — 43. *C. (B.) cristatum*, MUSORSTOM 4: stn DW 164, 9.70 × 8.40 mm. — 44-45. *C. (B.)* sp. cf. *diadematum*, MUSORSTOM 4: stn DW 204, 6.60 × 5.80 mm, 45 × 24. — 46-48. *C. (B.) cristatum*, holotype, 10.2 × 8.80 mm, 47 × 32, 48 × 112.

TABLE 10. — *Calliostoma (Benthastelena) diadematum*. Shell measurements (mm) and countings (MUSORSTOM 5: stns 255, 258, 270, 276, 295, 298).

Character	n	Range	Mean	SD
H	9	8.40-12.70	10.47	1.37
D	9	7.15-11.90	09.6	1.40
H/D	9	1.04-01.17	01.09	0.04
TW	9	6.50-07.70	07.08	0.35

REMARKS. — This species is similar to *C. (B.) katherina* from off New South Wales and Queensland (Figs 37-38), and is obviously closely related. *C. (B.) diadematum* differs from the Australian species, however, in numerous points of detail, including more exsert protoconch, coarser sculpture, considerably wider umbilicus, with the shoulder (P2) at adapical 3rd instead of submedian on later whorls. The two subadult specimens from off Chesterfield Islands and southern New Caledonia (Figs 44-45) differ from the Argo and Capel Banks type material (Figs 40-42) in having less prominent nodules on P2, and in having S2 stronger at the same stage of growth. These specimens could equally well represent divergent isolated populations of *C. (B.) diadematum* or distinct species.

ETYMOLOGY. — Crowned (Latin).

*Calliostoma (Benthastelena) cristatum* sp. nov.

Figs 43, 46-48, 127, 156; Table 11

TYPE MATERIAL. — Holotype (10.2 × 8.80 mm, 7.75 TW) MNHN. Paratypes: 9 MNHN, 1 AMS C201708, 2 NMNZ M262473, M262475.

TYPE LOCALITY. — S. New Caledonia, CHALCAL 2, stn DW 83, 23°20' S, 168°06' E, 200 m.

MATERIAL EXAMINED. — All type material. **New Caledonia**. LAGON: stn 444, 18°15' S, 162°59' E, 300-350 m, 2 lv (paratypes).

CHALCAL 2: stn DW 83, 23°20' S, 168°06' E, 200 m, 3 lv (holotype and 1 paratype MNHN, 1 AMS).

MUSORSTOM 4: stn DW 164, 18°33' S, 163°13' E, 255 m, 5 lv (paratypes: 4 MNHN, 1 NMNZ). — Stn DW 234, 22°15' S, 167°08' E, 350-365 m, 2 lv (paratypes: 1 MNHN, 1 NMNZ).

SMIB 5: stn DW 72, 23°42' S, 168°01' E, 400 m, 1 dd (paratype).

DISTRIBUTION (Fig. 156). — Off Récifs d'Entrecasteaux, northern New Caledonia, and off southern New Caledonia (type loc.), 200-400 m, living at 200-365 m.

DESCRIPTION. — *Shell* up to 10.2 mm high, glossy, stout. Spire narrowly and rather evenly conical, 1.90-2.28 × as high as aperture, mean spire angle 57-63°, anomphalous.

*Colour* of tip of apical fold yellowish brown, rest of protoconch colourless, translucent. First 2 teleoconch whorls, translucent white, subsequent whorls white with broad, irregular, pale yellowish brown maculations, summits of P2-P4 alternately streaked white and yellowish brown. Base white or buff white, 1 or 2 outer and/or inner basal spirals often spotted yellowish brown.

*Protoconch* 380-400 μm wide, sculptured with network of fine, crisp threads that enclose roughly hexagonal spaces, apical fold tip rounded, terminal varix strong.

*Teleoconch* of up to 7.75 whorls: 1st eighth whorl with fine crisp spiral threads, delineated by strong, rounded varix and growth scar. Whorls convex, P3 peripheral, base weakly convex, sharply contracted below P4, last adult whorl becoming evenly convex. Spiral cords on spire and base prominent; axial costae strong on 1st 4 or 5 whorls, obsolete or persisting weakly thereafter. P2-P4 commencing immediately after post larval scar, strong, after 3rd whorl becoming narrowly and sharply angulate in section and flange-like, P2 adapically upturned, P4 partly covered by succeeding whorls. P1 absent or commencing on mid 3rd - early 4th whorl, remaining weak. S2 absent or commencing late 5th - late 6th whorl, remaining weak. Fine tertiary spirals frequently

present on last adult whorl, several in each interspace. Nodules (P2, P3) roundly conical, rather sharp, becoming more or less irregular in size, either persisting throughout or almost obsolete after 4th or 5th whorl. Base with 11-19 weak, inner 2 or 3 weakly nodular, others more or less smooth. Raised collabral growth lines throughout, stronger on base.

Aperture subquadrate. Outer lip thin at rim, strongly thickened within, especially on abapical side. Inner lip thick. Parietal inductura extremely thin.

*Animal.* External anatomy, radula (Fig. 127) and jaws similar to those of *C. (B.) diadematum* sp. nov.

TABLE 11. — *Calliostoma (Benthastelena) cristatum*. Shell measurements (mm) and countings (LAGON: stn 444, MUSORSTOM 4: stns DW 164, DW 234, CHALCAL 2: stn DW 83).

Character	n	Range	Mean	SD
H	12	7.65-10.2	8.99	0.76
D	12	6.75-8.80	8.02	0.64
H/D	12	1.05-1.18	1.12	0.49
TW	12	6.80-7.75	7.09	0.27

REMARKS. — *Calliostoma (Benthastelena) cristatum* is similar to *C. (B.) katherina* and *C. (B.) diadematum* sp. nov. in radular and jaw morphology and in gross shell facies, so the three species are evidently related. *C. (B.) cristatum* differs from *C. (B.) diadematum* in lacking an umbilicus, from *C. (B.) katherina* in that P2 is set higher on late teleoconch whorls, and from both species in having weaker secondary sculpture and much finer nodules on late teleoconch whorls. The nodules on the spire whorls tend to weaken from the fourth or fifth whorl in southern specimens but remain relatively stronger in northern specimens, especially on P2 (Figs 43, 46). I am unable to detect any other significant differences between northern and southern specimens, which seem to be regional variants of a single species.

ETYMOLOGY. — Crested (Latin).

*Calliostoma (Benthastelena) coronatum* sp. nov.

Figs 49-51, 128, 156; Table 12

TYPE MATERIAL. — Holotype (10.5 × 8.50 mm, 7.25 TW) MNHN. Paratypes: 8 MNHN, 1 NMNZ M262474.

TYPE LOCALITY. — S. New Caledonia, CHALCAL 2, stn DW 83, 23°20' S, 168°06' E, 200 m.

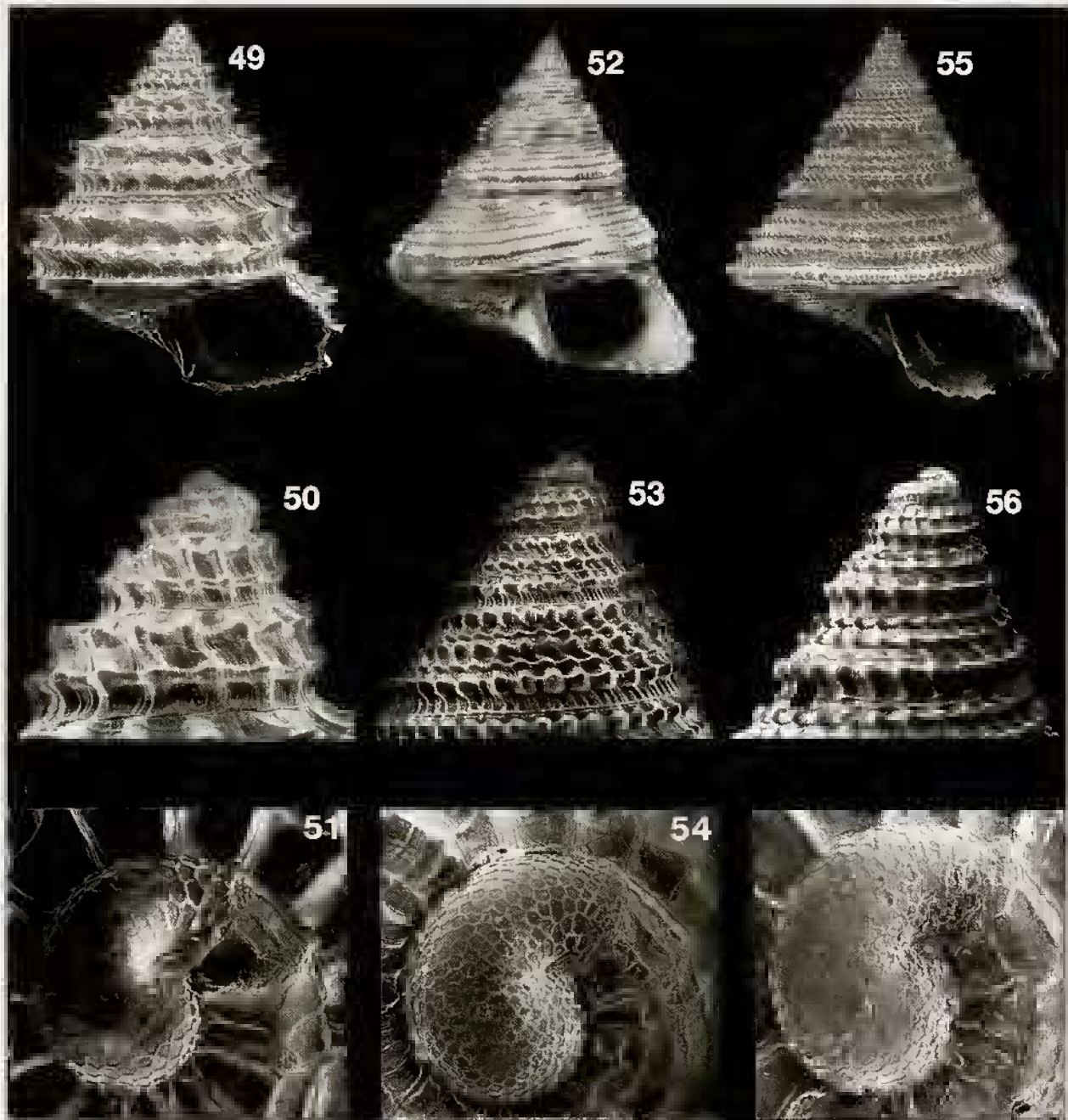
MATERIAL EXAMINED. — All type material. **New Caledonia.** LAGON: stn 394, 22°44' S, 167°06' E, 309 m, 1 lv (paratype). — Stn 395, 22°48' S, 167°08' E, 313 m, 1 lv (paratype). — Stn 396, 22°40' S, 167°09' E, 284 m, 1 dd (paratype). — Stn 497, 18°57' S, 163°28' E, 255 m, 1 lv (paratype). CHALCAL 2: stn DW 83, 23°20' S, 168°06' E, 200 m, 2 lv (holotype, paratype NMNZ). MUSORSTOM 4: stn CP 172, 19°01' S, 163°16' E, 275-330 m, 1 dd (paratype). — Stn CC 173, 19°02' S, 163°19' E, 250-290 m, 1 dd (paratype). — Stn CC 175, 18°59' S, 163°17' E, 355 m, 1 lv (paratype). — Stn DW 227, 22°46' S, 167°20' E, 300 m, 1 dd (paratype).

DISTRIBUTION (Fig. 156). — Off Grand Récif de Cook, northern New Caledonia, and off southern New Caledonia, 200-355 m, living at 200-355 m.

DESCRIPTION. — *Shell* up to 10.9 mm high, glossy, stout, spire rather narrowly conical, 1.73-1.77x as high as aperture, mean spire angle 55-62°, anomphalous.

*Protoconch* white; teleoconch whorls pale buff, 1st 2 whorls with yellowish brown spots on spirals, following whorls with

narrow, irregular, white axial bands, small irregular yellowish brown patches, and irregular yellowish brown streaks at summits of spiral cords. P4 alternately maculated with yellowish brown and white. Base pale buff, occasionally uniformly pigmented though usually outer and inner or all



FIGS 49-57. — Genus *Calliostoma*, subgenus *Benthastelena*. — 49-51, *Calliostoma (Benthastelena) coronatum*, holotype, 10.5 × 8.50 mm, 50 × 37, 51 × 116. — 52, *C. (B.) tosaense*, MUSORSTOM 6: stn CP 465, 22.4 × 20.4 mm. — 53-54, *C. (B.) tosaense*, MUSORSTOM 5: stn 379, 53 × 18, 54 × 100. — 55-57, *C. (B.) pertinax*, holotype, 11.5 × 9.60 mm, 56 × 19, 57 × 128.

spirals alternately spotted yellowish brown and white. Pale green nacreous layer showing through translucent outer shell layer on spire.

*Protoconch* 333-370  $\mu$ m wide, sculptured with network of fine, crisp threads that enclose roughly hexagonal spaces, apical fold tip, rounded, terminal varix strong.

*Teleoconch* of up to 7.40 whorls, 1st eighth whorl with crisp spiral threads, delineated by strong, rounded varix. Whorls convex, angulated at P4, periphery becoming rounded on last

adult whorl, base weakly convex. Prominent spiral cords on spire and base; axial costae strong on 1st 4 whorls, almost obsolete on subsequent whorls. P2-P4 commencing immediately after post larval scar, higher than broad after 3rd whorl, P2 and P3 very strong and similar throughout; P4 weaker, partly covered by succeeding whorls; P1 commencing mid 3rd - mid 5th whorl, weak throughout; few fine tertiary spirals appearing in primary interspaces on last adult whorl. Nodules small and rounded on P1; very strongly axially compressed.

sed. gently adapically upturned, and sharply and narrowly angulate in lateral section on P2 and P3. Base with 7-14 more or less similar spiral cords, nodules small, low, rounded; radially pleated, more strongly in southern than in northern specimens. Fine collabral growth lines throughout, stronger

on base. Aperture subcircular. Outer lip thin at rim, thickened within, strongly so abapically. Inner lip thick. No parietal inductura.

*Animal.* External anatomy, radula (Fig. 128) and jaws similar to those in *C. (B.) katherina*.

TABLE 12. — *Calliostoma (Benthastelena) coronatum*. Shell measurements (mm) and countings (LAGON: stns 394, 395, 396, 497, CHALCAL 2: stn DW 83, MUSORSTOM 4: stns CP 172, CC 173, CC 175, DW 227).

Character	n	Range	Mean	SD
H	10	7.20-10.90	9.60	1.17
D	10	6.60-09.00	8.18	0.69
H/D	10	1.08-01.33	1.17	0.08
TW	10	6.30-07.40	7.04	0.39

REMARKS. — *Calliostoma (Benthastelena) coronatum* bears a superficial resemblance to *C. (B.) diadematum*, from which it differs, however, in numerous sculptural details. More obvious differences include a lack of an umbilicus, lack of secondary spiral cords on all but the last adult whorl, and in that P2 and P3 are more similar to each other. Northern specimens differ from southern specimens in having weaker axial sculpture on the base, but otherwise appear to be indistinguishable.

ETYMOLOGY. — Crowned (Latin).

*Calliostoma (Benthastelena) tosaense* (Kuroda & Habe, 1961)

Figs 52-54, 154, 156; Table 13

*Tristichotrochus tosaensis* Kuroda & Habe in Habe, 1961: 10, app. 3, pl. 5, fig. 14.

Other references:

*Tristichotrochus tosaensis* - HABA, 1964: 14, pl. 5, fig. 14. — AZUMA, 1961: text fig. 1.

*Calliostoma (Tristichotrochus)* sp. cf. *tosaensis* - MARSHALL, 1979: 538, fig. 7GH.

*Calliostoma (Tristichotrochus) tosaensis* - KOSUGE, 1984: 6, pl. 2, figs 11-12.

TYPE MATERIAL. — Holotype NSMT.

TYPE LOCALITY. — Tosa Bay, Japan.

MATERIAL EXAMINED. — **New Zealand.** NZOI, stn K858, 30°34.2' S, 178°29.8' W, off Curtis I., Kermadec Is. 465-501 m, 1 dd (NZOI).

**Chesterfield Islands.** MUSORSTOM 5: stn 379, 19°53' S, 158°40' E, Chesterfield Reefs, 370-400 m, 1 dd.

**Loyalty Islands.** MUSORSTOM 6: stn DW 459, 21°01' S, 167°31' E, off Lifou, 425 m, 1 dd. — Stn CP 465, 21°04' S, 167°32' E, off Lifou, 480 m, 1 dd.

**Japan.** Tosa Bay, ca. 100-200 m, 2 spms (NMNZ).

**Philippine Islands.** Bohol Straits, ca. 150-200 m, 3 spms (NMNZ).

DISTRIBUTION (Figs 153, 156). — Southern Japan, Philippine Islands, Chesterfield Islands, Loyalty Ridge, Kermadec Islands, ca. 100-501 m. Depth range of living animals unknown.

TABLE 13. — *Calliostoma (Benthastelena) tosaense*. Shell measurements (mm) and countings.

H	D	H/D	TW	
09.6	09.0	1.07	6.20	MUSORSTOM 5: stn 379
16.8	16.0	1.05	7.30	Bohol Straits (NMNZ)
19.3	18.7	1.03	7.80	Tosa, Japan (NMNZ)
20.8	19.8	1.05	8.00	Tosa, Japan (NMNZ)
22.0	20.8	1.06	8.00	Bohol Straits (NMNZ)
22.4	20.4	1.10	8.40	MUSORSTOM 6: stn CP465
23.0	21.6	1.06	8.30	Bohol Straits (NMNZ)

REMARKS. — I am unable to detect any taxonomically significant differences between the specimens examined (Table 13), suggesting that a single exceptionally widely distributed species is represented. This species is distinctive among *Benthastelena* species in the combination of large size (height up to 22.8 mm), weakly convex teleoconch whorls, lack of shoulder angulation, sharply pointed nodules on spire, and peripheral P3 and S3.

*Calliostoma (Benthastelena) pertinax* sp. nov.

Figs 55-57, 155

TYPE MATERIAL. — Holotype (11.5 × 9.60 mm, 7.50 TW) and 2 paratypes MNHN.

TYPE LOCALITY. — S. New Caledonia. BIOCAL, stn CP 108, 22°03' S, 167°06' E, 335 m.

MATERIAL EXAMINED. — All type material. **New Caledonia**. LAGON: stn 993, 20°15' S, 163°53' E, 375-400 m, 1 dd (paratype).

BIOCAL: stn CP 108, 22°03' S, 167°06' E, 335 m, 1 dd (holotype).

MUSORSTOM 4: stn CC 247, 22°09' S, 167°13' E, 435-460 m, 1 dd (paratype: 10.7 × 9.40 mm, 7.40 TW).

DISTRIBUTION (Fig. 155). — Off northern and southern New Caledonia, 335-460 m (dead).

DESCRIPTION. — *Shell* up to 11.5 mm high, glossy, of moderate thickness, spire evenly conical, 2.00-2.31x as high as aperture, mean spire angle 57°, anomphalous.

*Colour* of tip of protoconch apical fold yellowish brown, rest of protoconch and most of 1st teleoconch whorl pale buff, 2nd whorl yellowish brown, subsequent whorls white. P3, S3, P4 and basal spirals spotted yellowish brown.

*Protoconch* 400 µm wide, sculptured with network of fine, crisp threads that enclose roughly hexagonal spaces, apical fold lip rounded, terminal varix strong.

*Teleoconch* of up to 7.50 whorls; 1st eighth whorl with crisp spiral threads, delineated by strong rounded varix and growth scar. First 2 whorls convex, 3rd whorl becoming almost flat, subsequent whorls almost flat, suture weakly impressed, periphery angulate. S3 peripheral, base weakly convex. Spire and base with prominent, rounded spiral cords that multiply by intercalation; axial costae strong on 1st 4 whorls, almost obsolete on subsequent whorls. Nodules on

spire roundly conical in axial section, laterally compressed, adapical extremities overhanging bases of spirals; basal nodules lower, rounded. P2-P4 commencing immediately after post larval scar; P2 and P3 strong and similar on 1st 2 whorls, P3 larger on subsequent whorls; P1 commencing on mid 2nd whorl, enlarging to resemble P2; P4 weakest, partly covered by succeeding whorls. S1 commencing late 7th - early 8th whorl, weak; S2 commencing mid - late 3rd whorl, enlarging to resemble P1 and P2; S3 commencing mid 3rd - start 4th whorl, becoming as large as P3 and peripheral. Tertiary spirals weak, 2 or 3 at end of last adult whorl, 1 per interspace. Base with 10-12 similar primary spiral cords, a secondary in most interspaces on last half whorl. Fine collabral growth lines throughout. Aperture subquadrate. Outer lip thin at rim, thickened within, strongly so on abapical side. Inner lip thick. Parietal inductura thin.

*Animal* unknown.

REMARKS. — *Calliostoma (Benthastelena) pertinax* bears a general resemblance to *C. (B.) tosaense* (Fig. 53) in early teleoconch morphology but differs in numerous details of teleoconch sculpture. These differences include much later appearance of S1, more rapid enlargement of S3, and



lack of radial pleats between P3 and P4 on the early teleoconch whorls. Judging from the slight constriction and descent of the end of the last whorl, the holotype of *C. (B.) pertinax* is evidently an adult, so the species attains about half the size of *C. (B.) tosaense*. Although it differs in sculptural details, *C. (B.) pertinax* is strikingly similar to *C. sueri* Finlay, 1923 (BEU & MAXWELL, 1990: pl. 19j) and *C. fragile* Finlay, 1923 from the Lower Miocene of New Zealand. The latter species, incidentally, is the type species of *Venustas* Allan, 1926.

ETYMOLOGY. — Firm (Latin).

#### Subgenus *AMPULLOTROCHUS* Monterosato, 1890

*Ampullotrochus* Monterosato, 1890: 145. Type species (by monotypy): *Trochus granulatus* Born, 1778; Recent, Europe.

DIAGNOSIS. — *Shell* up to about 30 mm high, spire narrowly conical, periphery angulate, anomphalous, all teleoconch whorls but 1st more or less flat-sided. P1-P3 commencing immediately or P1 commencing later than P2 and P3, axial sculpture strong on early teleoconch whorls, persistent in some species, producing fine, crisp reticulation; nodules rounded or roundly conical, enlarged at periphery in some species, elsewhere small. External anatomy, radula and jaws similar to those in *Calliostoma (s. str.)*.

REMARKS. — *Ampullotrochus* is allowed subgeneric status for a group of species that differ from *Calliostoma (s. str.)* primarily in having strongly flattened, finely nodular early teleoconch whorls, and axial costae that are stronger, more sharply defined and persistent. The combination of sculptural character states, particularly on the early teleoconch whorls, produces a distinctive facies, which, however, is difficult to quantify or more objectively describe. The two groups are sharply delineated, although both exhibit considerable degrees of interspecific variation. Apart from the type species (Fig. 21) and the taxa described below, the subgenus includes *C. (A.) gubbiolii* Nofroni, 1984 (western Mediterranean and north western Africa) and *Tristichotrochus iris* Kuroda & Habe, 1961 (southern Japan), while several undescribed species occur off the Philippines Island (NMNZ).

Shells of *Ampullotrochus* species are superficially similar to those of some species of *Astele*, all of which differ, however, in having stronger spiral lirae on the first teleoconch whorl, while the nodules on P3 are typically alternately enlarged on the early teleoconch whorls. Moreover, *Astele* species are extremely distinctive in that the innermost marginal teeth are relatively huge and extremely stout, each with a large secondary cusp on the inner side. *Astele*, as here interpreted, includes (as a synonym) *Salsipotens*, the type species of which (*Trochus armillatus* Wood, 1828) has similar radular and early teleoconch morphology. Although *A. armillatum* is more narrowly conical than *A. subcarinatum* and lacks an umbilicus, narrowly conical species with umbilicuses occur in the Australian Tertiary (e.g. *Calliostoma seuuoruata* Chapman, 1926). Moreover, the southern Australian Recent species *Astele ciliare* (Menke, 1843) is both anomphalous and as broadly conical as *A. subcarinatum*.

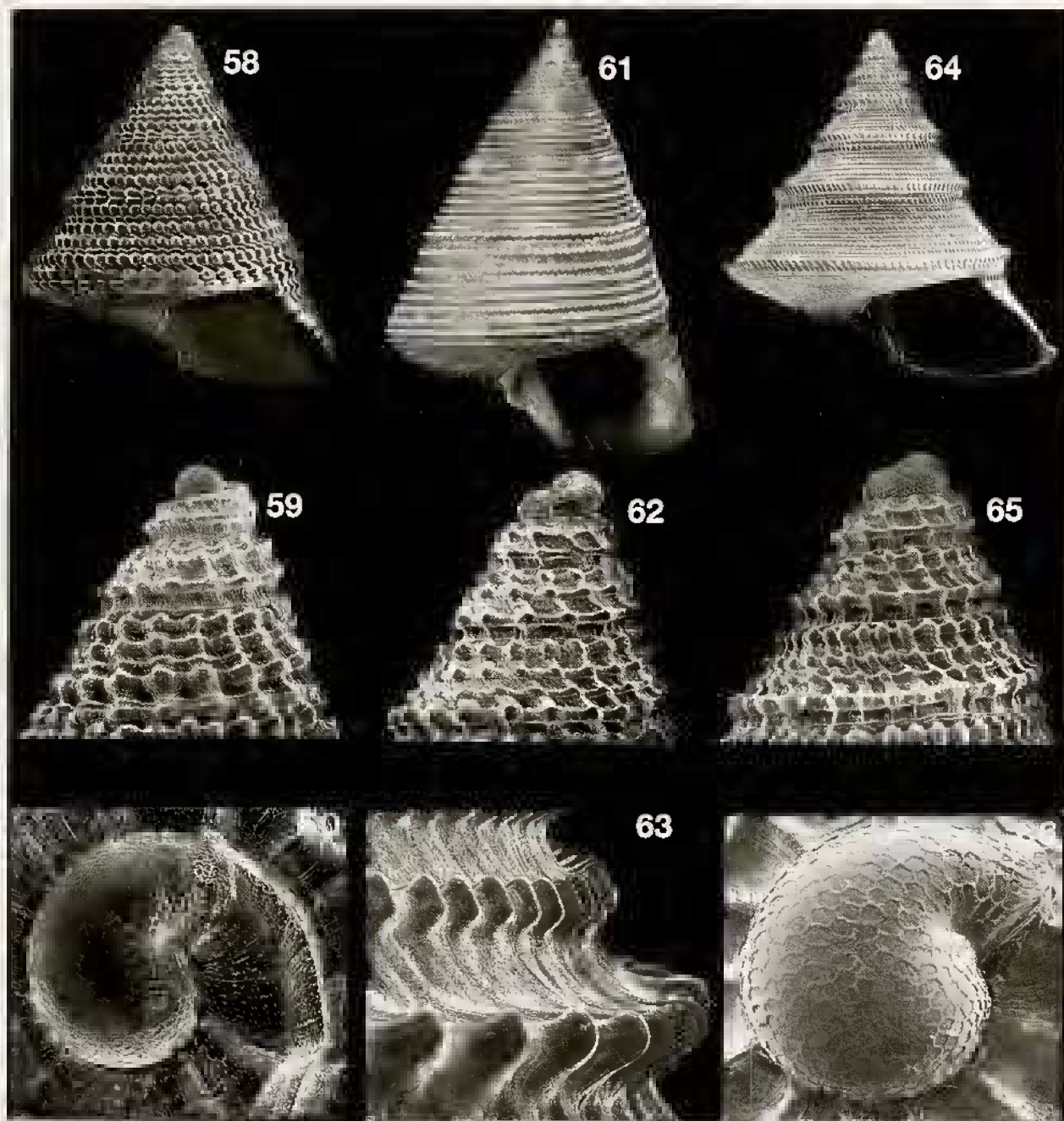
#### *Calliostoma (Ampullotrochus) xanthos* sp. nov.

Colour Plate: Figs 58-60, 129, 155; Table 14

*Calliostoma (Tristichotrochus)* sp. cf. *simplex* - MARSHALL, 1979: 537, figs 7C-D only (not *C. simplex* Schepman, 1908).

TYPE MATERIAL. — Holotype MNHN.

TYPE LOCALITY. — S. New Caledonia, CHALCAL 2, stn DW 76, 23°41' S, 167°45' E, 470 m.



FIGS 58-66. — Genus *Calliostoma*, subgenus *Ampullotrochus*. — 58-60, *Calliostoma (Ampullotrochus) xanthos*, holotype, 8.00 × 6.90 mm, 59 × 29, 60 × 104. — 61, *C. (A.) peregrinum*, holotype, 27.4 × 19.5 mm. 62-63, *C. (A.) peregrinum*, paratype, SMNB 4; stn DW 53, 62 × 25, 63 × 36 (detail of adult spire sculpture). — 64-66, *Calliostoma (A.) heros*, holotype, 11.6 × 10.2 mm, 65 × 26, 66 × 128.

**MATERIAL EXAMINED.** — **New Caledonia.** CHALCAL 2: sub DW 76, 23°41' S, 167°45' E, 470 m, 1 dd (holotype).

**Loyalty Islands.** MUSORSTOM 6: stn DW 459, 21°01' S, 167°31' E, 425 m, off Lifou, 1 lv.

**New Zealand.** NZOI stn K826(3), 28°48' S, 177°48' E, 390-490 m, off Raoul I., Kermadec Is, 25.7.1974, 1 dd (NZOI).

**DISTRIBUTION** (Fig. 155). — Off Lifou, Loyalty Islands (425 m), south of Ile des Pins, southern New Caledonia (470 m, alive), off Raoul Island, Kermadec Islands (390-490 m).

DESCRIPTION. — *Shell* (immature holotype) 8.00 mm high, glossy, stout; spire narrowly and evenly conical, 2.48x higher than aperture, mean spire angle 54°, anomphalous.

*Colour* of protoconch and 1st teleoconch whorl pale buff, 2nd and most of 3rd whorl white, subsequent whorls pale buff; S3 and P4 yellowish brown between nodules, base white.

*Protoconch* 420 µm wide, sculptured with network of fine threads that enclose roughly hexagonal spaces, apical fold tip tightly rounded, terminal varix strong.

*Teleoconch* of 6.50 whorls; 1st quarter whorl with crisp spiral threads and strong varix, delineated by growth scar and low varix. First whorl strongly convex, 2nd whorl becoming weakly convex, subsequent whorls flat with flush suture; periphery angulate, S3 and P4 peripheral, base weakly convex. Spire and base with prominent, rounded, nodular spiral cords that multiply by intercalation; axial costae strong on 1st 3.5 whorls, weakening and becoming obsolete over next whorl. Nodules on spire rounded on 1st 3 whorls; thereafter in lateral profile sharply shelved adapically, rounded abapically, on S3 and P4 elliptical and axially compressed in plan view and semicontiguous, elsewhere rounded. Basal nodules considerably smaller, rounded. P2-P4 commen-

ing immediately after post larval growth scar; P2 and P3 strong and similar throughout; P4 narrower, almost entirely exposed on spire; P1 commencing at start of 2nd whorl, as large as P2 and P3 by 3rd whorl. Secondary spirals enlarging to resemble primaries, S1 commencing early 6th whorl, S2 and S3 commencing mid 3rd whorl. Fine eollabral growth lines throughout. Base with 16 spiral cords in front of parietal area, outer 3 weaker, closes. Aperture subquadrate. Outer lip thin at rim, thickened within. Inner lip thick. Parietal glaze very thin.

*Animal* (holotype). Snout dorsoventrally flattened, nearly twice as long as broad, tip laterally expanded and edged with crowded, slender papillae. Cephalic tentacles narrowly tapered, rather short, little longer than snout; eyestalks at outer bases continuous with prominent cephalic lappets. Left and right neck lobes very large, thin in section. Epipodial tentacles small, 3 right and 4 left. Foot large, long and narrow, sides with rounded pustules. Operculum typical, reddish brown.

*Radula* (Fig. 129) similar to that of *C. (A.) granulatum* but with 6 instead of 5 pairs of lateral teeth, each with more narrowly tapered cutting area.

TABLE 14. — *Calliostoma (Ampullotrochus) xanthos*. Shell measurements (mm) and countings.

H	D	H/D	TW	
08.0	06.90	1.16	6.50	Holotype
14.6	12.80	1.14	8.50	MUSORSTOM 6: stn DW 459
19.6	15.20	1.29	9.40	NZOI stn K826(3)

REMARKS. — Although similar to the holotype in gross facies and apparently conspecific, the specimens from Lifou and Raoul Island exhibit some sculptural differences. In the Lifou specimen, P1 enlarges more rapidly on the 1st whorl, and S2 and S3 commence earlier (early 3rd and mid 2nd whorls respectively), but the first four whorls are otherwise similar. Following the 4th whorl, P1, P2, S2 and P3 become much wider, gradually dividing medially, while they are sharply shelved both adapically and abapically (shelved adapically, rounded abapically in holotype). Since multiplication of spire spirals by fission is extremely rare in normal calliostomatids, it seems probable that the Lifou specimen has grown abnormally, perhaps due to injury associated with a repaired fracture early on the 3rd whorl. The Raoul Island specimen (MARSHALL, 1979: figs 7C-D), similar to the holotype in early teleoconch facies, differs from it in the later appearance of S2 (early 8th whorl) and tertiary spirals (late 7th whorl), and differs from both the holotype and the Lifou specimen in having considerably stronger, more widely spaced nodules on S3 and P4. The Raoul Island specimen is interpreted as either an inter or intrapopulational variant.

*C. xanthos* corresponds in a general way with the original description and illustration of *C. quadricolor* Schepman, 1908. Unfortunately the only known syntype (ZMA, "Siboga", stn 49A, Sape Strait, Flores, Indonesia, 69 m) is clearly neither the originally described nor the illustrated specimen, which was thus presumably the one recorded from "Siboga", stn 257 (off Kai Is, Indonesia, 52 m) and evidently lost (MOOLENBEEK pers. comm.). The extant syntype (height 6.60 mm, diameter 6.10 mm), now bleached and etched due to prolonged storage in acidic alcohol, differs from *C. (A.) xanthos* in the earlier appearance of P1, and in that S3 becomes peripheral and larger than P4.

The Raoul Island specimen was originally thought to be related to *C. simplex* Schepman, 1908 (MARSHALL, 1979), but the holotype of that species differs in colour and sculptural details. *C. simplex* is much closer to *C. (F.) comptum* and thus probably belongs in subgenus *Fautor*.

*Calliostoma (Ampullotrochus) peregrinum* sp. nov.

Figs 61-63, 130, 153; Table 15

*Calliostoma (Tristichotrochus)* sp. cf. *simplex* - MARSHALL, 1979: 537, figs 7E-F only (not *C. simplex* Schepman, 1908).

TYPE MATERIAL. — Holotype and 4 paratypes MNHN.

TYPE LOCALITY. — S. New Caledonia, SMIB 4, stn DW 52, 23°41' S, 168°1' E, 235-250 m.

MATERIAL EXAMINED. — **New Caledonia.** SMIB 3: stn DW 8, S. New Caledonia, 24°45' S, 168°08' E, 233 m, 1 dd.

SMIB 4: stn DW 45, 24°46' S, 168°09' E, 245-260 m, 1 lv (paratype). — Stn DW 52, 23°41' S, 168°1' E, 235-250 m, 1 lv (holotype). — Stn DW 53, 23°40' S, 168°00' E, 250-270 m, 1 dd (paratype).

SMIB 5: stn DW 75, 23°41' S, 168°01' E, 270 m, 1 dd.

**Loyalty Islands.** SMIB 5: stn DW 90, 22°19' S, 168°42' E, 340 m, 1 dd (paratype). — Stn DW 93, 22°20' S, 168°42' E, 255 m, 1 lv (paratype).**New Zealand.** NZOI stn Z2098, 28°39.5' S, 173°01' E, Betty Guyot, N. Three Kings Rise, New Zealand, 841 m, 4.9.1967 1 dd (NZOI).

DISTRIBUTION (Fig. 154). — South of Loyalty Islands and south of Ile des Pins, southern New Caledonia, 233-340 m (living at 235-260 m) and northern Three Kings Rise, northern New Zealand, 841 m (dead).

DESCRIPTION. — *Shell* up to 27.4 mm high, glossy, stout; spire narrowly conical, weakly cyrtocoenoid, 2.11-2.31x higher than aperture, mean spire angle 51-55° anomphalous.*Colour* of tip of apical fold pale buff, rest of protoconch and most of 1st teleoconch whorl white; next 2 or 3 whorls buff white with irregular yellowish brown maculations. Subsequent whorls pale yellowish brown, P3 irregularly alternately spotted white and yellowish brown until last adult whorl, other spirals translucent white.*Protoconch* 420-470 µm wide, sculptured with network of fine threads that enclose roughly hexagonal spaces. Apical fold tip rounded, terminal varix rounded.*Teleoconch* of up to 9.80 whorls. 1st eighth whorl with crisp spiral threads, delineated by growth scar and strong, rounded varix. First and most of 2nd whorl convex, subsequent whorls flat with flush suture; periphery angulate, tightly rounded at maturity, P3 peripheral; base weakly convex. Spire and base with prominent spiral cords, spire spirals multiplying by intercalation; axial costae strong on 1st 3 whorls, weakening on 4th whorl, becoming obsolete on 5th whorl. Nodules on 1st 3 whorls rounded, on subsequent spirewhorls somewhat prism-shaped (*i.e.* rather sharply angulate though with flattened summits), most prominent on P3; nodules on basal spirals weaker, rounded. P2-P4 commencing immediately after post larval growth scar, P2 and P3 strong and similar on 1st 2 whorls, P3 thereafter stronger, peripheral. P1 a fine thread on 1st whorl, becoming as large as P2 on 2nd whorl; P4 partly covered by succeeding whorls. Secondary spirals enlarging to resemble P1 and P2, S1 commencing mid 4th whorl, S2 commencing early to mid 3rd whorl. Tertiary spirals 2, enlarging to resemble P1, P2 and secondaries, commencing on 4th or 5th whorl in P2-S2 and S2-P3 interspaces. Spire spiral interspaces about as wide as each spiral on early whorls, becoming considerably wider than each spiral. Base with 14 or 15 similar rounded spiral cords. Fine collabral growth lines throughout. Aperture subquadrate. Outer lip thin at rim, thickened within. Inner lip thick. Parietal inductura thin, translucent.*Animal.* External anatomy unknown (dried).*Radula* (Fig. 130) with 6 pairs of lateral teeth, outer 2 pairs lacking serrated tips, other teeth and jaws similar to those in *C. (A.) granulatum*.TABLE 15. — *Calliostoma (Ampullotrochus) peregrinum*. Shell measurements (mm) and countings.

H	D	H/D	TW	
17.0 (est.)	14.7	1.16	8.50 (est.)	SMIB 3: stn DW 8
20.2	16.0	1.26	9.00	SMIB 4: stn DW 53
21.0 (est.)	17.0	1.23	9.30 (est.)	SMIB 4: stn DW 45
27.4	19.5	1.40	9.80	Holotype

REMARKS. — *Calliostoma (Ampullotrochus) peregrinum* differs from *C. (A.) xanthos* in having a mottled colour pattern on the early teleoconch whorls, and in lacking the dark pigmentation on S3 and P4. It differs further in sculptural details, particularly in having substantially finer nodules and

more widely spaced spiral cords. It is apparently most closely related to the southern Japanese species *C. (A.) iris*, from which it differs in having stronger spiral cords, especially on the periphery, with nodules that are more sharply bevelled on their adapical and abapical sides.

ETYMOLOGY. — Travelling about (Latin), alluding both to its distribution and changing taxonomic status.

*Calliostoma (Ampullotrochus) heros* sp. nov.

Colour Plate: Figs 64-66, 131, 153; Table 16

TYPE MATERIAL. — Holotype and 3 paratypes MNHN.

TYPE LOCALITY. — Loyalty Islands, MUSORSTOM 6, stn DW 482, 21°21' S, 167°47' E, off Maré I., 375 m.

MATERIAL EXAMINED. — **Loyalty Islands.** MUSORSTOM 6: stn 459, 21°01' S, 167°31' E, 425 m, 2 dd (paratypes). — Stn DW 482, 21°21' S, 167°47' E, off Maré I., 375 m, 1 lv (holotype). SMIB 5: stn DW 87, 22°19' S, 168°41' E, 370 m, 1 dd. — Stn DW 93, 22°20' S, 168°42' E, 255 m, 1 dd (paratype).

DISTRIBUTION (Fig. 154). — Off Loyalty Islands, 255-425 m, living at 375 m.

DESCRIPTION. — *Shell* up to 14.4 mm high, glossy, lightly built; spire narrowly conical, weakly coeloconoid, 1.92-2.0 × as high as aperture, mean spire angle 58-62°, umbilicus narrow.

*Colour* of protoconch and most of 1st teleoconch whorl translucent white. Subsequent spire whorls yellowish brown with paler patches (about 6 on 7th whorl), P3 closely alternately spotted yellowish brown and white. Base pale yellowish brown, with or without 2 spiral rows of yellowish brown streaks midway between periphery and columella.

*Protoconch* 470-480 µm wide, sculptured with network of fine threads that enclose roughly hexagonal spaces. Apical fold tip rounded, terminal varix strong.

*Teleoconch* of up to 7.80 whorls, growth scar immediately following protoconch. First whorl convex, subsequent whorls sharply angulated at P3, shoulder slope steep and concave, base weakly convex. Spire and base with prominent, rounded spiral cords that multiply by intercalation; axial costae strong on 1st 4 whorls, finer and closer on all subsequent whorls, including base. Nodules on S3 strongest, rounded, conical, forming close saw-tooth serration; nodules on other spire whorls small, rounded, crowded. P2-P4 commencing immediately; P2 and P3 strong throughout, P3 strongest, peripheral; P1 commencing late on 1st whorl, rapidly enlarging to

resemble P2; P4 partly covered by succeeding whorls. Secondary spirals enlarging to resemble primaries, S1 commencing mid to late 3rd whorl, S2 commencing late 2nd - early 3rd whorl, S3 absent. Tertiary spirals slowly enlarging to resemble primaries and secondaries, 1 per interspace, earliest commencing between P2 and S2 on early to late 4th whorl, others commencing in varying order and position. Base with 20-24 low, rounded spiral cords, nodules rounded, strongest on inner 2 spirals and very weak elsewhere in subadult holotype, nodules on other spirals enlarging on last adult whorl. Umbilicus narrow, conical, diameter 8.4 - 10.2 % of shell diameter, partly overhung by inner lip rim. Aperture subquadrate. Outer lip thin at rim modestly thickened within. Inner lip thin, rim free. Parietal inductura present only in adults, extremely thin, translucent.

*Animal.* Snout fringed with prominent papillae. Cephalic tentacles long and slender, flattened, narrowly tapered, prominent eyestalks with well developed eyes at outer bases. Neck lobes prominent, thin, left lobe considerably larger than right. Epipodial tentacles slender, 3 on each side.

*Radula* (Fig. 131) similar to that of *C. (A.) granulosum* but with 6 instead of 5 pairs of lateral teeth, their tips more narrowly tapered.

TABLE 16. — *Calliostoma (Ampullotrochus) heros*. Shell measurements (mm) and countings.

H	D	H/D	TW	
14.4	11.5	1.25	8.50	SMIB 5: stn DW 93
13.7	12.6	1.09	7.75	MUSORSTOM 6: stn DW 459
11.6	10.2	1.14	7.80	Holotype

REMARKS. — This extremely distinctive species differs from all other known *Ampullotrochus* species in its fine sculpture, pagodiform spire, and concave-sided spire whorls.

ETYMOLOGY. — Named after Virginie Heros (MNHN).

*Calliostoma (Ampullotrochus) alisi* sp. nov.

Figs 67-69, 132, 157

TYPE MATERIAL. — Holotype (14.7 × 12.7 mm, 7.60 TW) and 1 paratype (13.8 × 11.9 mm, 7.50 TW) MNHN.

TYPE LOCALITY. — Loyalty Islands, MUSORSTOM 6, stn CP 464, 21°02'S, 167°32' E, off Lifou, 430 m.

MATERIAL EXAMINED. — All type material. **Loyalty Islands**. MUSORSTOM 6: stn 459, 21°01' S, 167°31' E, 425 m, 1 lv (paratype). — Stn CP 464, 21°02' S, 167°32' E, off Lifou, 430 m, 1 lv (holotype).

DISTRIBUTION (Fig. 157). — Off Lifou, Loyalty Islands, 425-430 m (living).

DESCRIPTION. — *Shell* up to 14.7 mm high, glossy, stout; spire narrowly and rather evenly conical, 1.77-1.90x as high as aperture; mean spire angle 57°, anomphalous.

*Colour* of spire pale orange, base and nodules on S3 white.

*Protoconch* 430 μm wide, sculptured with network of fine threads that enclose roughly hexagonal spaces, apical fold lip broadly rounded, terminal varix strong.

*Teleoconch* of up to 7.60 whorls; 1st quarter whorl with 5 spiral threads, clearly delineated by strong, rounded varix and growth scar. First whorl convex, subsequent whorls more or less flat; periphery sharply angulated, surmounted by S3, overhanging subsequent whorls; base weakly convex. Spire with prominent, rounded, nodular, spiral cords that multiply by intercalation, interspaces broader than each spiral; nodules prominent, roundly conical, adapical edges sharply shelved, summits slightly but distinctly upturned; axial costae rounded, persistent throughout. P1 weak and P2 and P3 strong and similar on 1st whorl; P4 weak throughout and partly covered by succeeding whorls; P1 rapidly enlarging and resembling P2 on 2nd whorl, broader than P2 on 3rd - 5th whorls, after which as broad as P2; P3 more prominent

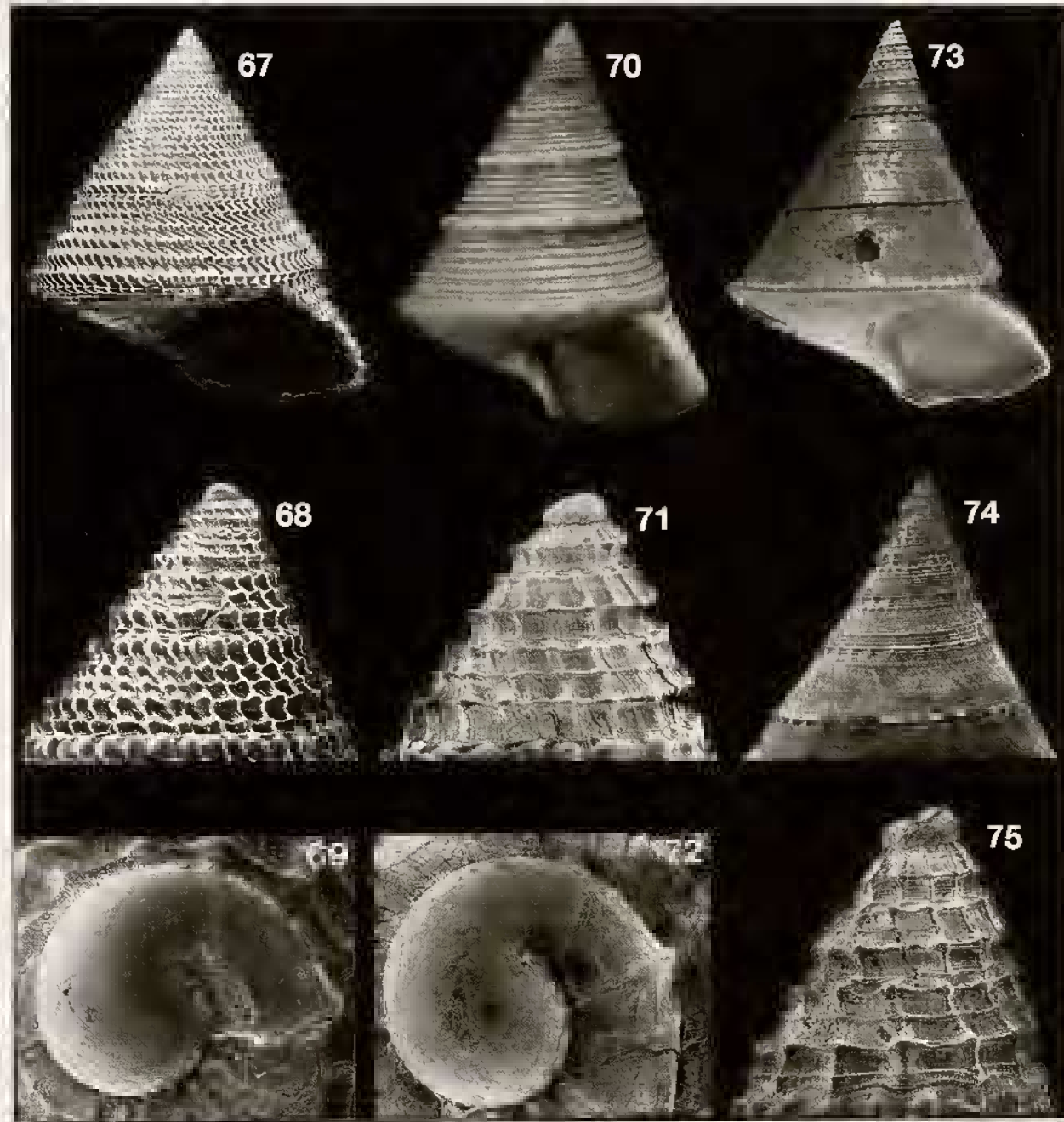
than P1 and P2 after 1st whorl. S1 commencing on mid 4th - mid 5th whorl, S2 commencing on early - mid 3rd whorl, both enlarging to resemble P2; S3 commencing on mid 3rd whorl, close beside P4, becoming peripheral and slightly larger than P3. Base with 10 or 11 similar, rounded spiral cords with bluntly rounded nodules. Fine collabral growth lines throughout, spiral interspaces finely granulate on earliest whorls. Aperture subquadrate. Outer lip thin at rim, thickened within, especially abapically. Inner lip thick. Parietal inductura very thin.

*Animal*. Snout subrectangular, longer than broad, tip laterally eared, densely papillate. Cephalic tentacles slender, tapered, prominent cystalks with well developed eyes at outer bases. Neck lobes very prominent, thin, left lobe considerably larger than right, both occupying more than half length of (contracted) epipodial fringe. Epipodial tentacles small, tapered, 2 on each side.

*Radula* (Fig. 132) with the formula  $\infty + 8 + 1 + 8 + \infty$ , generally similar to that of *C. (A.) granulatum*, which has only 5 pairs of lateral teeth at maturity.

REMARKS. — *Calliostoma (Ampullotrochus) alisi* bears a general similarity to *C. (Fautor) scobinatum* (Adams in Reeve, 1863) and *C. (F.) houbricki* sp. nov., but differs from both in colour and colour pattern, in being larger relative to the number of whorls, in having a larger protoconch (width 430 μm vs. 300 μm and 350-370 μm respectively), and in that S2 commences on the third teleoconch whorl. Despite these similarities to *Fautor* species, *C. (A.) alisi* exhibits gross teleoconch facies that are closer to *Ampullotrochus*, particularly the flattened early teleoconch whorls and strong, persistent axial sculpture. Moreover, the lateral radular teeth are not as slender as in *Fautor* species and more closely resemble those in *C. (A.) granulatum*, *heros* and *peregrinum*.

ETYMOLOGY. — After N.O. "Alis".



Figs 67-75. — Genera *Calliostoma* (*Ampulloirochus*) and *Bathyfautor*. — 67-69, *Calliostoma* (*Ampulloirochus*) *alisi*, holotype, 14.7 × 12.7 mm, 68 × 15, 69 × 100. — 70, *Bathyfautor rapuhia*, holotype, 22.8 × 17.7 mm. — 71-72, *B. rapuhia*, paratype, Wanganella Bank, south of Norfolk Island, 757-660 m, NZOI P-950, 71 × 22, 72 × 116. — 73-75, *B. coriolis*, holotype, 18.7 × 16.2 mm, 74 × 4, 75 × 21.

Genus *Bathyfautor* gen. nov.

Type species: *Bathyfautor rapuhia* sp. nov.; Recent, northern New Zealand.

DIAGNOSIS. — *Shell* up to about 23 mm high, white conical, anomphalous, periphery angulate, teleoconch whorls flat-sided. P3 commencing immediately. P1 and P2 commencing on 2nd and 3rd whorls respectively, or P1 and P2 commencing on 2nd and 1st whorls respectively. Teleoconch spirals

multiplying by intercalation: axials restricted to early whorls, strong between P3 and S3, intersections with conical nodules, spirals becoming smooth on later whorls in some species; base typically with a broad smooth median band. *Radula* with the formula  $\infty + 5 + 1 + 5 + \infty$ , central tooth broad with broadly angulate tip, lateral teeth broad-based with narrowly tapered tips. Marginal teeth similar to those in *Calliostoma* (*s. lat.*). Animal with prominent left and right cephalic lappets extending posteriorly from eyestalks, otherwise similar to that in *Calliostoma* (*s. lat.*).

REMARKS. — Apart from the new species described below, this group includes *Calliostoma multispinosum* Schepman, 1908 (Indonesia and Philippine Islands), an undescribed species from off Rowley Shoals, Western Australia (NMNZ M 257425) and probably *Kombologion babelica* Hahe, 1961 (southern Japan). Their shells are distinctive in being white with flat-sided whorls and an angulate periphery. Three of the species (described below) are rendered highly distinctive by the late appearance of P1 and P2, especially the latter, though these spirals appear earlier in the other species. *C. multispinosum* (holotype ZMA 3.08.74, plus 2 additional specimens in MNHN from MUSORSTOM 2 stations 44 and 77, off the Philippines) and the species described below share a distinctive smooth median basal spiral band. All of the species have particularly strong axial costae between P3 and S3 and exhibit a distinctive gross early teleoconch facies that is difficult to quantify or objectively describe — compare, for example, the illustrations of early teleoconchs of *Bathyfautor* species (Figs 71, 75, 77) with those of superficially similar *Aupullotrochus* and *Benthastelena* species (Figs 53, 56, 59, 62, 65, 68). The only well preserved animal seen (of *B. rapuhia* sp. nov.) differs from those of all other species examined during the present study in having prominent cephalic lappets that extend posteriorly from behind the bases of the eyestalks.

ETYMOLOGY. — From the Greek *bathus* (deep) and generic name *Fautor* (gender masculine).

*Bathyfautor rapuhia* sp. nov.

Figs 70-72, 133; Table 17

TYPE MATERIAL. — Holotype NZOI H-600. Paratypes: 3 NZOI, 1 NMNZ M117283, 1 MNHN.

TYPE LOCALITY. — N. New Zealand, NZOI stn U582, 31°52.0' S, 172°26.0' E. Three Kings Rise, 790-780 m, 5.2.1988, R.V. "Rapuhia".

MATERIAL EXAMINED. — **New Zealand.** NZOI stn U582, 31°52.0' S, 172°26.0' E, Three Kings Rise, 790-780 m, 2 lv (holotype NMNZ).

**Southern Norfolk Ridge.** NZOI stn P8, 32°40.8' S, 167°26.8' E. Wanganella Bank, 757-660 m, 4 dd (paratypes: 3 NZOI, 1 MNHN).

DISTRIBUTION. — Three Kings Rise, northern New Zealand; and Wanganella Bank, southern Norfolk Ridge, 660-790 m, living at 780-790 m.

DESCRIPTION. — *Shell* up to 22.8 mm high, glossy, of moderate thickness, spire narrowly and rather evenly conical, 2.17-2.30x as high as aperture, mean spire angle 51-53°, anomphalous.

*Colour* uniform buff white, pale green nacreous layer showing through translucent outer layer in spiral interspaces.

*Protoconch* 470-500  $\mu$ m wide, sculptured with network of fine threads that enclose roughly hexagonal spaces, apical fold tip rounded, terminal varix strong.

*Teleoconch* of up to 8.90 whorls; 1st eighth whorl with crisp spiral threads, delineated by strong rounded varix and growth scar. First 2 whorls angulated at P3, subsequent whorls more or less flat, suture almost flush; periphery

angulate, S3 peripheral; base weakly convex. Spire with prominent, rounded spiral cords that multiply by intercalation; axial costae strong on 1st 4 whorls, becoming obsolete on 5th whorl; nodules roundly conical, strongest at S3, gradually becoming obsolete after 4th - 6th whorl. P3 and P4 commencing immediately, P3 strong throughout; P1 commencing early on 2nd whorl, rapidly enlarging to resemble P3; P2 commencing on mid 3rd whorl, slowly enlarging to resemble P3; P4 weak throughout, partly covered by succeeding whorls. S1 and S2 enlarging to resemble adjacent primaries. S1 commencing early 5th - 6th whorl, S2 early 5th - 7th whorl, S3 mid - late 3rd whorl. Tertiary spiral commencing close to adapical side of S3 on mid 6th - 7th



whorl, another sometimes appearing on abapical side on mid 6th - late 7th whorl; adapical spiral largest, resembling summit of S3; additional tertiaries appearing on last few adult whorls, 1 per interspace. S3 and associated 1 or 2 tertiaries surmounting prominent peripheral bulge. Base with fine spiral threads between P4 and strong, rounded outer spiral cord; 3 or 4 smooth, rounded spiral cords on inner third; intermediate zone broad, smooth apart from few spiral threads beside outer cord, obscure spiral lines, and collabral growth lines. Aperture subquadrate. Outer lip thin at rim, modestly thickened within. Inner lip rather thick. Parietal glaze extremely thin.

*Animal.* Snout longer than broad, tip expanded and covered with crowded, slender papillae. Cephalic tentacles of

moderate length, tapered, eyestalks with well developed eyes at outer bases. Cephalic lappets prominent, continuous with eyestalks. Neck lobes large, thin, right longer, left broader. Epipodial tentacles 4 on each side. Foot long and narrow, sides papillate. Operculum multispiral.

*Radula* (Fig. 133) with the formula  $\infty + 5 + 1 + 5 + \infty$ . Central tooth broadest, tip broadly angulate, finely serrate. Lateral teeth broad-based, tips slender, finely serrate. Innermost pair of marginals very large, laterally compressed, terminal cusp largest, 3 or 4 stout subterminal cusps. Outer marginals narrowing outwards, tips narrowly tapered, outwardly more finely serrate. Jaw plates ovate, elements not markedly elongate anteriorly.

TABLE 17. — *Bathyaufator rapuhia*. Shell measurements (mm) and countings.

H	D	H/D	TW	
09.10	07.55	1.20	6.60	NZOI stn P8
19.50	15.50	1.26	8.75	NZOI stn P8
20.00	16.00	1.25	8.90	NZOI stn P8
22.80	17.70	1.29	8.80	Holotype

REMARKS. — Among previously described calliostomatines *Bathyaufator rapuhia* is extremely distinctive in the combination of large, narrowly conical, white shell, angulate periphery, flat-sided spire whorls, and especially the late appearance of P1 and P2. The unicarinate (P3) first teleoconch whorl is strikingly similar to those in *Thysanodontinae*, though the radula, jaw and early teleoconch microsculpture are entirely different.

ETYMOLOGY. — After R.V. "*Rapuhia*".

*Bathyaufator caledonicus* sp. nov.

Figs 76-78, 134, 157; Table 18

TYPE MATERIAL. — Holotype (11.5 × 10.4 mm, 6.80 TW) MNHN. Paratypes: 10 MNHN, 1 AMS C201709, 1 NMNZ M262479.

TYPE LOCALITY. — S. New Caledonia, BIOCAL, stn DW 48, 23°00' S, 167°29' E, 775 m.

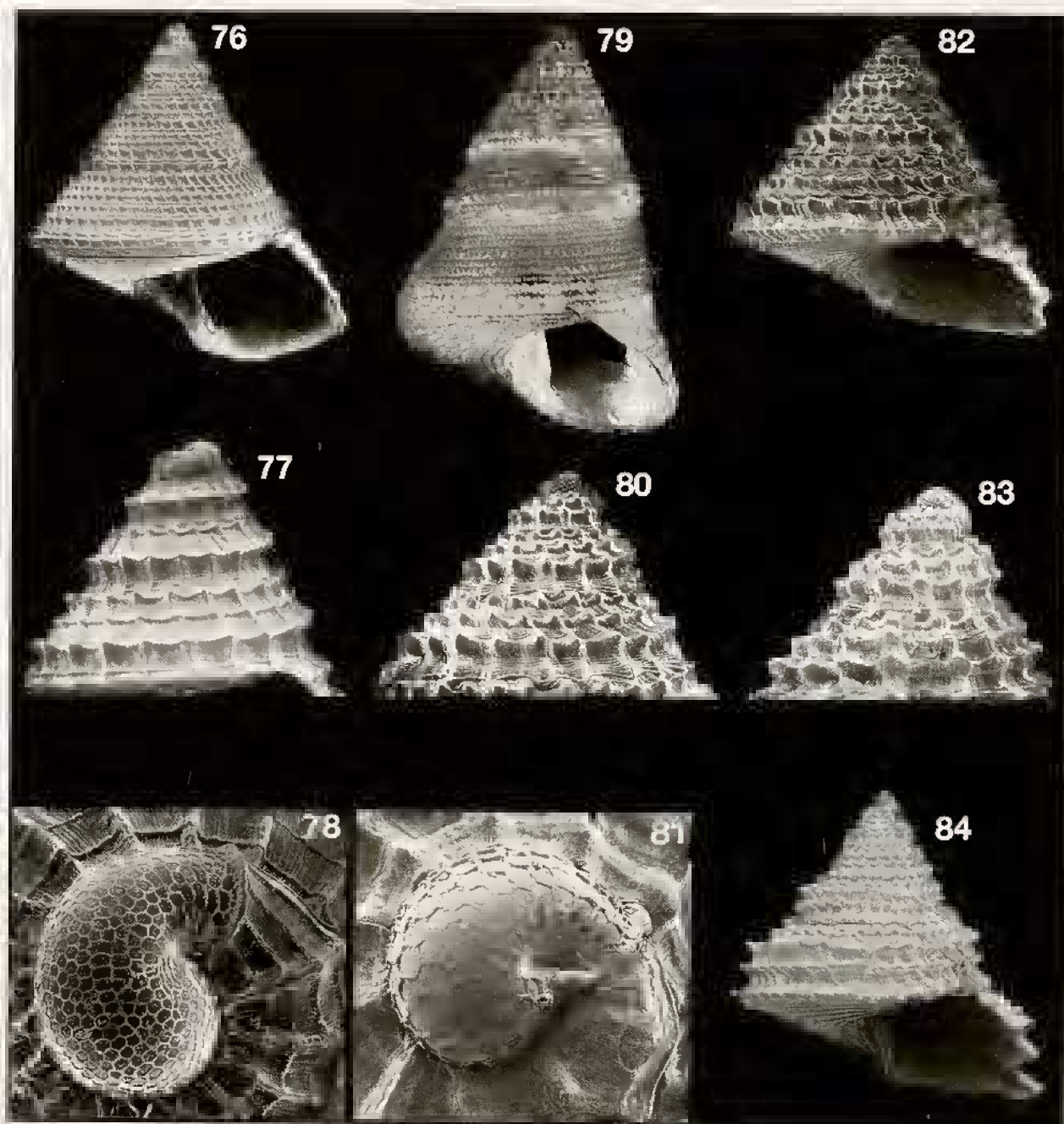
MATERIAL EXAMINED. — **New Caledonia.** BIOCAL: stn DW 48, 23°00' S, 167°29' E, 775 m, 3 dd (holotype and paratypes: 1 MNHN, 1 NMNZ). — Stn DW 51, 23°05' S, 167°45' E, 680-700 m, 1 lv (paratype). — Stn DW 53, 23°09' S, 167°43' E, 975-1005 m, 1 dd. MUSORSTOM 4: stn DW 159, 18°46' S, 163°16' E, 585 m, 2 dd (paratypes). — stn DW 160, 18°42' S, 163°13' E, 668 m, 5 lv (paratypes: 1 AMS, 4 MNHN). — stn DW 161, 18°39' S, 163°11' E, 550 m, 2 lv (paratypes).

DISTRIBUTION (Fig. 157). — Grand Passage, northern New Caledonia and south of Ile des Pins, southern New Caledonia, 550-1005 m, living at 550-700 m.

DESCRIPTION. — *Shell* up to 11.5 mm high, glossy, of moderate thickness, spire narrowly and rather evenly conical, 1.53-1.88 × as high as aperture, mean spire angle 61-63°, very narrowly umbilicate.

*Colour* uniform white.

*Protoconch* 470-500 μm wide, sculptured with network of fine threads that enclose roughly hexagonal spaces, apical fold tip rounded, terminal varix prominent of up to 6.80 whorls; 1st eighth whorl with crisp spiral threads, delineated by strong rounded varix and growth scar. First 3 whorls



FIGS 76-84. — Genera *Bathyaufator*, *Dactylastele* and *Coralastele*. — 76, *Bathyaufator caledonicus*, holotype, 11.5 × 10.4 mm. — 77-78, *Bathyaufator caledonicus*, paratype, BIOCAL: stn DW 51, 77 × 20, 78 × 100. — 79, *Dactylastele poupineli*, holotype, 11.7 × 8.40 mm. — 80-82, *Dactylastele poupineli*, Senez Reef, Noumea Lagoon, New Caledonia, 3-6 m, MNHN, 3.90 × 4.20 mm, 80 × 22, 81 × 92. — 83, *Coralastele allanae*, Murray Island, Queensland, intertidal, AMS C29298, × 60. — 84, *Coralastele allanae*, Broadhurst Reef, Queensland, AMS C155293, 7.50 × 7.70 mm (immature).

angulated at P3, angulation weakening on 4th whorl, subsequent whorls flat or shallowly concave, suture weakly impressed; periphery angulate, S3 peripheral; base weakly convex, evenly curving into umbilicus. Spire with prominent, rounded spiral cords that multiply by intercalation; axial costae strong on 1st 4 whorls, weakening on 5th whorl; weak or obsolete thereafter, number and relative size variable after 3rd whorl, 26-45 on 5th whorl. Nodules roundly conical,

shelved adapically, contiguous on S3 and P4. P3 and P4 commencing immediately after post larval scar, P3 strong throughout; P1 commencing early on 2nd whorl, rapidly enlarging to resemble P3; P2 commencing mid 2nd - mid 3rd whorl, enlarging to resemble P1 and P3; P4 weak throughout, partly covered by succeeding whorls. Secondary spirals enlarging to resemble primaries; S1 commencing mid - late 4th whorl, S2 commencing start 4th -late 5th whorl, S3

commencing mid 2nd - late 3rd whorl. Tertiary spiral commencing close to adapical side of S3 on mid 4th - early 6th whorl, usually another close to abapical side of S3 commencing late 5th - early 7th whorl, both remaining weak and resembling summit of S3 throughout. Other tertiary spirals commencing in varying orders at various stages of growth, remaining weaker than adjacent spirals, 1 per interspace. Basal spirals rounded, multiplying by intercalation, developing rounded nodules with increasing size, spirals

either 9-11 and evenly distributed, or more or less obsolete from broad median zone. Fine collabral growth lines throughout. Aperture subquadrate. Outer lip thin at rim, little thickened within. Inner lip of moderate thickness; rim thin, overhanging umbilicus. Parietal inductura extremely thin.

*Animal.* External anatomy unknown (available animals dry).

Radula (Fig. 134) and jaws similar to those of *B. rapuhia*.

TABLE 18. — *Bathyaufator caledonicus*. Shell measurements (mm) and countings (BIOCAL: stn DW 48, MUSORSTOM 4: stns DW 159, DW 160, DW 161).

Character	<i>n</i>	Range	Mean	SD
H	9	06.30-11.50	8.40	1.69
D	9	06.05-10.40	7.83	1.43
H/D	9	01.00-01.14	1.07	0.04
TW	9	05.25-06.80	5.85	0.54

REMARKS. — Compared with *Bathyaufator rapuhia*, which it resembles in early teleoconch morphology, *B. caledonicus* differs in being more broadly conical (mean spire angle 61-63° instead of 51-53°), in lacking a peripheral bulge, and in that the nodules do not become obsolete on later whorls. There is considerable variation in the relative size and number of axial costae after the third teleoconch whorl, specimens with narrower, more crowded axials tending to have smaller more sharply pointed nodules. Although the samples are too small for statistical purposes, most specimens from northern New Caledonia have more numerous axial costae than southern specimens, the latter including the holotype (number of axials on 5th teleoconch whorl: range 26-45, mean 37.3, SD 6.56, *n*=6, as against range 28-35, mean 30.6, SD 3.78, *n*=3). Since there appear to be no other correlated differences between coarsely and finely sculptured specimens, all of the material is considered to represent a single polymorphic species.

ETYMOLOGY. — New Caledonian.

*Bathyaufator coriolis* sp. nov.

Figs 73-75, 154

TYPE MATERIAL. — Holotype (18.7 × 16.2 mm, 8.90 TW) and 2 paratypes MNHN.

TYPE LOCALITY. — Chesterfield Islands, MUSORSTOM 5, stn DC 357, 19°37' S, 158°46' E, 630 m.

MATERIAL EXAMINED. — **Chesterfield Islands**, MUSORSTOM 5: stn 357, 19°37' S, 158°46' E, 630 m, 1 dd (holotype).

CORAIL 2: stn DE 13, 21°03' S, 160°55' E, Lansdowne Bank, 700-705 m, 1 dd (paratype). — Stn DE 14, 21°01' S, 160°57' E, Lansdowne Bank, 650-660 m, 1 dd (paratype).

DISTRIBUTION (Fig. 153). — Off Chesterfield Islands (type loc.) and Lansdowne Bank, 630-705 m (dead).

DESCRIPTION. — Shell up to 22.0 mm high, glossy, lightly-built, spire narrowly conical, weakly coeloconoid, 2.28-2.34x as high as aperture, mean spire angle 56°, very narrowly umbilicate.

Colour uniform white.

*Protoconch* 480-500 μm wide, sculptured with network of fine, crisp threads that enclose roughly hexagonal spaces, apical fold tip rounded, terminal varix strong.

*Teleoconch* of up to 9.60 whorls; 1st eighth whorl with 5 crisp spiral threads, delineated by growth scar and strong, rounded

varix. First whorl angulated at P3, next whorl weakly convex, subsequent whorls flat, suture almost flush; periphery angulate, S3 peripheral; base weakly convex, evenly curving into umbilicus. Spire with prominent rounded spiral cords that multiply by intercalation, nodules roundly conical; axial costae strong on 1st 3 whorls, becoming obsolete on 4th whorl. P3 and P4 commencing immediately after post larval scar, P3 strong; P1 commencing early on 2nd whorl, rapidly enlarging to resemble P3; P2 commencing at start of 3rd whorl, remaining weaker than P1 and P3; P4 weak throughout. S3 commencing mid 3rd whorl, becoming as large as P1 and P3. Tertiary spiral commencing abapically beside S3 on late 4th - 5th whorl; another abapically on mid 6th - late 8th, whorl resembling summit of S3 throughout, additional tertiaries intercalating between P3 and S3. P1-P3 weakening

on 5th whorl, P1 becoming obsolete on 6th or 8th whorl, P2 on 5th whorl; P3 on 7th or 8th whorl; last few adult spire whorls smooth apart from S3 and associated 2 tertiaries, some additional fine tertiaries mainly on abapical third, obscure spiral lines, and fine collabral growth lines; last half of last adult whorl finely lirate throughout. Base with crowded lirae between P4 and low, smooth, rounded outer spiral cord; 2 or 3 strong, rounded, widely spaced, weakly nodular spiral cords beside umbilicus; elsewhere smooth apart from obscure spiral lines and collabral growth lines; last half of last adult whorl lirate throughout. Aperture subquadrate. Outer lip thin at rim, modestly thickened within. Inner lip of moderate thickness; rim thin, overhanging umbilicus. Parietal inductura extremely thin.

*Animal unknown.*

REMARKS. — *Bathyauctor coriolis* differs from both *B. rapulua* and *B. caledonicus* in the obsolescence of spire spirals other than S3 and P4 on late teleoconch whorls. It differs further in being more broadly conical than *B. rapulua* and more narrowly conical than *B. caledonicus* (mean spire angles respectively 56°, 51-53°, and 61-63°).

ETYMOLOGY. — After N.O. "*Coriolis*".

#### Genus *DACTYLASTELE* gen. nov.

Type species: *Trochus (Zizyphinus) poupineli* Montrouzier 1875; Recent, tropical western Pacific.

DIAGNOSIS. — Shell stout, anomphalous, up to 13 mm high, periphery rounded at maturity, spire whorls weakly convex. Protoconch apical fold tip tightly pinched. Spiral cords of moderate size, nodular. P1-P4 very rapidly enlarging on 1st teleoconch whorl, P4 strongly nodular, especially on early whorls, spiral interspaces on spire spirally lirate throughout or (in *duplicatus*) non-lirate. Periostracum thin, smooth, simple.

REMARKS. — *Dactylastele* is introduced for a compact group of species comprising *Trochus poupineli* Montrouzier, 1875 (tropical western Pacific), *Calliostoma burnupi* Smith, 1899 (southern Africa), *C. nevillei* Sowerby, 1905 (Sri Lanka), and *Zizyphinus duplicatus* A. Adams, 1851 (described from unknown locality, several lots of conspecific material examined from Bombay — syntypes BMNH 196846). All of these are highly distinctive in the very rapid enlargement of P1-P4 on the first teleoconch whorl, in having P4 strongly nodular on the earliest teleoconch whorls, and in having an unusual colour pattern comprising a narrow yellowish brown line in each spiral interspace. With the exception of *Z. duplicatus*, which is otherwise similar, these are further strongly characterised by the presence of fine interstitial spiral lirae.

*Dactylastele* is undoubtedly closely related to *Coralastele* Iredale, 1930 (type species *C. allanae* Iredale, 1930. Queensland — Figs 83-84), their species sharing similar protoconchs, strongly nodular P4 on early teleoconch whorls, spirally lirate interspaces, and fundamentally similar radulae. The distinctive radula has 7 pairs of slender lateral teeth with narrowly tapered, serrated tips; and slender narrow-based innermost marginal teeth that are little stronger than the adjacent marginals.

*Dactylastele* species differ from species of *Coralastele* in being anomphalous at maturity, in attaining smaller maximum size (shell height 13 mm instead of 21 mm), and in having substantially weaker spiral cords on later whorls. Moreover, the periostracum in *Coralastele* species is spirally flanged on the spiral cords and strongly axially laminar between the nodules, while it is thin, smooth and simple in *Dactylastele*. *Dactylastele* species differ further in that the predominant shell colour pattern is confined to the spiral interspaces rather than to the spiral cords as in *Coralastele*.

*Dactylastele* and *Coralastele* species are among the very few calliostomatids that occur in the littoral or shallow sublittoral in the tropical and subtropical Indo-Pacific.

Apart from the type species, taxa referable to *Coralastele* include *Gibbula punctocostata* A. Adams, 1853 (Philippines), *Eutrochus pulcherrimus* Sowerby, 1914 (southern Japan and Okinawa), and an undescribed species from Norfolk Island (AMS, NMNZ). The type specimens of *G. punctocostata* and *E. pulcherrimus* (BMHN 196896 and 1915.1.6.182 respectively) differ from each other and from the syntypes (AMS C57742) and topotypes of *C. allanae* in minor details, though I have seen insufficient additional material to ascertain the constancy of these differences. While they may well all represent local populations of a single polymorphic species, I am presently disinclined to suggest that they are synonyms.

ETYMOLOGY. — From the Greek *Daktylios* (ring) and generic name *Astele*, alluding to the distinctive colour pattern (gender feminine).

*Dactylastele poupineli* (Montrouzier, 1875)

Figs 79-82, 135, 155

*Trochus (Zizyphinus) poupineli* Montrouzier in SOUVERBIE & MONTROUZIER, 1875: 40, pl. 4, fig. 6.

Other references:

*Trochus poupineli* — FISCHER, 1879: 387, pl. 116, fig. 3.

*Calliostoma poupineli* — PILSBRY, 1890: 350, pl. 17, fig. 41.

*Calliostoma (Fautor) poupineli* — IREBE, 1942: 274, pl. 28, figs 12a-b.

*Fautor poupineli* — HABE, 1961: 9, pl. 5, fig. 1; 1964: 13, pl. 5, fig. 1.

NOT *Calliostoma poupineli* — THIELE, 1930: 565 (= *Calliostoma (Fautor) cf. comptum* (A. Adams, 1854).

TYPE MATERIAL. — Holotype, Muséum d'Histoire Naturelle de Bordeaux, France.

TYPE LOCALITY. — Northern New Caledonia, Ile Art.

MATERIAL EXAMINED (62 specimens). — **Japan**. Off Kyoto, 6 dd (5 LACM, 1 NMNZ). — Off Kii, 1 dd (LACM). — Tosa Bay, 91 m, 3 dd (USNM). — Okinawa, 2 dd (NSMT).

**Philippines**. Off Masoinit Is., Palawan, 2-6 m, 1 lv (LACM).

**Queensland**. Murray I., Torres Strait, in crevices of madreporae, 3 lv (AMS). — Off inner side of Carter Reef, 18 m, 15.1.1980, W.F. Ponder, 1 dd (AMS). — Low Isles, Nov 1928, T. Iredale, G.P. Whitley & A. Livingstone, 2 dd (AMS). — Michaelmas Cay, May-June 1926, T. Iredale & G.P. Whitley, 1 dd (AMS). — Little Upolu Cay, off Cairns, intertidal, 19.7.1970, I. Loch, 1 dd (AMS). — Little Broadhurst Reef, off Townsville, subtidal, 14.4.1974, I. Loch, 1 lv (AMS). — Off W side Gillett Cay, Swains Reef, 64-73 m, 17-19.10.1962, 2 dd (AMS). — Off North West I., off Yeppoon, 31 m, T.A. Garrard, 1 dd (AMS). — North West I., 5.1931, T. Iredale, M. Ward & G.P. Whitley, 1 dd (AMS). — Barren I., Yeppoon, 8 m, 12.1972, N. Coleman, 2 lv (AMS). — Off Masthead I., Capricorn Group, 31-37 m, 25-29.10.1904, C. Hedley, 1 dd (AMS). — Mooloolabah, N of Caloundra, N. & V. Gomersal, 1 dd (AMS). — Shelley Beach, Caloundra, beach, J. Voorwinde, 1 dd (AMS).

**Lord Howe Island**. R.S. Bell (25 specimens in 4 lots AMS).

**New Caledonia**. 22°17.95' S, 166°19.57' E, Senez Reef, Noumea Lagoon, 3-6 m. P. Bouchet and B.A. Marshall, 23.11.1992, 3 lv (MNHN).

"*Vauban*" 1978-79: stn 40, 22°30' S, 166°24' E, 250-350 m, 3 dd (MNHN).

**Loyalty Islands**. Lifu. C. Hedley (1 AMS). — J. Brazier, 1 dd (AMS).

**Fiji**. Levuka, Ovalau, 10.1919, W.R.B. Oliver, 1 dd (NMNZ).

DISTRIBUTION (Fig. 155). — Japan, Okinawa, Philippines, Queensland, Lord Howe Island, New Caledonia, Loyalty Islands, Fiji, intertidal to 350 m, living intertidally to 8 m amongst coral.

DESCRIPTION. — *Shell* (New Caledonian specimens) up to 11.7 mm high, glossy, stout; spire narrowly conical, very weakly cyrtocoenoid, 2.17x as high as aperture; mean spire angle 51°, anomphalous.

*Colour* of tip of apical fold reddish brown, protoconch elsewhere colourless and translucent. Subsequent whorls buff white, spiral interspaces on spire each with fine yellowish brown spiral line, P4 spotted yellowish brown, base buff white.

*Protoconch* 300 µm wide, sculptured with network of fine, crisp threads that enclose roughly hexagonal spaces, apical fold tip narrowly tapered, terminal varix strong.

*Teleoconch* of up to 6.60 whorls, no post larval growth scar or varix. First whorl convex, subsequent whorls almost flat, suture essentially flush; periphery angulated at P4, tightly rounded on last adult whorl; base weakly convex. Spiral cords on spire and base prominent, multiplying by intercalation; axial costae strong on 1st 3 whorls, almost obsolete thereafter. P1-P4 commencing immediately; P1 commencing later than P2, rapidly enlarging to resemble P2 by end of 1st whorl; P3 and P4 stronger than P1 and P2 throughout; P4

almost entirely exposed on spire. Secondary spirals enlarging to resemble P1 and P2, S1 commencing mid 4th whorl, S2 commencing early 4th whorl, S3 absent. Tertiary spirals remaining weaker than primaries, one commencing mid 5th whorl between suture and P1, another commencing late 5th whorl between P2 and S2. Nodules roundly conical on spire, strong on P3 and P4 on 1st 3 whorls, becoming irregular in size on P3 and P4 from mid 3rd whorl, the largest nodules larger than those on other spirals. Base with 13 similar, rounded spiral cords with small rounded nodules. Spiral interspaces on all spire whorls with crowded spiral lirae, fine collabral growth lines throughout. Aperture subquadrate. Outer lip thin at rim, rather strongly thickened within. Inner lip thick. Parietal inductura extremely thin.

*Animal*. External anatomy unknown (available material dry).

*Radula* (Fig. 135) with the formula  $\infty + 7 + 1 + 7 + \infty$ . Innermost marginal slender, little stouter than adjacent marginals and not as strongly differentiated from them as in most other Calliostomatinae. Radula otherwise rather similar to those in *Calliostoma* (*s. lat.*), as is jaw.

REMARKS. — *Dactylastele poupineli* is highly distinctive in the combination of very rapid development of P1-P4 on the first teleoconch whorl, the strong nodules on P4, the fine interstitial spiral lirae, and the colour pattern. *Dactylastele poupineli* is one of the most widely distributed calliostomatids in the western Pacific, which suggests that it has a free-floating larval stage (lecithotrophic) of exceptionally long duration.

*Calliostoma (Fautor) comptum* has been frequently treated as a synonym of *D. poupineli* (e.g. FISCHER, 1879; IKEBE, 1942; HABE, 1961; KOSUGE, 1984), although they actually differ in numerous details of colour pattern, sculpture and radular morphology. Their protoconchs are, moreover, quite different in sculpture (Fig. 6 vs. Fig. 81) and size (width 500 µm in *C. comptum*). As suggested by BRAZIER (1895), and supported by HEDLEY (1913: 279), ADAMS (1855) erred in recording *C. comptum* from New Caledonia, since the syntypes (BMNH 1968177) are indistinguishable from the narrow New South Wales form of the species, which is widely distributed in southern Australia and unknown from elsewhere.

### Genus *LAETIFAUTOR* Iredale, 1929

*Laetifautor* Iredale, 1929: 271. Type species (OD): *Calliostoma trepidum* Hedley, 1907 (= *Calliostoma deceptum* Smith, 1899); Recent, northern Australia.

Synonym:

*Spicator* Colton & Godfrey, 1935: 14. Type species (OD): *Calliostoma spinulosum* Tate, 1893; Recent, southern Australia. (Syn. nov.).

DIAGNOSIS. — *Shell* up to 9 mm high, anomphalous, stout, higher than broad at maturity. Protoconch sculpture network very widely open. Teleoconch spirals strong to very strong, axials strong and persistent throughout, strong sharp nodules at intersections. *Radula* with the formula  $\infty + 1 + 1 + 1 + \infty$ . Central and lateral teeth extremely slender with hair-like serrated tips, tightly cramped between bases of massive innermost marginals. Marginals relatively fewer in number per transverse row than in most other calliostomatine groups, inner teeth with enlarged terminal cusp.

REMARKS. — The type species of *Laetifautor* (Fig. 90) and *Spicator* (Fig. 86) have essentially similar shell and radular morphologies (Figs 136-137) and it is impossible to justify segregation of *Spicator* from the prior *Laetifautor*. Apart from the Australian type species, the genus includes *Zizyphinus rubropunctatus* A. Adams, 1851 (Queensland, southern Japan, Okinawa, Ryukyu Islands and Philippines), an undescribed species from off the Philippine Islands (NMNZ M257491), and *L. fundatus* sp. nov. from New Caledonia (see below).

As a group *Laetifautor* is extremely distinctive in the combination of small shell size, strong teleoconch sculpture and highly reduced number of radular teeth. The adult radula in *Laetifautor* is strikingly similar to those of juvenile calliostomatines with otherwise typical adult radulae (see WARÉN, 1990: 180, 186, fig. 6C). Thus development of the radula is retarded through paedomorphosis, as is also probably the teleoconch, since the juvenile and adult facies are strikingly similar.

*Laetifautor fundatus* sp. nov.

Figs 85, 87, 89, 157

TYPE MATERIAL. — Holotype (6.00 × 4.60 mm, 5.50 TW) MNHN.

TYPE LOCALITY. — S. New Caledonia, LAGON, stn 133, 22°24' S, 166°52' E, 59-62 m.

MATERIAL EXAMINED. — Only known from the type material.

DISTRIBUTION (Fig. 157). — Off southern New Caledonia, 59-62 m (dead).

DESCRIPTION. — *Shell* (holotype) 6.00 mm high, glossy, very stout; spire narrowly conical, 2.00x as high as aperture, weakly cyrtocooid; mean spire angle 55°, anomphalous.

*Colour* pale yellowish brown, small reddish brown spots between spirals and axials on spire and base.

*Protoconch* 400 µm wide, sculptured with network of fine, crisp threads that enclose roughly hexagonal spaces, apical fold tip rounded, terminal varix strong.

*Teleoconch* of 5.50 whorls; 1st eighth whorl with fine, crisp spiral threads, delineated by strong, rounded varix and growth scar. Whorls convex, 1st whorl most strongly so, P3 peripheral; base rather sharply retracted below P4, periphery becoming rounded on last adult whorl; base weakly convex. Spiral cords and axial costae rounded, strong, similar and similarly spaced on spire, weaker on base. P2-P4 commencing

immediately after post larval scar, P2 and P3 strong and similar throughout; P1 commencing on mid 1st whorl, becoming strong though remaining weaker than P2 and P3; P4 almost entirely exposed on spire, weakest. S3 commencing late on 2nd whorl close beside P4, becoming more prominent than P4 though remaining weaker than P1; S1 commencing late on last adult whorl, weak. Nodules on spire roundly conical, prominent on P1, very prominent on P2 and P3, blunter on P4. Base with 2 weak spiral cords close beside P4; followed by 6 strong, rounded spiral cords with low, rounded nodules, outermost spiral strongest, a weak secondary spiral on its inner side. Aperture subquadrate. Outer lip rapidly and very strongly thickened within. Inner lip thick. Parietal inductura thin.

*Animal* unknown.

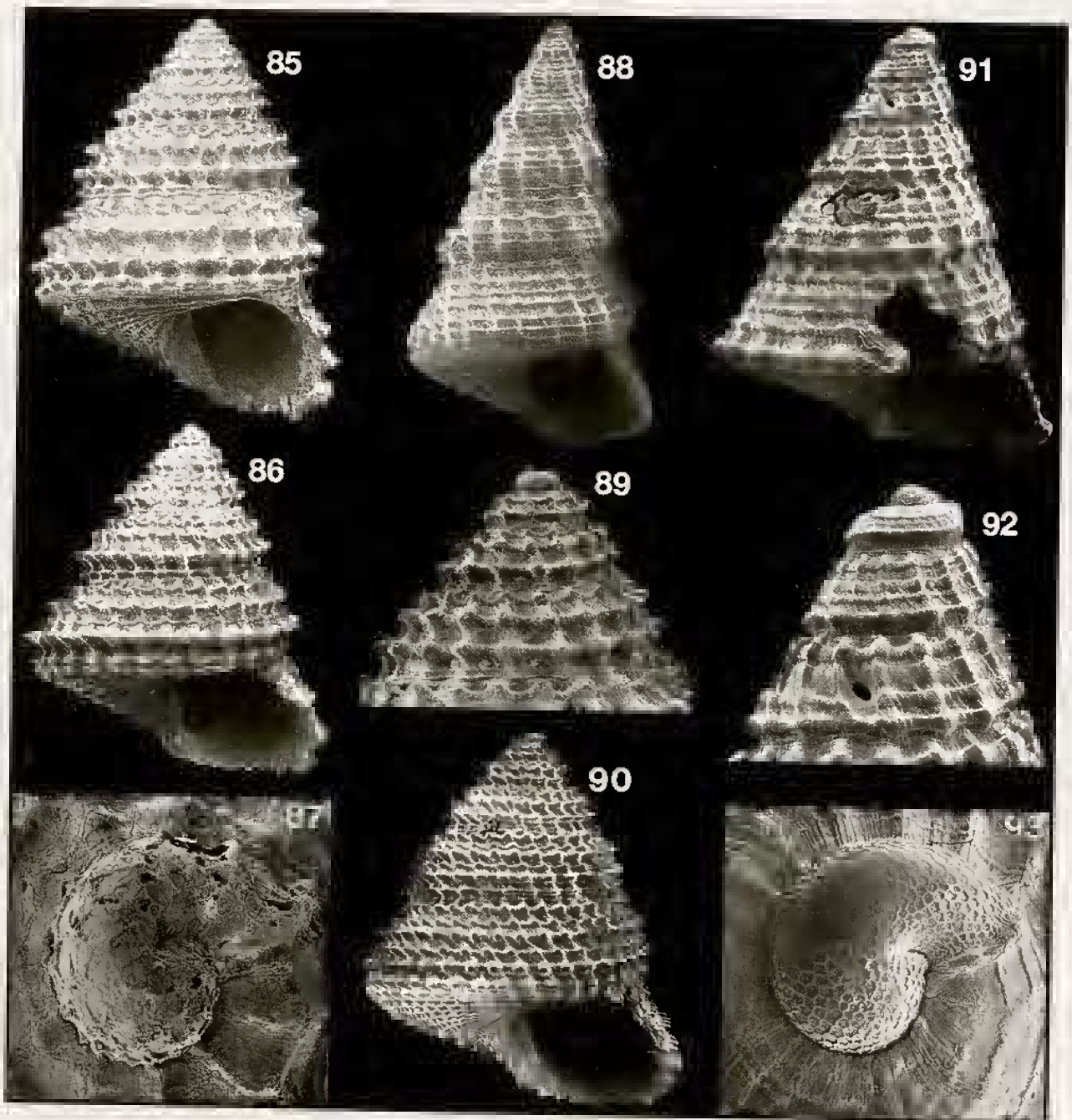
REMARKS. — This species is extremely distinctive in its small size, colour pattern, prominent nodules, and strong spiral and axial sculpture on the spire. It is obviously closely related to *L. rubropunctatus* (A. Adams, 1853), which it resembles in general shell facies, including the colour pattern on the spire. Compared with the holotype of *L. rubropunctatus* (BMNH 196842) and specimens from Okinawa (2 lots LACM), Mindanao, Philippine Islands (1 lot LACM), and Queensland (6 lots AMS), *L. fundatus* differs in having blunter, less prominent nodules, especially on S3, a larger protoconch (width 400 µm vs. 300-320 µm), and pigment spots in the interspaces of the basal spirals instead of on the summits of the spiral cords.

ETYMOLOGY. — From the Latin *fundatus* (firm, grounded).

Genus *SELASTELE* gen. nov.

Type species: *Calliostoma omustum* Odhner, 1924: Recent, northern New Zealand.

DIAGNOSIS. — *Shell* up to 9.80 mm high, spire narrowly conical, anomphalous. P2 and P3 commencing immediately, P1 enlarging slowly on 1st 1 or 2 whorls, axial sculpture strong and persistent. *Radular* formula ca. 10 + 8 + 1 + 8 + ca. 10. Marginal 1 relatively small, stout; central and lateral teeth very long and narrowly tapered, exceedingly thin in section.



FIGS 85-93. — Genera *Laetifautor* and *Selastele*. — 85, 87, 89, *Laetifautor fundatus*, holotype, 6.00 × 4.60 mm, 87 × 72, 89 × 23. — 86, *Laetifautor spinulosus*, Moonta Bay, South Australia, South Australian Museum D18836, 5.80 × 5.10 mm. — 88, *Selastele onustum*, off Three Kings Islands, northern New Zealand, 128 m, NMNZ M34251, 9.85 × 5.50 mm. — 90, *Laetifautor trepidus*, off Swain's Reef, Queensland, 100 m, AMS C154363, 6.15 × 4.85 mm. — 91-93, *Selastele pictum*, holotype, 5.45 × 4.20 mm, 92 × 38, 93 × 116.

REMARKS. — The type species of *Selastele* (Fig. 88) is very distinctive in the combination of small shell size, narrowly conical spire and unusual radula. The radula (Figs 138-139) has fewer marginal teeth per transverse row and a relatively weaker innermost marginal than any known calliostomatid other than thysanodontines, which, however, have entirely different tooth and early teleoconch morphologies. In contrast, the number of lateral teeth (8 pairs per transverse row) is



exceptionally high for a calliostomatid of this size, although there are more numerous laterals in a few (larger) species, such as *Venustatrochus georgianus* Powell, 1951. While the number of laterals is high, overall development of the radula in *Selastele* is retarded, evidently as the result of a paedomorphic process. One of two undescribed species from New Zealand (NMNZ) has an even more weakly developed radula, a sub-adult with 4.5 teleoconch whorls having teeth that are almost gelatinous. The group is represented in southern Australia by the Recent species *Calliostoma retiarium* Hedley & May, 1908.

ETYMOLOGY. — From the Greek *selasma* (shining) and generic name *Astele* (neuter).

*Selastele pictum* sp. nov.

Figs 91-93, 158

TYPE MATERIAL. — Holotype (5.45 × 4.20 mm, 6.10 TW) MNHN.

TYPE LOCALITY. — S. Loyalty Islands, SMIB 5, stn DW 87, 22°19' S, 168°41' E, 370 m.

MATERIAL EXAMINED. — Only known from the type material.

DISTRIBUTION (Fig. 158). — Southern Loyalty Islands, dead, 370 m.

DESCRIPTION. — *Shell* (holotype) 5.45 mm high; spire narrowly and evenly conical, 2.7 × as high as aperture, mean spire angle 50°; anomphalous.

*Colour*. Protoconch white; first half teleoconch whorl orange, following 3.5 whorls with orange spots on P3, elsewhere translucent white, brilliantly nacreous though thin translucent outer shell layer.

*Protoconch* 350 μm wide, sculptured with dense network of fine, crisp threads that enclose roughly hexagonal spaces. Extreme tip of apical fold tightly pinched, terminal varix strong.

*Teleoconch* of 6.10 whorls; 1st tenth whorl sculptured with crisp spiral threads and minute granules, sharply delineated by growth scar. First whorl convex, subsequent whorls flat, periphery angulate, base flat. Sculpture of rounded spiral cords that multiply by intercalation and gradually enlarge, and persistent axial costae; rounded nodules at intersections. P1, P2, S2, P3 and P4 commencing immediately; P2 and P3 strong and similar on 1st 1.5 whorls, after which P2 widens and weakens, becoming obsolete early on 3rd whorl; P3

peripheral, strongest throughout. P1 and S2 commencing as fine threads, both rapidly enlarging on 2nd whorl to become almost as large as P3, similar throughout. Late on 3rd whorl 2 tertiary spirals resolve between P1 and S2 in space formerly occupied by P2, then rapidly enlarge to resemble P1 and S2. P4 weak throughout, almost entirely covered by succeeding whorls. A tertiary spiral intercalating between S2 and P3 late on last adult whorl. Base with 8 similar spiral cords that are weaker and more weakly nodular than spire spirals; a weak tertiary spiral between outermost spiral and P4. Axial costae weak and crowded on 1st half whorl, thereafter strong on spire and weak on base with interspaces wider than each axial; collabral on 1st whorl and on base, non-collabral to varying degrees on subsequent whorls. Fine collabral growth lines throughout, prosoeline on spire, opisthocyrt on base. Aperture subquadrate. Inner lip of moderate thickness, almost orthoeline, parietal glaze very thin, outer lip rim broken back, thin.

*Animal* unknown.

REMARKS. — Compared with *Selastele pictum*, the southern Australian species *S. retiarium* differs in having P2 stronger and persistent throughout, with P3 also stronger and set higher on each whorl. Apart from several sculptural details, the New Zealand type species (Fig. 88) differs in having each teleoconch whorl concave on the adapical half and convex abapically.

ETYMOLOGY. — Painted (Latin).

TRIBE FAUTRICINI nov.

Type genus: *Fautrix* gen. nov.

DIAGNOSIS. — First teleoconch whorl with strong spiral lirae and crowded axial riblets. Teleoconch whorls convex, sculptured with spiral cords that multiply by intercalation, and axial riblets that become obsolete on later whorls. Spire spirals nodular, basal spirals nodular or smooth. Narrowly umbilicate. Aperture simple. Head very broad, snout broadly rounded in front. Foot short

and broad, folded from end to end when retracted. Radular formula  $\infty + 8-9 + 1 + 9-8 + \infty$ . Central and lateral teeth narrowly elliptical, thin in section, faces concave, tips pointed and non-serrate. Lateral teeth apparently multiplying during ontogenesis by progressive morphological transformation of marginal teeth. Marginal teeth in early ontogenesis all long and thin in section, with broad, blunt, finely serrate tips. In later ontogenesis inner 9 pairs of marginal teeth becoming progressively stouter and vertical cutting area with strong cusps forming on inner edges, terminal cusp becoming progressively larger relative to subterminal cusps.

REMARKS. — This new tribe is introduced for *Fautrix* gen. nov., the type species of which (see below) differs markedly from all other known calliostomatids in having a much broader head, a shorter and broader foot that when retracted is folded from end to end instead of from side to side, and an entirely unique radular ontogenesis and morphology. Unique features of the radula include the elliptical, cusplless central and lateral teeth, the morphologically sharply differentiated inner and outer marginal teeth, the very stout inner marginal teeth, and the blunt-tipped outer marginal teeth. Other unique features of the radula are the similarity of the inner 9 pairs of marginal teeth, and the relatively small innermost marginal. By contrast all other calliostomatids have a single enlarged innermost pair of marginals, while the outer teeth exhibit a rather smooth outward morphological gradation. The most remarkable and significant features of the radula, however, are the apparent formation of lateral teeth by transformation of marginals and the profound morphological changes in marginal tooth morphology into late ontogenesis.

As recently demonstrated by WARÉN (1990), the innermost marginal in Calliostomatinae becomes greatly enlarged at a very early stage of development and prior to formation of the central and lateral teeth. He showed that the lateral teeth arise pair by pair through intercalation within the central field, unlike all other known trochoideans in which laterals are multiplied by progressive morphological transformation of marginal teeth. In a study of four calliostomatine species, WARÉN (1990) found that the central tooth and first pair of laterals were formed when specimens had 1.5-3 teleoconch whorls and that the other lateral teeth appear rather abruptly when the shell has 3.5-4.5 teleoconch whorls. Apart from a progressive increase in the number of teeth, there is relatively little change in marginal tooth morphology between juveniles with 0.5 teleoconch whorls and adults in these species (WARÉN, 1990: figs 6 A-D). Since there can be no doubt that the calliostomatine radula is derived from a standard trochoidean plan, it is concluded that the radula in *Fautrix* is more primitive than that in Calliostomatinae (plesiomorphic) and that Fautricini either represents the common basal stock or is an offshoot from it.

Fautricini is here interpreted as a grade of lower calliostomatines rather than as a discrete phylogenetic radiation, for which the category of subfamily would be more appropriate.

*Fautrix* species are living representatives of a group of (undescribed) genera that were richly speciated in the Miocene of Australia. These exhibit an astonishing variety of bizarre shell shapes and sculptural types that have no parallel among hitherto known calliostomatids (descriptions in prep.).

#### Genus *FAUTRIX* gen. nov.

Type species: *Fautrix candida* sp. nov.

DIAGNOSIS. — As for the tribe.

REMARKS. — The shells of *Fautrix* species bear a general resemblance to that of the Japanese species *Calliostoma* (*Calotropis*?) *akoya* Kuroda, 1942, type species of *Akoya* Habe, 1961. *Fautrix* species differ, however, in numerous details of teleoconch sculpture, while the radula of *Akoya akoya* is typically calliostomatine and essentially similar to that in *Benthastelena*. *Akoya* may be related to *Otukaia* Ikebe, 1942 but, it might also be a deep water representative of the group typified by *Calliostoma* (s. lat.) *unicum* (Dunker, 1860). See under subfamily diagnosis for additional remarks.

ETYMOLOGY. — Patroness (Latin) (gender feminine).

*Fautrix candida* sp. nov.

Figs 94-96, 98, 140-147, 157; Table 19

TYPE MATERIAL. — Holotype and 2 paratypes MNIN.

TYPE LOCALITY. — S. New Caledonia, SMIB 4, stn DW 60, 23°00' S, 167°22' E, S. New Caledonia, 500-535 m.

MATERIAL EXAMINED. — **New Caledonia.** SMIB 4: stn DW 60, 23°00' S, 167°22' E, 500-535 m, 1 lv (holotype). — Stn DW 61, 23°00' S, 167°22' E, 520-550 m, 1 dd (paratype).

CHALCAL 2: stn DW 76, 23°41' S, 167°45' E, 470 m, 1 lv (paratype).

**S. Norfolk Ridge.** NZOI stn 196, 32°10.8' S, 167°21.2' E, Wanganella Bank, 356 m, 25.7.75, R.V. "Tangaroa", 1 lv (NZOI).**N. New Zealand.** Off Three Kings Islands (ca.100 specimens in 7 lots NMNZ).

DISTRIBUTION (Fig. 157). — Off southern New Caledonia (470-550 m), Wanganella Bank, southern Norfolk Ridge (356 m), and off Three Kings Islands, northern New Zealand (200-805 m), living at 206-535 m.

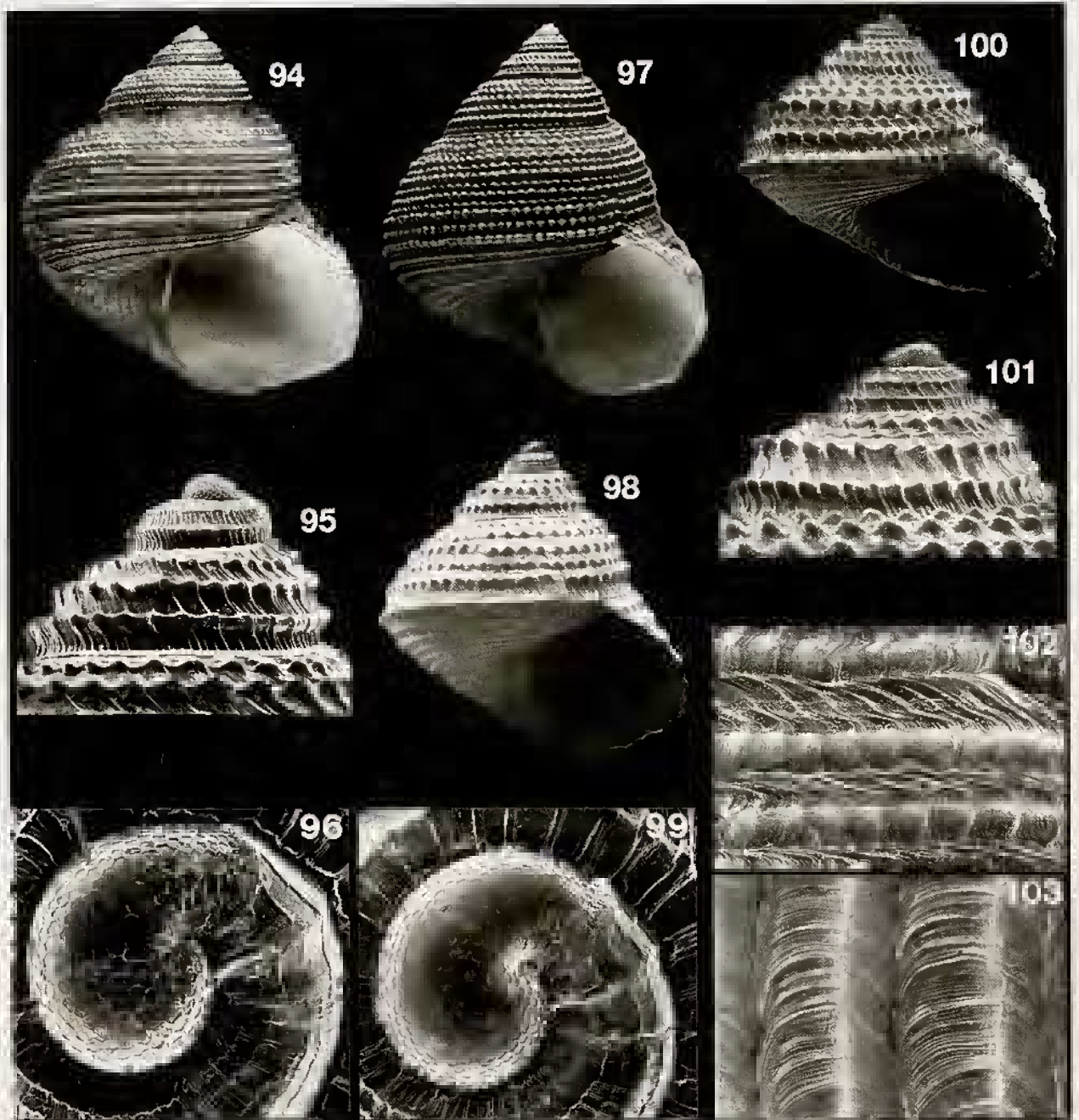
DESCRIPTION. — *Shell* up to 14.0 mm high, glossy, thin, spire broadly conical, weakly cyrtocoenoid 0.93-1.19x as high as aperture, mean spire angle 70-77°, very narrowly umbilicate, translucent white.*Protoconch* 400-420 µm wide, sculptured with dense network of fine crisp threads that enclose roughly hexagonal spaces, apical fold tip broadly rounded, terminal varix strong.*Teleoconch* of up to 5.00 whorls; 1st eighth whorl with crisp spiral threads and strong rounded varix, delineated by growth scar. Whorls strongly convex, periphery rounded; base weakly convex, evenly rounded into umbilicus at maturity. Spiral cords prominent, multiplying by intercalation, stronger on spire than on base; spire spirals with rounded nodules, P4 smooth, inner few basal spirals with rounded nodules, most outer basal spirals becoming weakly or very weakly nodular at maturity. Axial ribs fine, crisp and crowded on 1st half whorl, progressively enlarging and becoming more widely spaced over next full whorl, weakening over next half whorl, becoming obsolete on 3rd whorl. P1-P4 commencing immediately after post larval scar, P2-P4 similar throughout; P1 weaker on 1st whorl, rapidly enlarging to resemble P2-P4; P4 partly covered by succeeding whorls. Secondary spirals enlarging to resemble primaries. S1 commencing immediately or early - late 3rd whorl, S2 commencing late 2nd - late 3rd whorl, S3 commencing early 3rd - early 4th whorl; additional spirals intercalating at

varying positions and orders after 2nd whorl, enlarging to resemble primaries. Base with 8-10 major spiral cords in front of parietal area, others intercalating. Fine collabral growth lines throughout. Aperture subcircular. Outer lip thin at rim, slightly thickened within. Inner lip thick. Parietal inductura extremely thin.

*Animal.* Head very broad, snout broadly rounded in front, fringed with crowded slender papillae. Cephalic tentacles of moderate size, tapered, prominent eyestalks with developed eyes at outer bases. Cephalic lappets small, connected to and extending posteriorly from eyestalks. Left and right neck lobes large, broad. Epipodial tentacles 3 on each side. Foot broad and extremely short.*Radula* (Figs 140-147). Radula ribbon very long, cross-row formula  $\infty + 8-9 + 1 + 9-8 + \infty$ . Central tooth and inner 5 or 6 pairs of lateral teeth thin in section with concave faces, elliptical, tips tapered with irregular ragged edges. Outer 3 pairs of lateral teeth reduced. Marginal teeth similar in shells up to about 3.5 mm in width, slender, thin in section: tips blunt, broad, finely serrate. In larger specimens, inner 8 or 9 pairs of marginal teeth becoming much stouter than outer teeth, leading edge with strong terminal cusp and 4 or 5 smaller subterminal cusps, below them a prominent projection; innermost marginal smaller than adjacent marginals. Innermost marginals continuing to stouten into late ontogeny, terminal cusp becoming relatively much larger, and projection below cusps relatively stronger.TABLE 19. — *Fautrix candida*. Shell measurements (mm) and countings.

H	D	H/D	TW	
06.40	06.45	0.99	4.40	CHALCAL 2: stn DW 76
11.70	10.50	1.11	5.00	SMIB 4: stn DW 61
14.00	13.10	1.07	5.00	Holotype

REMARKS. — *Fautrix candida* is extremely distinctive in its strongly convex whorls, narrow umbilicus, nacreous white shell, crowded axials on the first teleoconch whorl, external anatomy and radular morphology. As described above the adult holotype, a subadult paratype, and a smaller



FIGS 94-103. — Genera *Fautrix* and *Thysanodonta*. — 94, *Fautrix candida*, holotype, 14.0 × 13.1 mm. — 95-96, *F. candida*, paratype, CUALCAL 2: stn DW 76, 95 × 34, 96 × 126. — 97, *F. aquilonia*, holotype, 14.0 × 12.6 mm. — 98, *F. candida*, off Three Kings Islands, New Zealand, 310 m, NMNZ M61466, 4.20 × 4.40 mm. — 99-101, *F. aquilonia*, paratype, MUSORSTOM 4: stn DW 156, 4.80 × 5.20 mm, 99 × 122, 101 × 29. — 102-103, *Thysanodonta eucosmia*, holotype, details of sculpture on last teleoconch whorl (102, × 28) and on base (103, × 67).

specimen from northern New Zealand, exhibit very pronounced differences in inner marginal tooth morphology. All of the specimens examined appear to be indistinguishable in shell morphology, so it would seem that the radula differences in the three different-sized specimens examined represent stages in development within a single species.

ETYMOLOGY. — Latin *candidus* (white).

*Fautrix aquilonia* sp. nov.

Figs 97, 99-101, 157; Table 20

TYPE MATERIAL. — Holotype MNHN. Paratypes: 2 MNHN, 1 NMNZ M262480.

TYPE LOCALITY. — N. New Caledonia, MUSORSTOM 4, stn DW 197, 18°51' S, 163°21' E, 550 m.

MATERIAL EXAMINED. — New Caledonia. MUSORSTOM 4: stn DW 156, 18°54' S, 163°19' E, 525 m, 1 dd (paratype). — Stn DW 197, 18°51' S, 163°21' E, 550 m, 3 dd (holotype and paratypes: 1 MNHN, 1 NMNZ).

DISTRIBUTION (Fig. 157). — Grand Passage, northern New Caledonia, 525-550 m (dead).

DESCRIPTION. — Shell up to 14 mm high, glossy, rather thin, spire broadly conical, weakly cyrtocooid, about 1.09 × as high as aperture at maturity, very narrowly umbilicate, translucent white.

*Protoconch* 400 μm wide, sculptured with dense network of fine, crisp threads that enclose roughly hexagonal spaces, apical fold tip broadly rounded, terminal varix strong.*Teleoconch* of up to 5.75 convex whorls; 1st eighth whorl sculptured with spiral lirae and strong, rounded varix, delineated by growth scar. Periphery rounded, base weakly convex, tightly rounded into umbilicus. Spiral cords prominent, multiplying by intercalation, stronger on spire than on base, nodules crowded, rounded, stronger on spire than on base, especially in juveniles. Axial riblets fine, crisp and crowded on 1st half whorl, progressively enlarging and becoming more widely spaced, weakening and becoming obsolete on 3rd whorl. P1-P4 commencing immediately after

post larval scar, resolving from fine threads, rapidly enlarging, P2-P4 similar throughout; P1 weaker on 1st 3 whorls, thereafter as strong as P2-P4; P4 partly covered by succeeding whorls. Secondary spirals enlarging to resemble primaries. S1 commencing on mid 2nd - mid 3rd whorl, S2 at about mid 3rd whorl, S3 on mid - late 3rd whorl. Tertiary spirals enlarging to resemble primaries and secondaries, a spiral commencing between suture and P1 on early 2nd - mid 4th whorl, additional tertiaries intercalating on mid 4th - early 5th whorl, adult specimen (holotype) with total of 12 spiral cords on spire on penultimate whorl. Base with 9-11, rounded primary spiral cords in front of parietal area, others intercalating. Fine collabral growth lines throughout. Aperture subcircular. Outer lip thin at rim, thickened within. Inner lip thick. Parietal inductura thin.

*Animal* unknown.TABLE 20. — *Fautrix aquilonia*. Shell measurements (mm) and countings.

H	D	H/D	TW	
04.80	05.20	0.92	3.70	MUSORSTOM 4: stn DW 156
06.25	06.00	1.04	4.10	MUSORSTOM 4: stn DW 197
07.45	07.90	0.94	4.60	MUSORSTOM 4: stn DW 197
14.00	12.60	1.11	5.75	Holotype

REMARKS. — *Fautrix aquilonia* differs from the southern New Caledonian species *F. candida* in having stronger, more strongly nodular spiral cords on the teleoconch, a thicker, heavier shell, and a tighter sculptural network on the protoconch.ETYMOLOGY. — Latin *aquilonius* (northern).

## Subfamily THYSANODONTINAE Marshall, 1988

REMARKS. — Members of Thysanodontinae are highly distinctive in having exceedingly slender, hair-like radular teeth tipped with backwardly inclined barbs (Figs 148-149). A distinctive feature of the shell not noted in the original diagnosis concerns the collabral growth lines, which are at first rather evenly prosocline on the spire and opisthocyrte on the base. With increasing shell size the growth lines on the spire become more or less orthocline on the spiral cords, and increasingly

strongly prosocline in the spiral interspaces (Fig. 102). The basal growth lines become sharply serrated, each serration coinciding with a sharply incised spiral groove on the summit or inner slope of or between each spiral cord; the growth lines between the serrations are opisthocyrt (Fig. 103). The profile of the apertural rim in adults (damaged in all material) is thus strongly stepped — prosocline on the spire and sharply scalloped on the base. The growth lines in Calliostomatini and Fautricini are either rather evenly prosocline on the spire and opisthocyrt on the base, or at most weakly undulant, and basal grooves are absent. The group is further characterized by the presence of a single prominent submedian carina (P3) on the first 1.5-2.5 whorls (Figs 105, 108, 111, 114), though some species of *Bathyfautor* gen. nov. are similarly sculptured.

Genus *Thysanodonta* Marshall, 1988

*Thysanodonta* Marshall, 1988: 217. Type species (OD): *Thysanodonta aucklandica* Marshall, 1988; Recent, New Zealand.

*Thysanodonta boucheti* Marshall, 1988

Fig. 158; Table 21

*Thysanodonta boucheti* Marshall, 1988: 219, figs 3G-I.

TYPE MATERIAL. — Holotype MNHN.

TYPE LOCALITY. — N. New Caledonia, LAGON, stn 444, Atoll de Surprise, 18°15' S, 162°59' E, 300-350 m.

MATERIAL EXAMINED. — **New Caledonia.** LAGON: stn 444, 18°15' S, 162°59' E, 300-350 m, 1 dd (holotype).

MUSORSTOM 4: stn DW 197, 18°51' S, 163°21' E, 550 m, 5 dd (MNHN, NMNZ M262477).

BIOCAL: stn DW 77, 22°15' S, 167°15' E, 440 m, 1 dd.

DISTRIBUTION (Fig. 158). — Northern and southern New Caledonia, 300-550 m (dead).

TABLE 21. — *Thysanodonta boucheti*. Shell measurements (mm) and countings (LAGON: stn 444, BIOCAL: stn DW 77, MUSORSTOM 4: stn DW 197).

Character	<i>n</i>	Range	Mean	SD
H	6	4.95-8.90	6.78	1.60
D	6	4.00-6.95	5.20	1.19
H/D	6	1.15-1.42	1.30	0.10
TW	6	5.25-6.75	6.05	0.54

REMARKS. — The only specimen known from southern New Caledonia (BIOCAL: stn DW 77) differs from the holotype and other northern specimens in being slightly more broadly conical, in being slightly larger relative to the number of whorls, and in having a stronger, more strongly nodular P4 (Table 21). In the absence of material from intermediate localities it is impossible to ascertain the status of this specimen, but it is tentatively interpreted as a regional variant of *T. boucheti*.

*Thysanodonta festiva* sp. nov.

Figs 104-106, 158

TYPE MATERIAL. — Holotype (6.60 × 4.60 mm, 6.90 TW) and 1 paratype dd (7.40 × 5.00 mm, 7.25 TW) MNHN.

TYPE LOCALITY. — S. New Caledonia, CHALCAL 2, stn DW 71, 24°42' S, 168°10' E, 230 m.

MATERIAL EXAMINED. — Only known from the type material.

DISTRIBUTION (Fig. 158). — Northern Norfolk Ridge, 230 m, dead.

DESCRIPTION. — *Shell* up to 7.40 mm high, glossy, stout, spire narrowly and evenly conical, 1.83-2.11x as high as aperture, mean spire angle 42-44°, anomphalous.

*Colour* of apical fold tip and adapical extremity of protoconch brown, protoconch elsewhere white. First 1.5 teleoconch whorls translucent dull mauve. Next 1.5 whorls with irregularly broken brown bands on P1-P3 and S2, P4 white with brown spots between nodules. Subsequent whorls either with much paler, gradually fading pigmentation on P1-P3 and S2, and white on S3, the spiral below it with few scattered brown spots; or white with S3 and spiral below it pale brown. Base either uniform white or with few narrow pale brown axial bands.

*Protoconch* 370 µm wide, sculptured with dense network of fine, crisp threads that enclose roughly hexagonal spaces, apical fold tip rounded, terminal varix strong.

*Teleoconch* of up to 7.25 whorls, 1st eighth whorl with crisp spiral threads, delineated by strong, rounded varix and growth scar. First whorl submedially angulated at P3, angulation weakening and vanishing on 2nd whorl, subsequent whorls flat, suture flush, periphery rounded, base

weakly convex. Spiral cords prominent, spire spirals with rounded nodules; P3 and P4 commencing immediately after post larval scar. P3 strong throughout; P4 weak, becoming fully fused with S3. P1, P2, S2 and S3 resolving on 2nd whorl, P1, P2 and S2 rapidly enlarging to resemble P3; S3 larger than others on 2nd and 3rd whorl, bifurcating on 3rd whorl to form 2 nodular spirals similar to P3. Axial costae strong and widely spaced on 1st 2 whorls, weaker, closer and becoming obsolete on 3rd whorl. Base with 8 or 10 strong, rounded similar, smooth spiral cords, each sharply grooved on inner slope. First and early 2nd whorl with fine, crisp spiral threads. Collabral growth lines on spire prosocline on early whorls, with increasing shell size becoming more or less orthocline on spiral cords and increasingly strongly prosocline between spirals. Basal collabral growth lines sharply serrated, the serrations coinciding with grooves on inner slopes of each spiral, opisthocyrt between serrations. Aperture subquadrate. Outer lip thin at rim, thickened within. Inner lip thick. Parietal inductura thin.

*Animal* unknown.

REMARKS. — *Thysanodonta festiva* differs from *T. boucheti* in being coloured instead of uniform white, in being more narrowly conical, and in having finer nodules, and 6 instead of 4 spiral cords on the adult spire whorls.

*Thysanodonta chesterfieldensis* sp. nov.

Figs 107-109, 154

TYPE MATERIAL. — Holotype (3.60 × 2.85 mm, 5.00 TW) and 1 paratype MNHN.

TYPE LOCALITY. — Chesterfield Islands, MUSORSTOM 5, stn 345, 19°40' S, 158°32' E, 305-310 m.

MATERIAL EXAMINED. — **Chesterfield Islands**, MUSORSTOM 5: stn 345, 19°40' S, 158°32' E, 305-310 m, 1 dd (holotype). — Stn 362, 19°53' S, 158°40' E, 410 m, 1 dd (paratype).

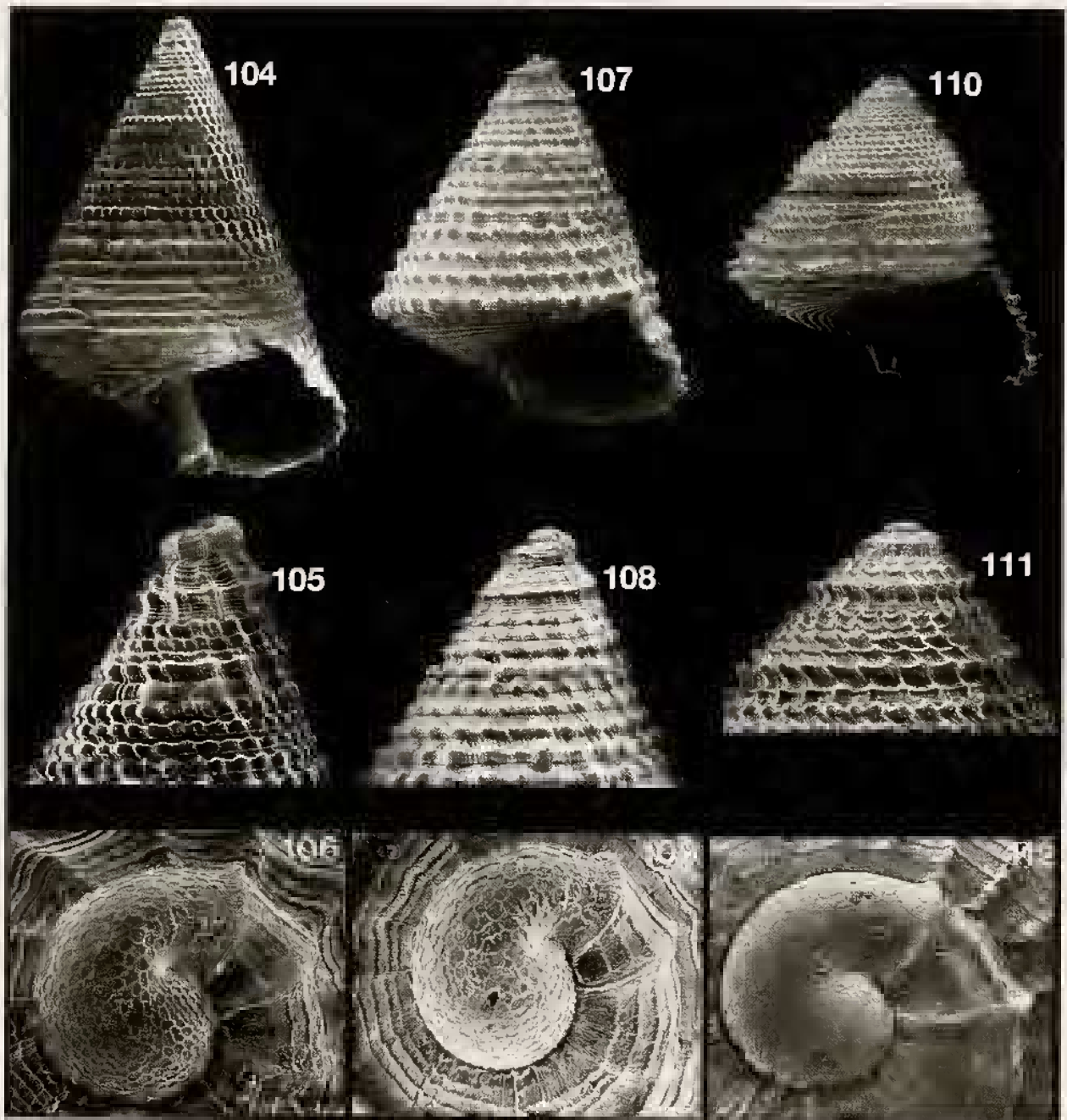
DISTRIBUTION (Fig. 153). — Off Chesterfield Islands, 305-410 m (dead).

DESCRIPTION. — *Shell* (immature holotype) 3.60 mm high, glossy, stout, spire narrowly conical, 1.77x higher than aperture, mean spire angle 52°, anomphalous.

*Colour* of adapical half of protoconch pale brown, elsewhere white. Subsequent whorls translucent white; P4 with reddish brown spots, scattered reddish spots on other spire spirals. Base translucent white.

*Protoconch* 370 µm wide, sculptured with dense network of fine, crisp threads that enclose roughly hexagonal spaces, apical fold tip rounded, terminal varix strong.

*Teleoconch* of 5.10 whorls; 1st eighth whorl with crisp spiral threads, delineated by strong, rounded varix and growth scar. First whorl submedially angulated at P3, angulation weakening and vanishing on 2nd whorl; subse-



Figs 104-112. — Genus *Thysanodonta*. — 104-106, *Thysanodonta festiva*, holotype, 6.60 × 4.60 mm, 105 × 28, 106 × 126. — 107-109, *T. chesterfieldensis*, holotype, 3.60 × 2.85 mm, 108 × 26, 109 × 126. — 110-111, *T. opima*, holotype, 9.10 × 8.80 mm, 111 × 18. — 112, *T. opima*, paratype, BIOCAL: stn DW 70, × 112.

quent whorls flat, suture flush, periphery angulated at P4, base weakly convex. Spiral cords prominent, rounded, P1-P4 with rounded nodules, basal spirals weaker, almost smooth; axial costae gradually resolving on 1st whorl, strong on 2nd whorl, weakening until obsolete on 3rd whorl. P3 and P4 commencing immediately after post larval scar; P3 strong throughout; P1 and P2 resolving early on 2nd whorl, rapidly enlarging to resemble P3; P4 either resembling P1-3 (paraty-

pe) or with weak median groove from mid 2nd whorl (holotype). Base with 8 similar, rounded spiral cords. First whorl with crisp spiral threads, becoming obsolete on 1st half of 2nd whorl. Fine collabral growth lines throughout, prosocline on spire, opisthocyrt on base. Aperture subquadrate. Outer lip thin at rim, thickened within. Inner lip thick. No parietal inductura.

*Animal unknown.*



REMARKS. — *Thysanodonta chesterfieldeensis* resembles *T. festiva* in having a colour pattern, yet differs from that species and resembles *T. boucheti* in having only 4 spiral cords on the spire whorls. It differs further from *T. boucheti* in having a more open network of hexagons on the protoconch, and in having axial sculpture on the early teleoconch that is less crisply defined.

*Thysanodonta opima* sp. nov.

Figs 110-112, 158

TYPE MATERIAL. — Holotype (9.10 × 8.80 mm, 5.75 TW) and 1 paratype (4.20 × 4.40 mm, 3.80 TW) MNHN.

TYPE LOCALITY. — S. New Caledonia, BIOCAL, stn DW 48, 23°00' S, 167°29' E, S, 775 m.

MATERIAL EXAMINED. — New Caledonia. BIOCAL: stn DW 48, 23°00' S, 167°29' E, 775 m, 1 dd (holotype). — Stn DW 70, 23°25' S, 167°53' E, 965 m, 1 dd (paratype).

DISTRIBUTION (Fig. 158). — South of Ile des Pins, southern New Caledonia, 775-965 m, dead.

DESCRIPTION. — Shell up to 9.10 mm high, glossy, stout, spire broadly conical, 1.36 × as high as aperture (adult); mean spire angle (adult) 62°, narrowly umbilicate, white.

Protoconch 350-370 μm wide, surface worn, apical fold tip rounded, terminal varix strong.

Teleoconch of up to 5.75 whorls; 1st eighth whorl with crisp spiral threads, delineated by strong, rounded varix and growth scar. First whorl submedially angulated at P3, angulation weakening on 2nd whorl, subsequent whorls weakly convex, suture almost flush; periphery angulated at P4, becoming tightly rounded on last adult whorl, base weakly convex. Spiral cords prominent, rounded, spire spirals with rounded nodules, basal spirals very weakly nodular at maturity; axial costae gradually resolving on 1st whorl, strong on 2nd and 3rd whorls, weakening on 4th whorl, obsolete thereafter. P3 and P4 commencing immediately after

post larval scar, P3 strong throughout; P4 weakest, entirely covered by succeeding whorls. P1 and P2 resolving on 2nd whorl, S1 and S2 late 2nd - early 3rd whorl, S3 late 2nd - start 3rd whorl, all gradually enlarging to resemble P3. Adult base with 11 strong, similar, rounded, medially grooved spiral cords. Shoulder on 1st 1.5 whorls with numerous fine, crisp spiral threads. Collabral growth lines on spire prosocline on early whorls, with increasing shell size becoming more or less vertical on spiral cords and increasingly strongly prosocline between spirals. Basal collabral growth lines sharply serrated, the serrations coinciding with grooves at summits of each spiral, opisthocyrt between serrations. Umbilical rim tightly rounded. Aperture subquadrate. Outer lip rim broken away, thickened. Inner lip of moderate thickness, overhanging umbilicus. Parietal inductura thin.

Animal unknown.

REMARKS. — *Thysanodonta opima* is distinctive among *Thysanodonta* species in having a uniform white shell, a broadly conical spire, and an umbilicus.

ETYMOLOGY. — Well-fed (Latin).

*Thysanodonta eucosmia* sp. nov.

Figs 113-115, 148-149, 158

TYPE MATERIAL. — Holotype (12.0 × 9.00 mm, 7.00 TW) MNHN. Paratypes: 47 MNHN, 1 AMS C201710, 1 BMNH 1995.017, 1 NMP, 1 NMNZ M262478, 1 USNM.

TYPE LOCALITY. — S. New Caledonia, BIOCAL, stn DW 33, 23°10' S, 167°10' E, 675-680 m.

MATERIAL EXAMINED. — All type material. New Caledonia. BIOCAL: stn DW 33, 23°10' S, 167°10' E, 675-680 m, 10 dd (holotype and paratypes: 5 MNHN, 1 AMS, 1 BMNH, 1 NMP, 1 USNM). — Stn DW 36, 23°09' S, 167°11' E, 650-680 m, 3 dd (paratypes). — Stn DW 46, 22°53' S, 167°17' E, 570-610 m, 13 dd (paratypes). — Stn DW 48, 23°00' S, 167°29' E, 775 m, 4 dd (paratypes). — Stn DW 51, 23°05' S, 167°45' E, 680-700 m, 5 lv (paratypes: 4 MNHN, 1 NMNZ). — Stn DW 66, 24°55' S, 168°22' E, 505-515 m, 2 dd (paratypes).



FIGS 113-115. — Genus *Thysanodonta*. *Thysanodonta eucosmia*, holotype, 12.0 × 9.00 mm, 115 × 135.

MUSORSTOM 4: stn DW 220, 22°58' S, 167°38' E, 505-550 m, 2 dd (paratypes). — Stn DW 222, 22°58' S, 167°33' E, 410-440 m, 1 dd (paratype). — Stn DW 223, 22°57' S, 167°30' E, 545-560 m, 1 dd (paratype).

CHALCAL 2: stn DW 76, 23°41' S, 167°45' E, 470 m, 5 lv (paratypes). — Stn DW 77, 23°38' S, 167°43' E, 435 m, 2 dd (paratypes).

SMIB 3: stn DW 1, 24°56' S, 168°22' E, 520 m, 2 dd (paratypes). — Stn DW 22, 23°03' S, 167°19' E, 503 m, 1 dd (paratype). — Stn DW 24, 22°59' S, 167°21' E, 503 m, 2 dd (paratypes).

DISTRIBUTION (Fig. 158). — Northern Norfolk Ridge, 410-775 m, living at 470-700 m.

DESCRIPTION. — *Shell* up to 12.0 mm, glossy, rather thin but strong; spire conical, 1.37-2.42x as high as aperture; mean spire angle 40-60°, anomphalous, translucent white.

*Protoconch* 350-400  $\mu$ m wide, sculptured with dense network of fine, crisp threads that enclose roughly hexagonal spaces, apical fold tip rounded, terminal varix strong.

*Teleoconch* of up to 7.00 whorls; 1st eighth whorl with crisp spiral threads, delineated by strong, rounded varix and growth scar. First 1.5 whorls sharply submedially angulated at P3, angulation weakening on next half whorl, subsequent whorls weakly convex or flat; periphery angulated at P4, becoming rounded at maturity; base weakly convex. Spiral cords prominent, rounded; axial costae fine on 1st whorl, gradually enlarging, strong on 2nd and 3rd whorl, becoming obsolete on 4th whorl. P3 and P4 commencing immediately after post larval scar; P3 very prominent, flange-like and adapically upturned on 1st 1.5 whorls, becoming less prominent on next half whorl, though remaining strong throughout; P4 partly covered by succeeding whorls; P1 and P2 commencing at about end of 2nd whorl, rapidly enlarging to resemble P3 and P4. S1 and S2 and frequently an extra spiral

commencing more or less simultaneously with P1 and P2, resembling them throughout; S3 commencing on about mid 2nd whorl, rapidly enlarging to resemble others. Additional spirals intercalate on or after 4th whorl so that there are 9-11 similar spiral cords on adult penultimate whorl. Nodules rounded on spire, much finer on base. Base with 9-13 strong, rounded, similar spiral cords, separated by sharply incised grooves, each spiral cord divided into 2 sectors by sharply defined step. Minute granules throughout. Collabral growth lines on spire prosocline on early whorls, with increasing shell size becoming more or less vertical on spiral cords and increasingly strongly prosocline between spirals. Basal collabral growth lines sharply serrated, the serrations coinciding with grooves between each spiral cord, opisthocyrt between serrations. First 1.5-2 whorls with numerous fine, crisp spiral threads. Aperture subcircular. Outer lip thin at rim, weakly thickened within, rarely thick. Inner lip moderately thickened. Parietal inductura very thin, translucent.

*Animal* unknown (dried).

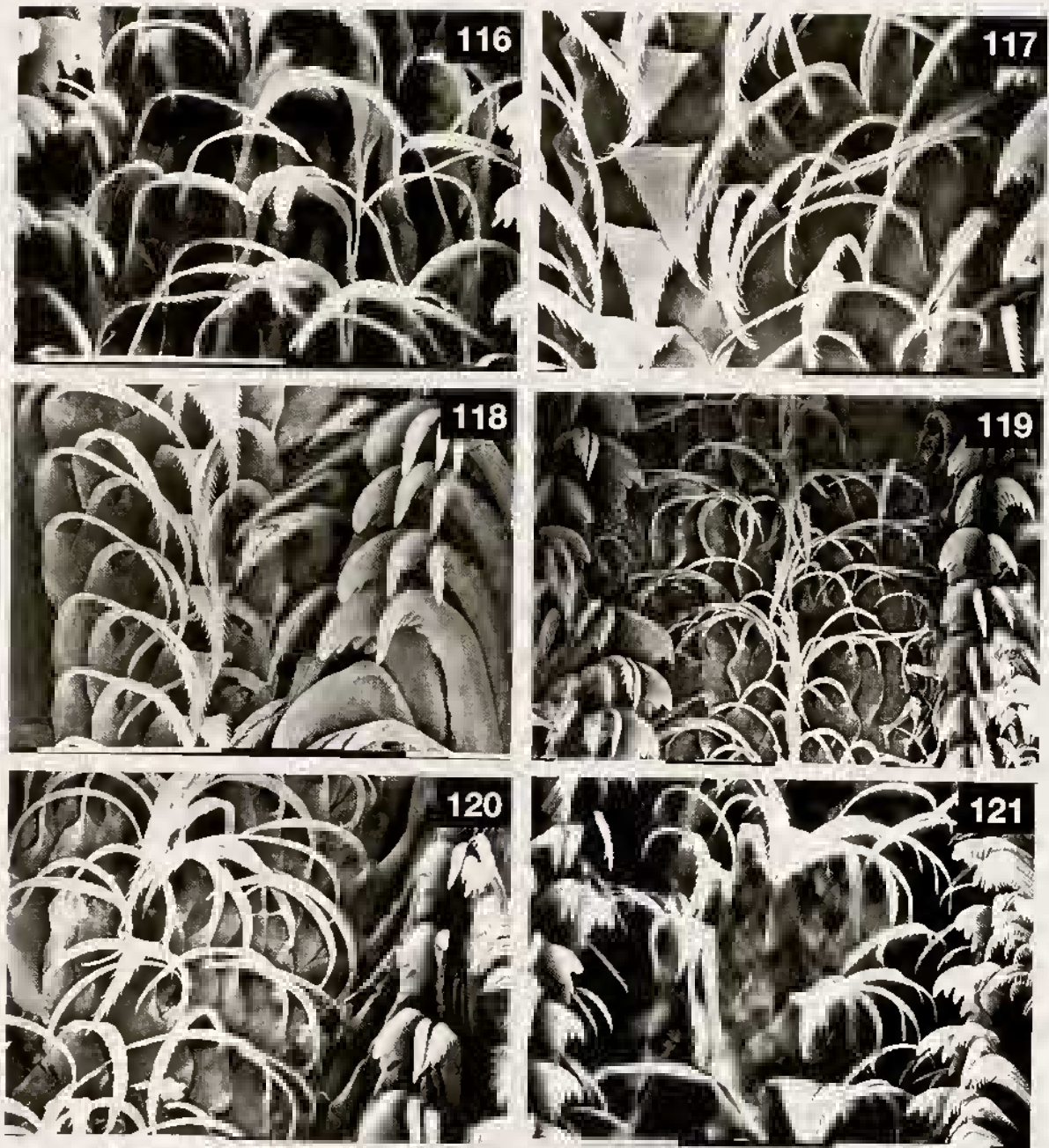
*Radula* (Figs 148-149) 6.50 mm long and 167  $\mu$ m wide, teeth typical of the subfamily.

TABLE 22. — *Thysanodonta eucosmia*. Shell measurements (mm) and countings (BIOCAL: stns DW 33, DW 48, DW 51, DW66, MUSORSTOM 4: stns DW 220, DW 222, DW 223, CHALCAL 2: stns DW 76, DW 77).

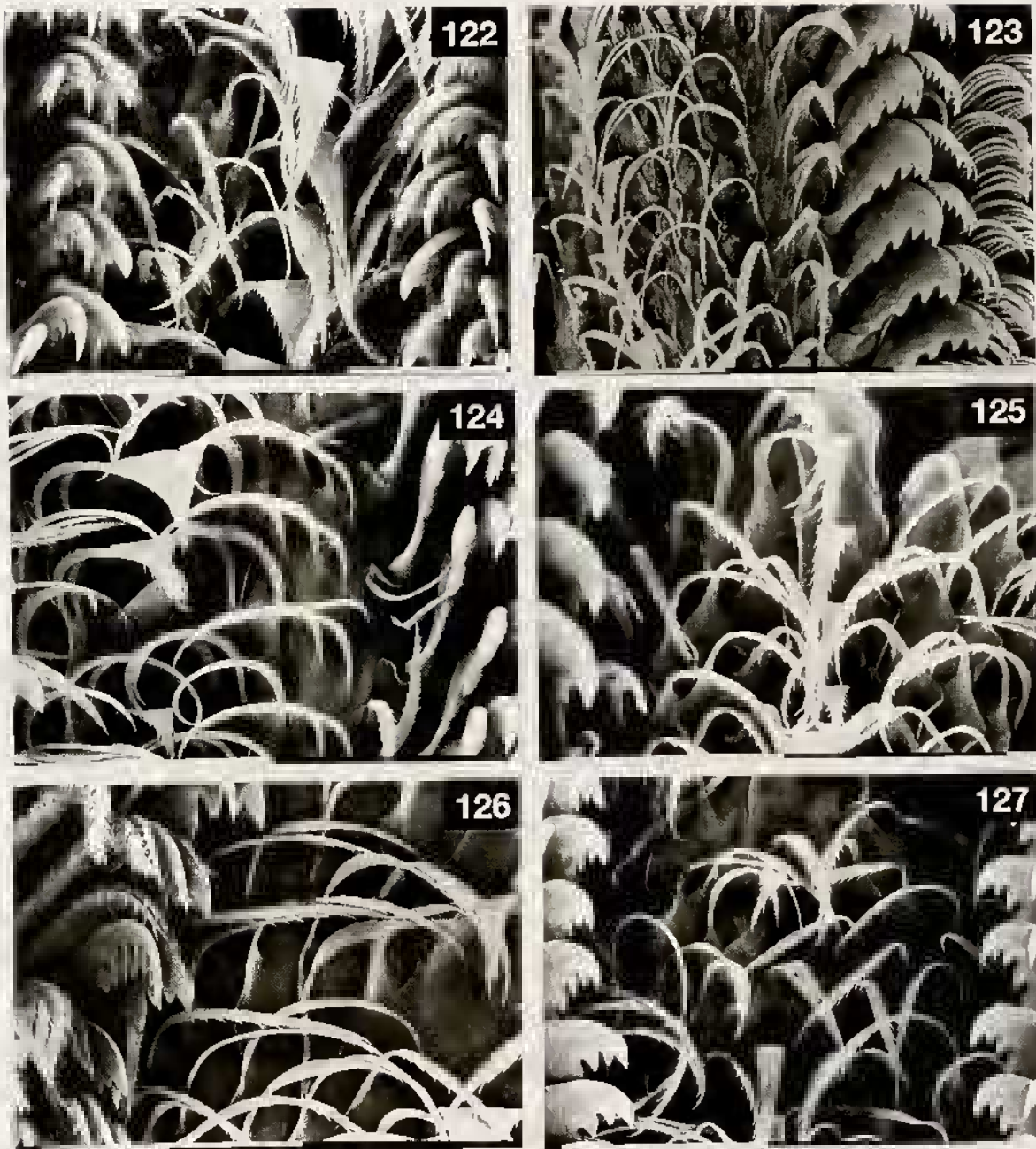
Character	n	Range	Mean	SD
H	15	5.35-12.00	7.91	1.94
D	15	4.35-09.00	6.28	1.44
H/D	15	1.16-01.47	1.26	0.09
TW	15	5.25-07.00	6.02	0.54

REMARKS. — *Thysanodonta eucosmia* is characterised by its numerous, narrow, finely nodular spire spirals, and in being covered with minute granules. Unlike other known *Thysanodonta* species, the basal grooves are situated on the inner sides of the spiral cords, rather than on their summits or inner slopes.

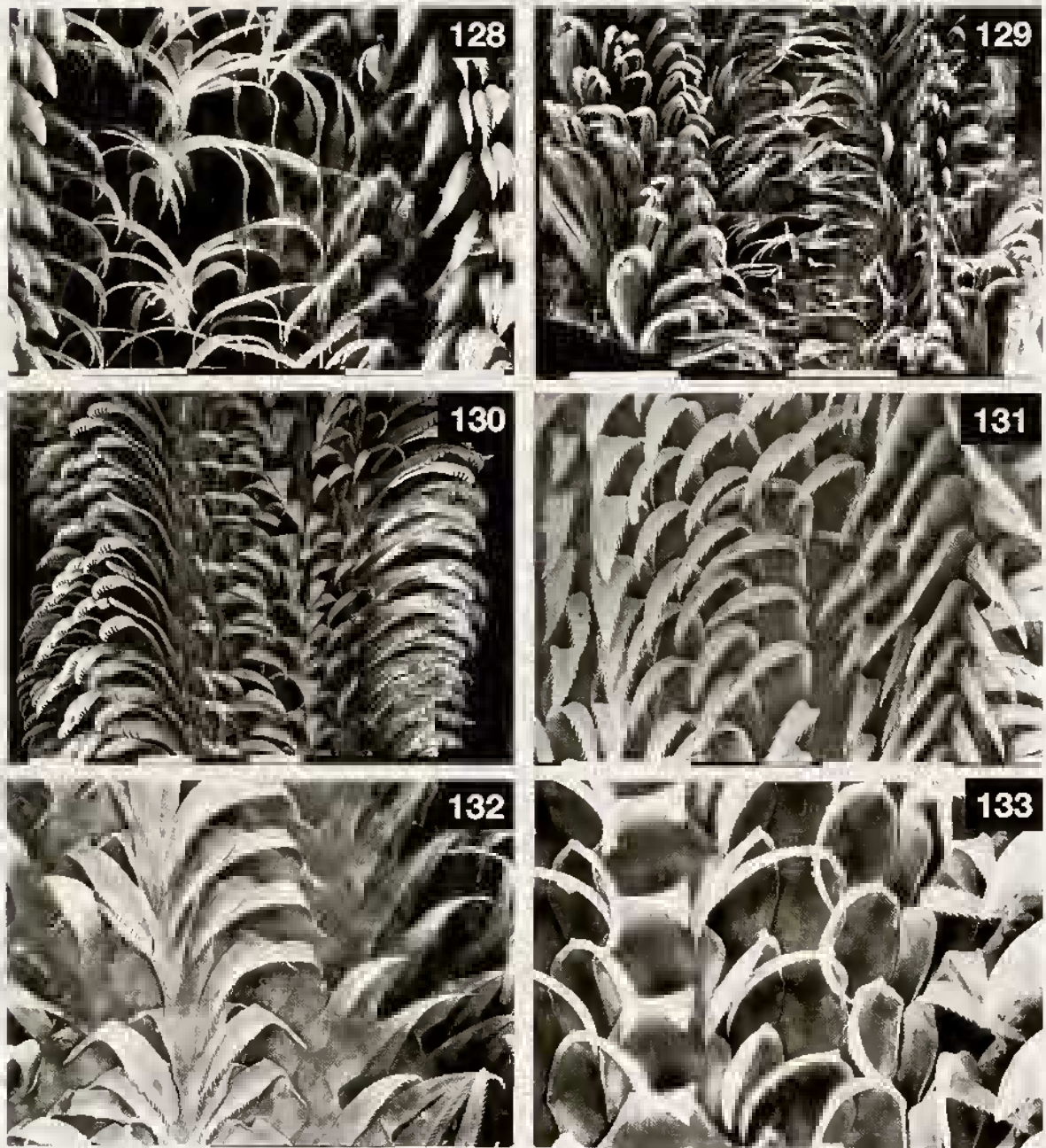
ETYMOLOGY. — Beautiful ornament (Greek).



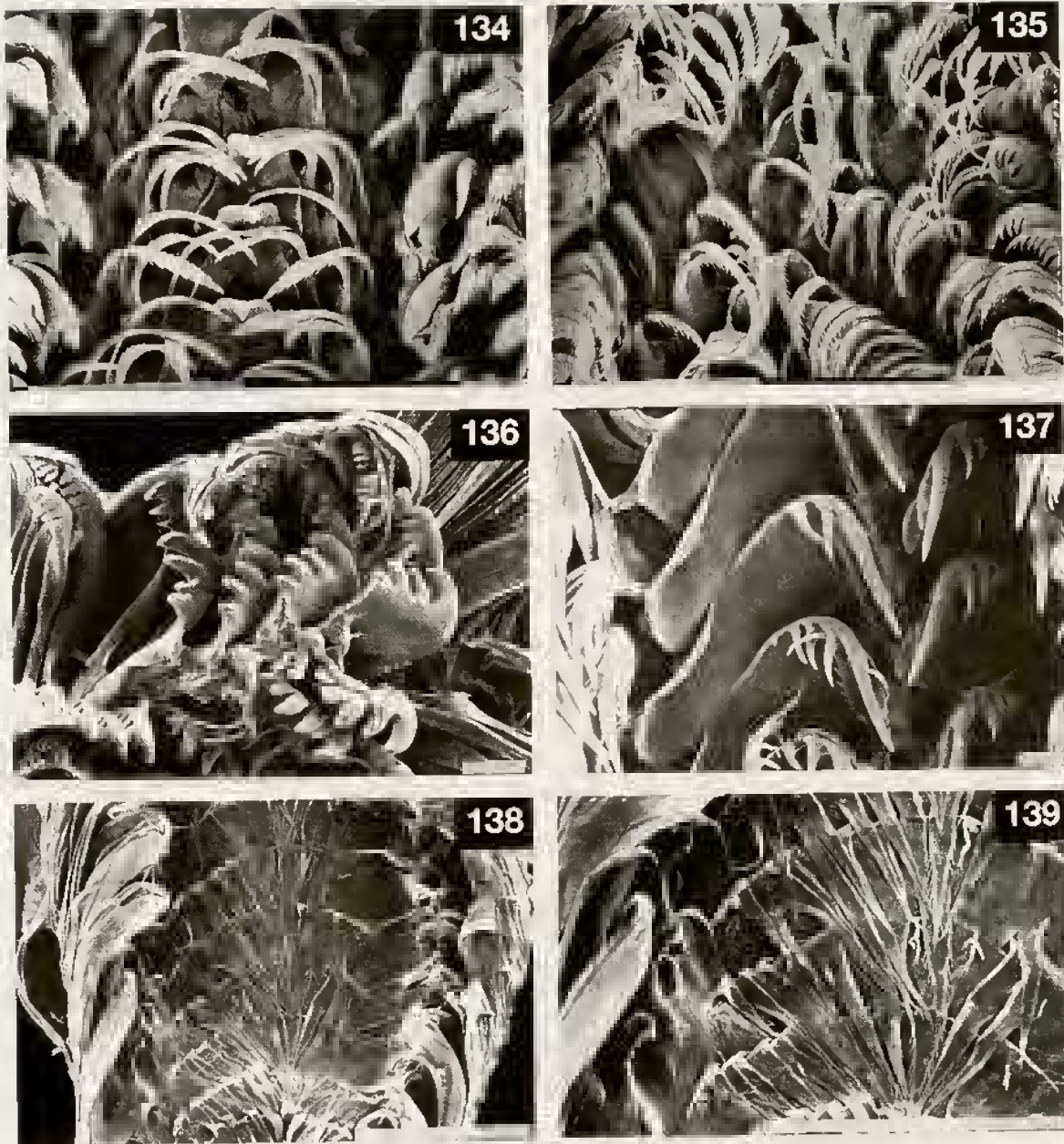
FIGS 116-121. — Central fields of adult radulae. — 116, *Calliostoma (Fautor) comptum*, off Sydney, New South Wales, AMS C161945. — 117, *C. (F.) boucheti*, ex paratype, CHALCAL 2: stn DW 74. — 118, *C. (F.) richeri*, ex paratype, LAGON: stn 352. — 119, *C. (F.) paradigmatum*, ex holotype. — 120, *C. (F.) metivieri*, ex holotype. — 121, *C. (F.) necopinatum*, ex paratype, LAGON: stn 444. Scale bars = 100  $\mu$ m.



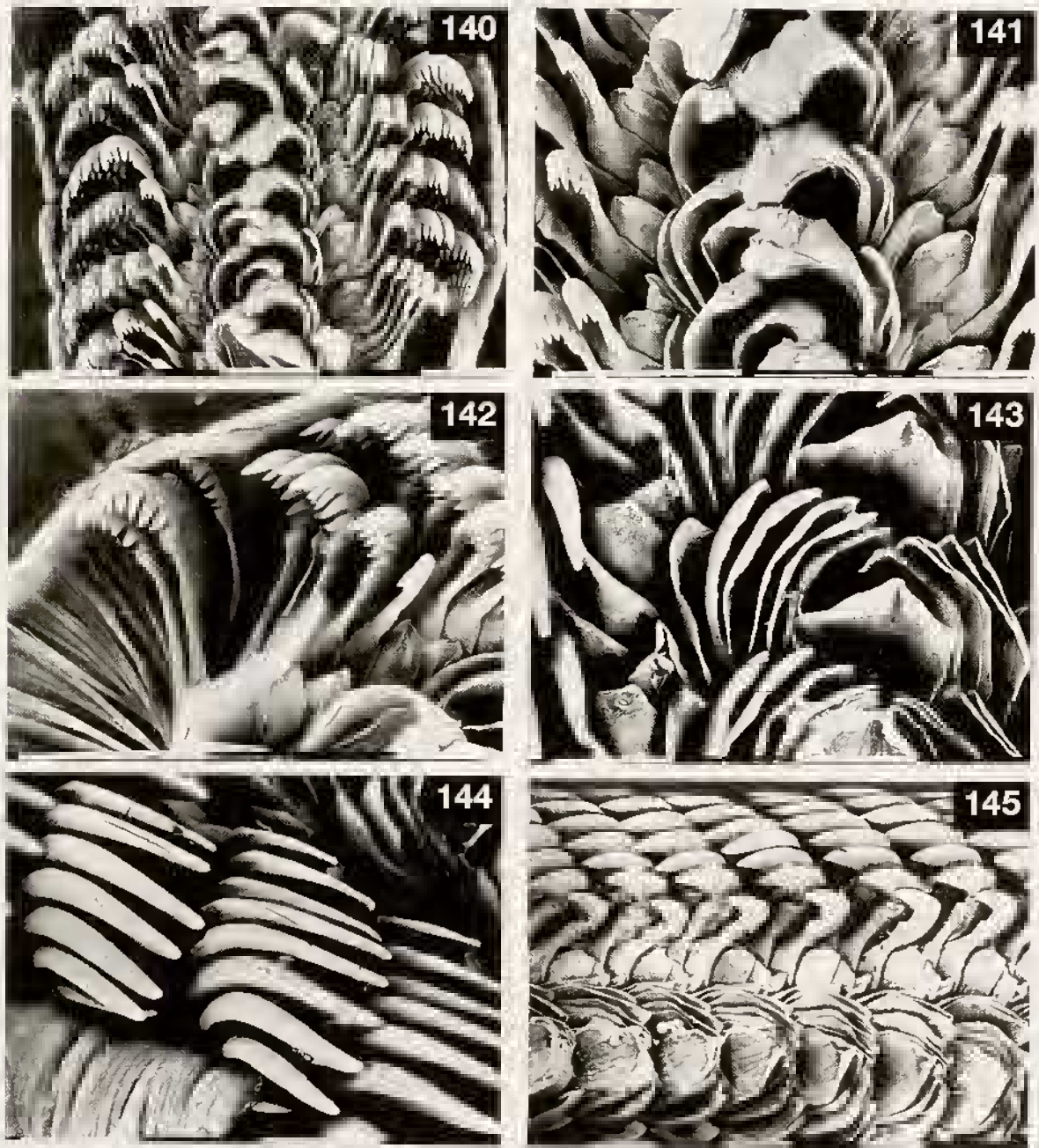
FIGS 122-127. — Central fields of adult radulae. — 122, *Calliostoma (Fautor) houbricki*, ex holotype. — 123, *C. (F.) periglypinum*, ex paratype, CHALCAL 2; stn DW 71. — 124, *C. (F.) chesterfieldense*, ex holotype. — 125, *C. (Benthastelena) katherina*, off Little Bay, Sydney, 183-192 m, AMS C152389. — 126, *C. (B.) diademanum*, ex holotype. — 127, *C. (B.) cristatum*, ex paratype, MUSORSTOM 4; stn DW 234. Scale bars = 100  $\mu$ m.



FIGS 128-133. — Adult radulae, full widths (129, 130) and central fields. — 128, *Calliostoma (Benthastelena) coronatum*, ex paratype, LAGON: stn 394. — 129, *C. (Anipullostochus) xanthos*, MUSORSTOM 6: stn DW 459. — 130, *C. (A.) peregrinum*, ex holotype. — 131, *C. (A.) heros*, ex holotype. — 132, *C. (A.) alisi*, ex holotype. — 133, *Bathyfautor rapuhia*, ex holotype. Scale bars = 100  $\mu$ m.

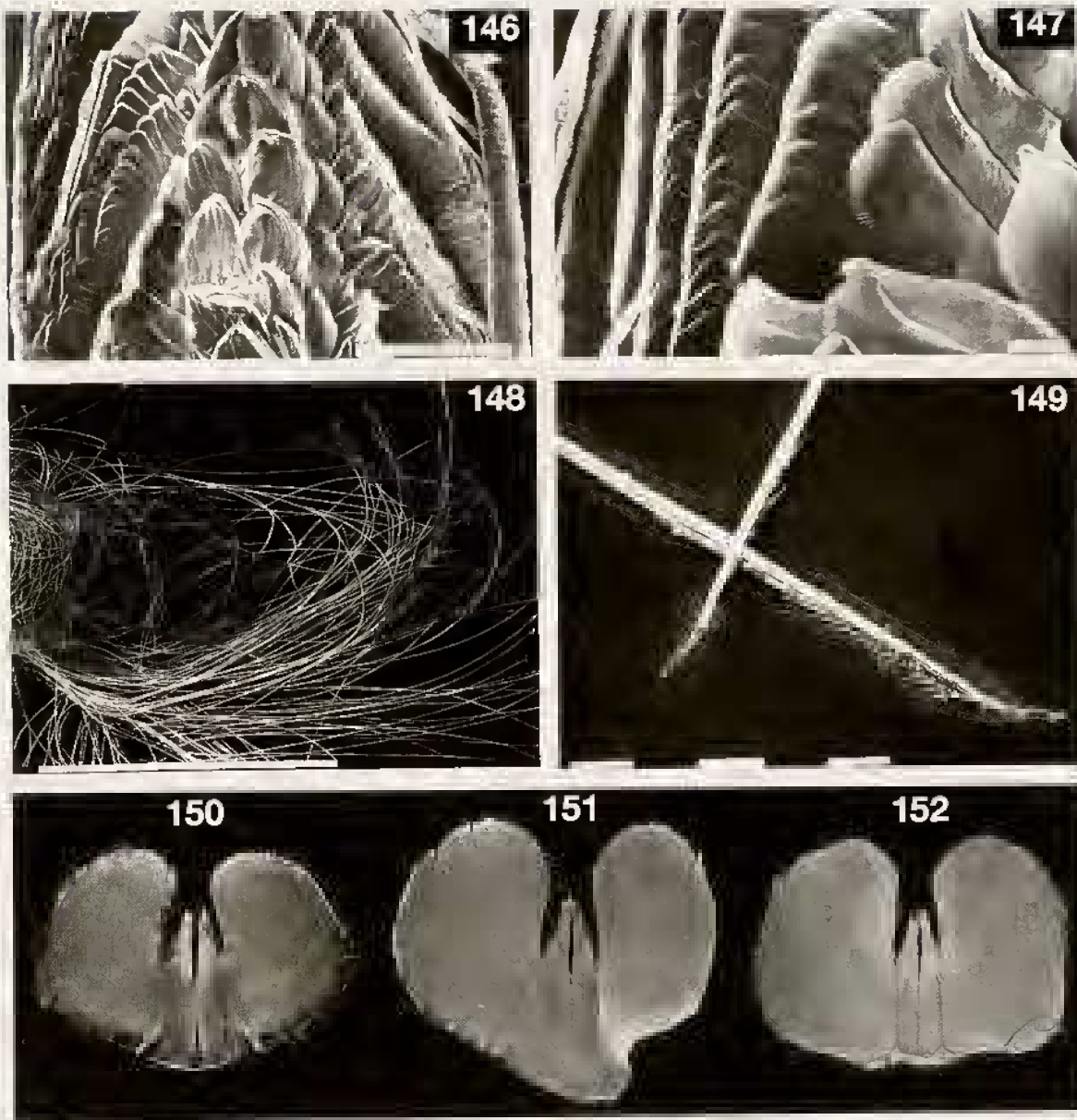


FIGS 134-139. — Radulae, central fields. — 134, *Bathysfautor caledonicus*, ex adult paratype, MUSORSTOM 4; stn DW 160. — 135, *Dactylastele poupineli* adult, off Barren Island, Queensland, 8 m, AMS C154352. — 136, *Laetifautor trepidus*, ex adult paratype, off Mast Head Reef, Queensland, 31-36 m, AMS C102804. — 137, *Laetifautor spinulosus*, adult, off Cape Donnington, South Australia, 18 m, NMNZ M237113. — 138-139, *Selastele ouustum*, off Three Kings Islands, northern New Zealand, 102 m, shell height 3.65 mm, NMNZ M34251. Scale bars 136, 137 = 10  $\mu$ m, others = 100  $\mu$ m.



Figs 140-145. — Radulae, *Faurix candida*. — 141-142, ex paratype, shell height 6.40 mm, CHALCAL 2: stn DW 76; note sharp transition between inner marginals and blunt — tipped, finely serrate outer marginals in figure 142. — 143-145, ex holotype, shell height 14.0 mm; note sharp transition between inner and outer marginals (Fig. 144), and enlarged terminal cusp on inner marginals (Fig. 145). Scale bars = 100  $\mu$ m.





FIGS 146-152. — Radulae and jaws. — **146-147**, *Fautrix candida*, radula *ex* shell 3.30 × 3.40 mm, off Three Kings Islands, northern New Zealand, 221-206 m, NMNZ M80659; note smooth morphological gradation through lateral and marginal teeth. — **148-149**, *Thysanodonta eucosmia*, radula *ex* adult paratype, CHALCAL 2; stn DW 76. — **150**, *Calliostoma (Fautor) bouchetti*, jaws *ex* paratype, CHALCAL 2; stn DW 74, × 35. — **151**, *C. (F.) vaubani*, jaws *ex* paratype, MUSORSTOM 4; stn DW 181, × 63. — **152**, *C. (Benthastelena) katherina*, off Little Bay, Sydney, 183-192 mm, AMS C152389, × 53. Scale bars 146 = 100 μm, 147 = 10 μm, 148 = 1 mm, 149 = 10 μm.

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Most of the few calliostomatid species reared in aquaria laid gelatinous egg masses, passed through a brief intracapsular veliger larval stage, and hatched as crawling young (ROBERT, 1902; LEBOUR, 1936; RAMON, 1990). *Calliostoma ligatum* (Gould, 1849) is known to be a broadcast spawner and to have a brief planktonic larval stage (HOLYOAK, 1988), which, together with the existence of a few species at exceptionally remote localities, indicates that at least some calliostomatids have more than minimal potential for dispersal by ocean currents. From a general standpoint, however, the majority of species evidently have rather limited potential for long distance dispersal in the plankton.

In the tropical and subtropical western Pacific, the only calliostomatids known to occur at localities separated by depths too great for the species and distances greater than 500 km are *Calliostoma (Benthastelena) tosaense*, *C. (Ampullostrochus) xanthos*, *C. (A.) peregrinum*, and *Dactylastele poupineli*. These species evidently owe their distributions to a drifting larval period of exceptional duration for the family. The other widely though patchily distributed species, *Laetifauctor rubropunctatus* and perhaps *Coralastele punctocostatum* (if *C. allanae* is a synonym), may eventually prove to have a more or less continuous distributions between Japan and Queensland via the Nansei Chain, the Philippines, and New Guinea. Of these six widely distributed species, three are intimately associated with coral reefs (*D. poupineli*, *L. rubropunctatus*, and *C. punctocostatum*).

The family is very poorly represented in the central Pacific. The only coral reef-associated calliostomatids known from the western-central Pacific east of longitude 150° E in the northern hemisphere and longitude 170° E in the southern hemisphere are respectively two apparently undescribed species from Kwajalein, Marshall Islands (JOHNSON 1990, 1991 — specimens NMNZ) and *Dactylastele poupineli* from Fiji (NMNZ). The only other calliostomatids known from the tropical and subtropical Pacific east of Melanesia and west of central America are *Calliostoma margaritissimum* Habe & Okutani, 1968 (off Midway Island, ca. 480 m), *C. imperialis* Kosuge, 1979 (NE off Midway Island, ca. 1000 m), and *C. doncorni* Kay, 1979 (off Hawaii, 250-280 m) — incidentally *Omphalotukaia midwayensis* Lan, 1990 is a species of *Calliotropis* Seguenza, 1903 (Trochidae, Eucyclinae). All of these species are known only from the localities mentioned.

My own (unpublished) studies of the Australian Recent and rich Tertiary calliostomatid fauna reveal that it is comprised almost entirely of archaic groups — mainly Fautricini and the *Astele* group — and that there is little evidence of inward or outward range expansions of respectively derived or old groups.

Of the distributional patterns revealed during the present study, one of the most striking is that of *Calliostoma (Benthastelena) katherina*, *C. (B.) diadematum*, *C. (B.) cristatum*, and *C. (B.) coronatum*, which occupy roughly parallel distributional arcs (Figs 154, 156). *C. (B.) katherina* (off Queensland coast) and *C. (B.) diadematum* may have originated from parent stock isolated by the opening of the Tasman Sea (Late Cretaceous — Late Paleocene) (KAMP, 1986). The absence from the Lord Howe Seamount Chain of characteristically Australian groups, such as the phylogenetically primitive *Astele* group, may indicate that depths in the northern Tasman Sea during early stages of its formation were too great for them but favourable for *Benthastelena* species, which currently range deeper than any other calliostomatids known from off Queensland (*C. (B.) katherina* to 281 m). The New Caledonian species *C. (B.) cristatum* and *C. (B.) coronatum* may in turn have originated from separate colonisations by early *C. (B.) diadematum* stock. A fifth component of the group, either a form of *C. (B.) diadematum* or a closely related species, is represented by single shells from the Chesterfield Reefs at the northern end of the Lord Howe Seamount Chain and off southern New Caledonia (Figs 154, 156).

New Caledonian species here referred to *C. (Ampullostrochus)* evidently have closest affinities with western Atlantic species, which suggests a Tethyan origin. So too perhaps does the presence of

*C. (Fautor)* species, if indeed the eastern Atlantic species *C. lithocolletum* Dautzenberg is consubgeneric.

Assuming that Calliostomatinae originated from Fautricini or its stem group, it is remarkable that none of the ancestral stock can be recognised among known Recent and Tertiary calliostomatids from anywhere else in the world beyond Australia, the New Caledonia area and northernmost New Zealand. The stem group was either much more widely distributed and is now long extinct (or unrecognised) elsewhere, or subfamily Calliostomatinae spread outwards from a southern (Gondwana) centre of origin. The latter option is favoured here. The distribution of subfamily Thysanodontinae, currently known only from southern Africa, Australia, New Caledonia and New Zealand also suggests a Gondwanian origin. It would not be surprising, therefore, if Fautricini and perhaps relatives of the *Astele* group were recognised off southern Africa, southern South America or Antarctica.

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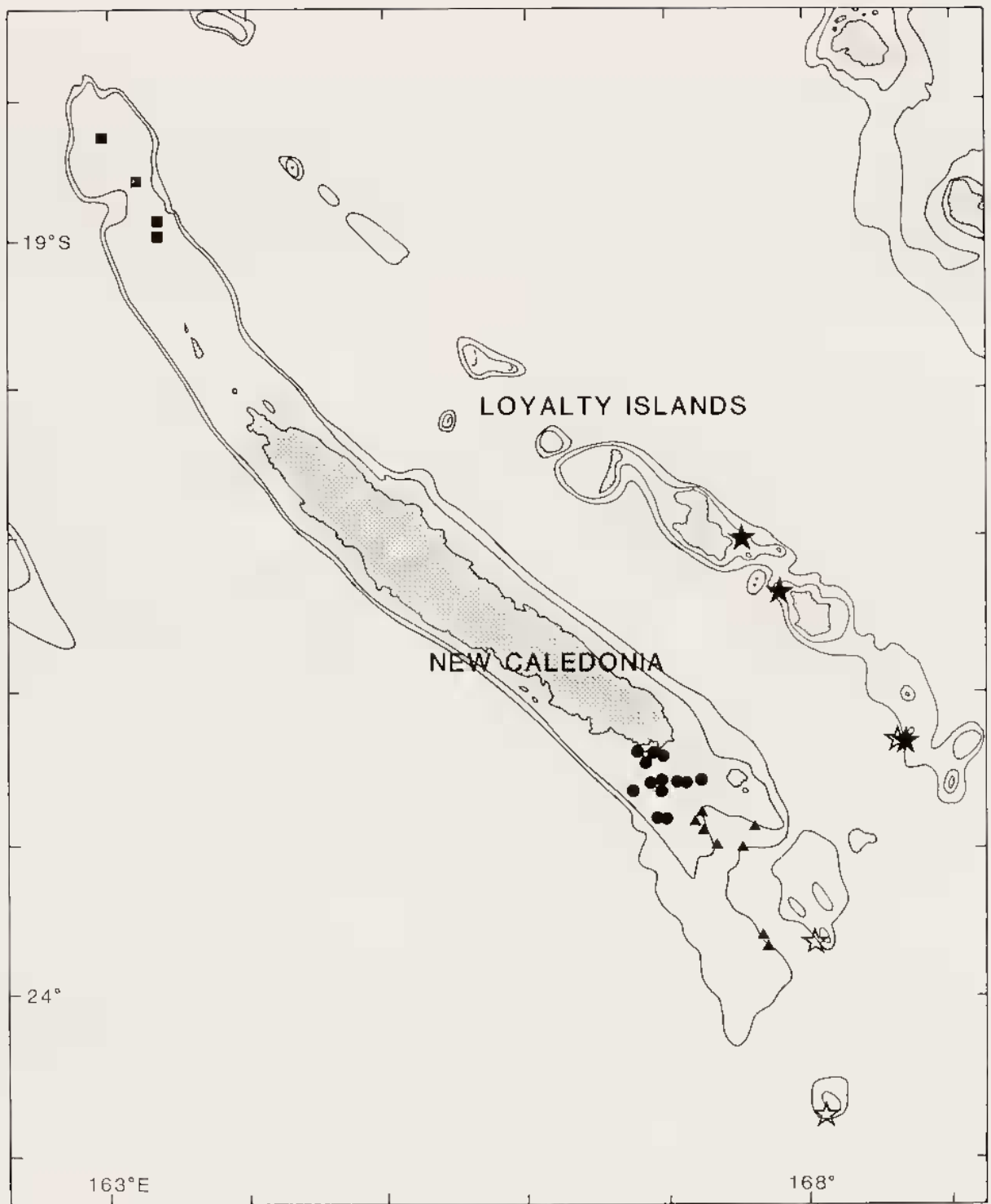


FIG. 153. Distribution of *Calliostoma (Fautor) richeri* (●), *C. (F.) vaubani* (■), *C. (F.) metivieri* (▲), *C. (Ampullotrochus) peregrinum* (☆) and *C. (A.) heros* (★).

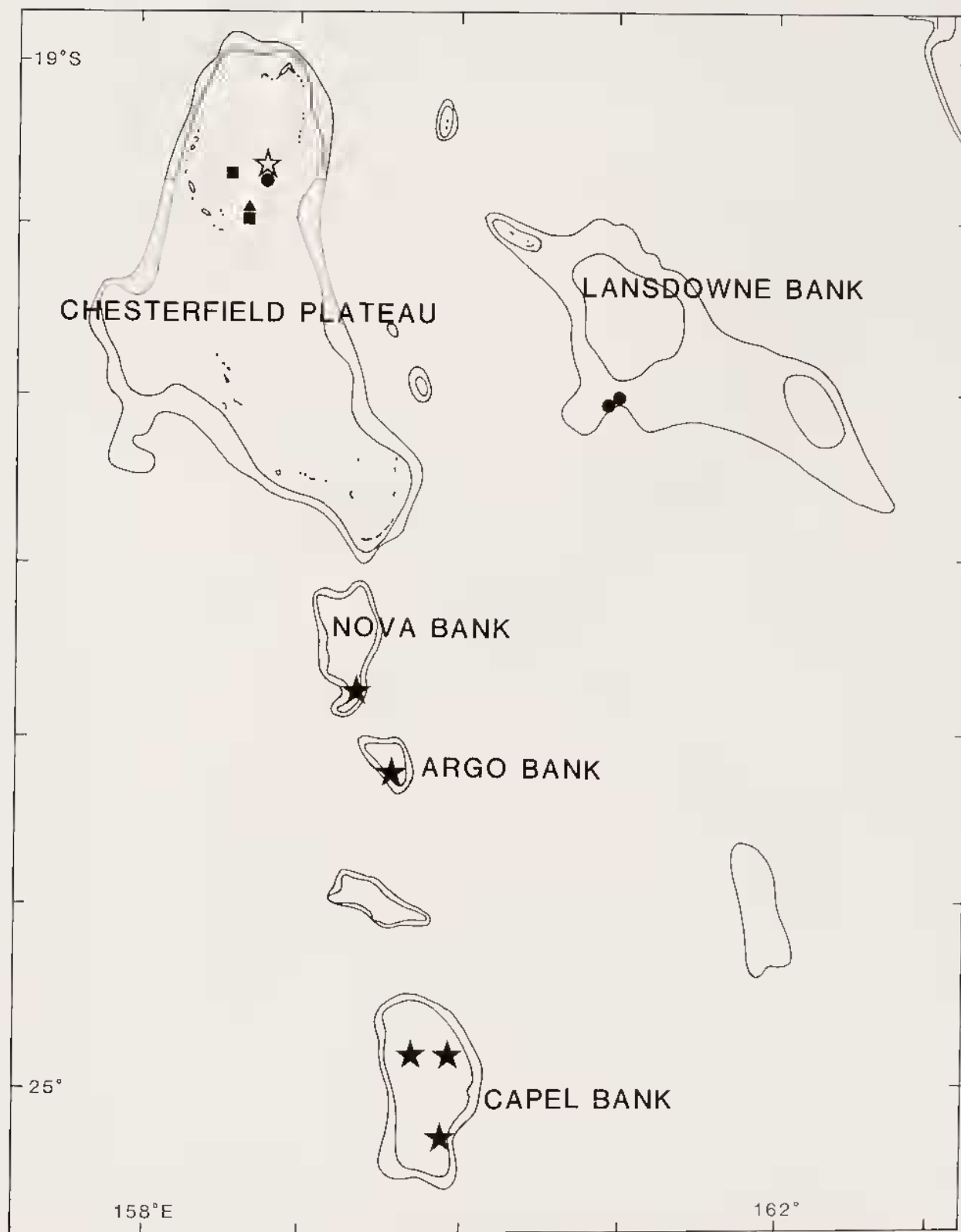


FIG. 154. - Distribution of *Calliostoma (Fautor) chesterfieldense* and *C. (Benthastelena) tosaense* (▲), *C. (B.) ihulematum* (★), *C. (B.) sp. cf. diadematum* (☆), *Bathyfautor coriolis* (●), and *Thysanodonta chesterfieldensis* (■).

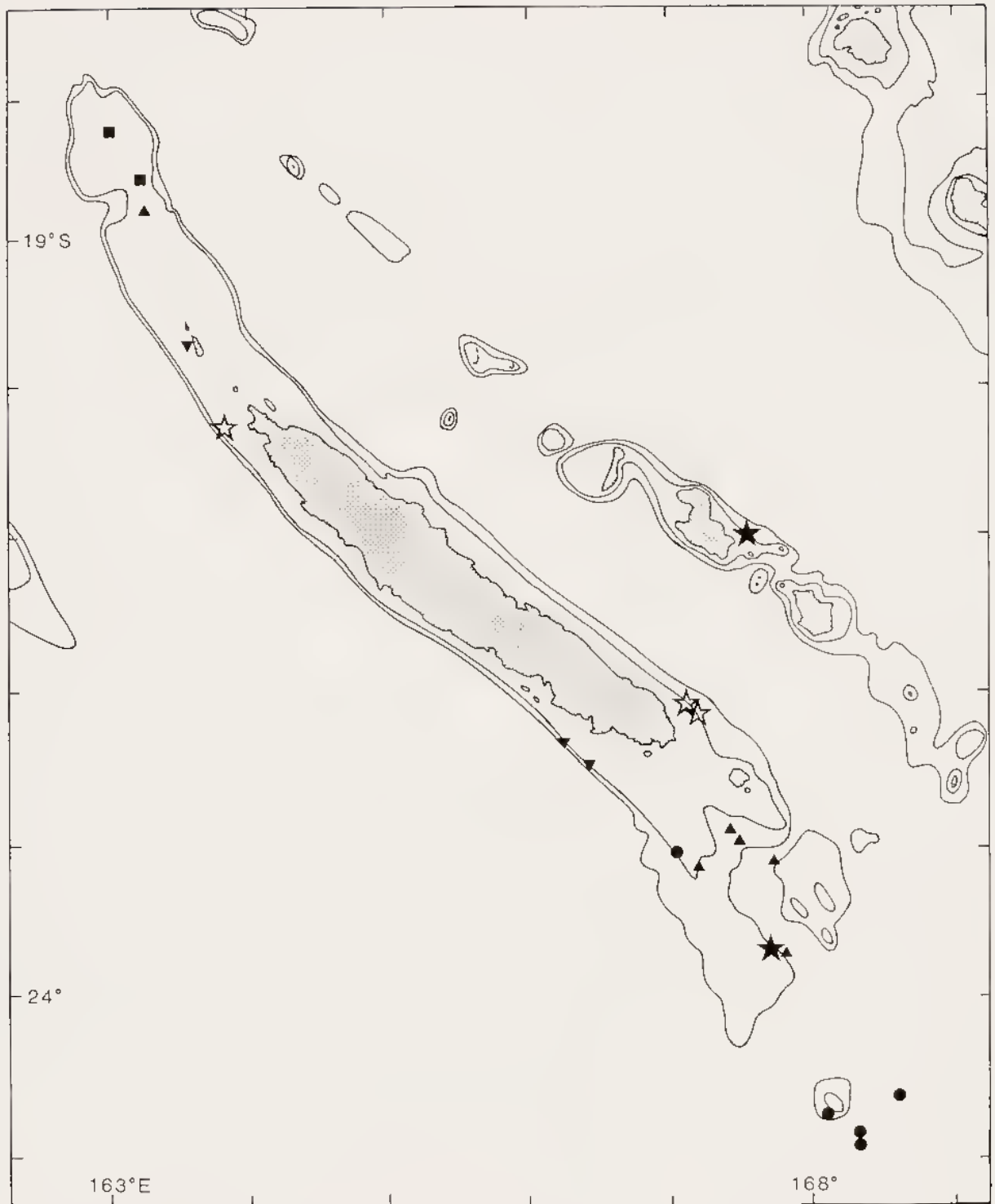


FIG. 155. Distribution of *Calliostoma (Fautor) boucheti* (●), *C. (F.) necopinatum* (■), *C. (F.) paradigmatum* (▲), *C. (Benthastelena) pertinax* (☆), *C. (Ampulloirochms) xanthos* (☆), and *Dactylastele poupineli* (▼).

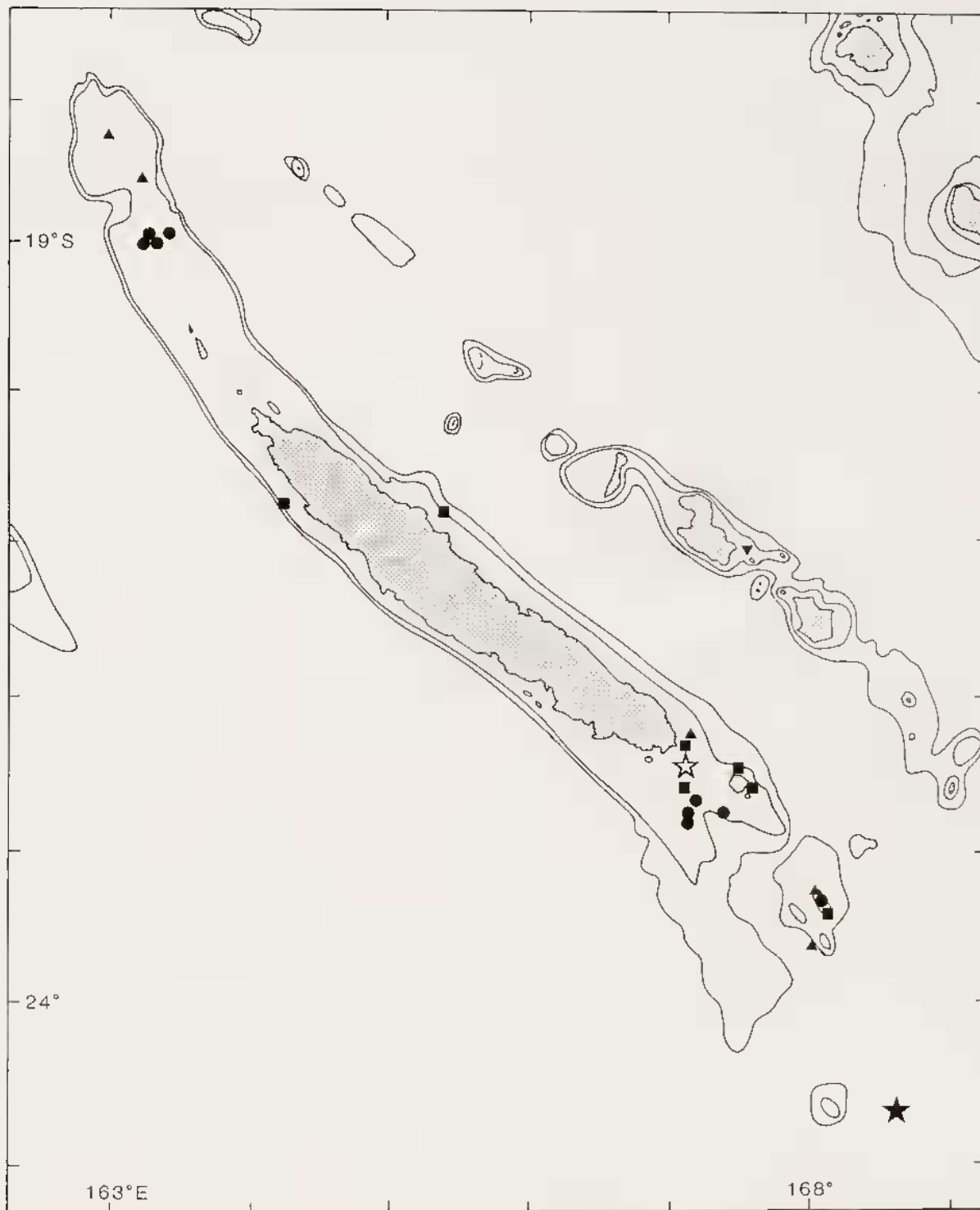


FIG. 156. -- Distribution of *Calliostoma (Fautor) houbricki* (■), *C. (F.)* sp. cf. *metivieri* (★), *C. (Beuthastelena) coronatum* (●), *C. (B.) cristatum* (▲), *C. (B.) tosaense* (▼), and *C. (B.)* sp. cf. *diadematum* (☆).

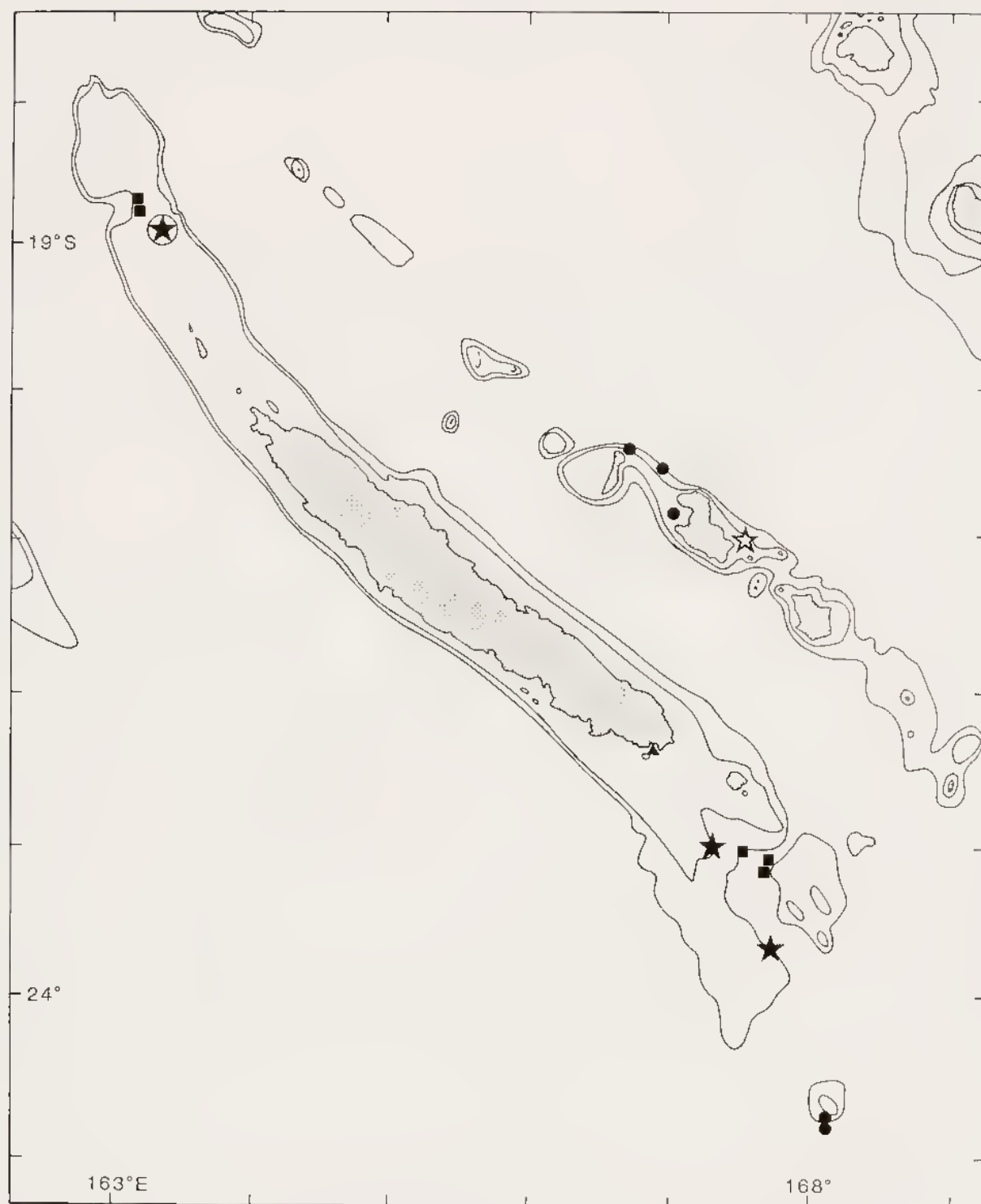


FIG. 157. — Distribution of *Calliostoma (Fautor) periglyptum* (●), *C. (Ampullatrochus) alisi* (☆), *Bathyfautor caledonicus* (■), *Laetifautor fundatus* (▲), *Fautorix aquilonia* (⊙), and *F. candidu* (★).





FIG. 158. — Distribution of *Selastele pictum* (⊙), *Thysanodonta boncheti* (★), *T. festiva* (☆), *T. opima* (■), and *T. eucosmia* (●).

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## APPENDIX 1

## LIST OF GENERA AND SUBGENERA OF CALLIOSTOMATIDAE

## CALLIOSTOMATINAE

- Akoya* Habe, 1961 (*Calliostoma* (*Calotropis*?) *nkoya* Kuroda in Ikebe, 1942).  
*Alertalex* Dell, 1956 (*Alertalex blacki* Dell, 1956). ? = *Otukaim* Ikebe, 1942.  
*Ampullotrochus* Monterosato, 1890 (*Trochus granulatus* Born, 1778).  
*Astele* Swainson, 1855 (*Astele subcarinata* Swainson, 1855).  
*Astelem* Iredale, 1924 (*Zizyphinus scitulus* A. Adams, 1854).  
*Bathyfautor* gen. nov. (*B. rapuhia* sp. nov.).  
*Benthastelena* Iredale, 1936 (*Benthastelena katherina* Iredale, 1936).  
*Calliostoma* Swainson, 1840 (*Trochus conulus* Linnaeus, 1758).  
*Calliotropis* Oliver, 1926 [Not *Calliotropis* Seguenza, 1903]. (*Trochus cuminghami* "Gray, 1834" — i.e. Griffith & Pidgeon, 1833 = *Trochus selectus* Dillwyn, 1817). = *Maurea* Oliver, 1926.  
*Callistoma*/Callistomus Herrmannsen, 1846 (emendations of *Calliostoma* Swainson, 1840).  
*Calotropis* Thiele, 1929. Replacement name for *Calliotropis* Oliver not Seguenza. = *Maurea* Oliver, 1926.  
*Carinator* Ikebe, 1942 (*Calliostoma* (*Carinator*) *makiyamai* Ikebe, 1942). Type material of *C. makiyamai* has not been seen and the relationships of *Carinator* are uncertain.  
*Conulus* Nardo, 1841 (*Trochus conulus* Linnaeus, 1758). = *Calliostoma* Swainson, 1840 (objective synonym).  
*Coralastele* Iredale, 1930 (*Coralastele allanae* Iredale, 1930).  
*Dactylastele* gen. nov. (*Trochus* (*Zizyphinus*) *poupineli* Montrouzier, 1875).  
*Dymares* Schwengel, 1942 (*Calliostoma* (*Astele*) *agalma* Schwengel, 1942 = *Calliostoma yucatecanum* Dall, 1881).  
*Elmerlinia* Clench & Turner, 1960 (*Calliostoma jujubinum* Gmelin, 1791).  
*Eucasta* Dall, 1889 (*Calliostoma* (*Eucasta*) *indiana* Dall, 1889).  
*Entrochus* A. Adams, 1864 (*Entrochus perspectivus* A. Adams, 1864 = *Astele subcarinata* Swainson, 1855). = *Astele* Swainson, 1840 (objective synonym).  
*Falsimargarita* Powell, 1951 (*Margarites gemma* Smith, 1915).  
*Fautor* Iredale, 1924 (*Zizyphinus comptus* A. Adams, 1854).  
*Fautrix* gen. nov. (*Fautrix candida* sp. nov.).  
*Fluxina* Dall, 1881 (*Fluxina brunea* Dall, 1881).  
*Jacintinus* Monterosato, 1889 (*Trochus conulus* Linnaeus, 1758). = *Calliostoma* Swainson, 1840 (objective synonym).  
*Kombalogion* Clench & Turner, 1960 (*Calliostoma bairdii* Verrill & Smith, 1880).  
*Kingotrochus* Ihering, 1902 (*Margarita coerulescens* King & Broderip, 1831). = *Photinula* H. & A. Adams, 1854 (objective synonym).  
*Laetifautor* Iredale, 1929 (*Calliostoma trepidum* Hedley, 1907).  
*Leiotrochus* Conrad, 1862 (*Leiotrochus distans* Conrad, 1862).  
*Maurea* Oliver, 1926 (*Trochus tigris* Gmelin, 1791).  
*Manniella* Oliver, 1926 (*Trochus punctulatus* Martyn, 1784). = *Maurea* Oliver, 1926.  
*Mucrinops* Finlay, 1926 (*Zizyphinus spectabilis* A. Adams, 1855). = *Maurea* Oliver, 1926.  
*Neocalliostoma* Castellanos & Fernandez, 1976 (*Calliostoma militaris* Ihering, 1907).  
*Omphalotukaia* Yoshida, 1948 (*Calliostoma* (*Otukaia*) *hajimeanum* Yoshida, 1948).  
*Otukaia* Ikebe, 1942 (*Calliostoma kibeiziebisi* Otuka, 1939).  
*Photina* H. & A. Adams in A. Adams, 1851 [Not *Photina* Burmeister, 1838]. (*Margarita coerulescens* King & Broderip, 1831). = *Photinula* H. & A. Adams, 1854.  
*Photinastoma* Powell, 1951 (*Trochus taeniatus* Wood, 1828).  
*Photinula* H. & A. Adams, 1854 (*Margarita coerulescens* King & Broderip, 1831).  
*Salsipotens* Iredale, 1924 (*Trochus armillatus* Wood, 1828). = *Astele* Swainson, 1855.  
*Selastele* gen. nov. (*Calliostoma onustum* Odhner, 1924).  
*Sinator* Cotton & Godfrey, 1935 (*Zizyphinus incertus* Reeve, 1863).  
*Spicator* Cotton & Godfrey, 1935 (*Calliostoma spinulosum* Tate, 1893). = *Laetifautor* Iredale, 1929.  
*Tristichotrochus* Ikebe, 1942 (*Calliostoma aculeatum* Sowerby, 1912). = *Benthastelena* Iredale, 1936.  
*Tropidotrochus* Parodiz, 1977 (*Zizyphinus virginicus* Conrad, 1875).  
*Venustas* Allan, 1926 (*Calliostoma fragile* Finlay, 1923).  
*Venustas* Finlay, 1927 (*Trochus tigris* Gmelin, 1791). = *Maurea* Oliver, 1926 (officially rejected name: ICZN Opinion 479).  
*Venustatrochus* Powell, 1951 (*Venustatrochus georgianus* Powell, 1951).  
*Zizyphinus* Gray, 1842 (*Trochus zizyphinus* Linnaeus, 1758).  
*Zizyphinus* Gray, 1847. Incorrect subsequent spelling of *Zizyphinus*.

## THYSANODONTINAE

- Carinastele* Marshall, 1988 (*Carinastele kristellae* Marshall, 1988).  
*Herbertina* Marshall, 1988 (*Herbertina eos* Marshall, 1988).  
*Thysanodonta* Marshall, 1988 (*Thysanodonta aucklandica* Marshall, 1988).

## APPENDIX 2

## GENUS GROUP TAXA REMOVED FROM CALLIOSTOMATIDAE

*Anceps* Kolesnikov, 1939 (*Trochus anceps* Eichwald, 1850) (as subgenus of *Calliostoma*). Judging from illustrations (EICHWALD, 1853: pl. 9, fig. 8; KOLESNIKOV, 1935: pl. 22, figs 31-33; KOJUMDGIEVA, 1969: pl. 28, figs 5-7), the type species seems more likely to be a trochid related to *Cantharidus* Montfort, 1810 (Trochinae: Cantharidini).

*Callistele* Cotton & Godfrey, 1935 (*Astele calliston* Verco, 1905) (as subgenus of *Astele*). From examination of type (AMS C21490) and additional material. *A. calliston* is a trochid related to *Chlorostoma* Swainson, 1840 (Trochinae: Cantharidini).

*Eocalliostoma* Haas, 1953 (*Calliostoma interruptum* Cox, 1949). Referred to Proconulinae by COX (1960). HICKMAN & MCLEAN (1990) tentatively treated Proconulinae as a synonym of Calliostomatinae, though there is absolutely no evidence that they are related.

*Eurastele* Coen, 1946 (*Astele (Eurastele) lusitana* Coen, 1946). The beachworm holotype of the type species (Hebrew University of Jerusalem No.36757) appears to belong to the local form of *Gibbula cineraria* (Linné, 1758) known as *Trochus strigosus* Gmelin, 1791 (Trochinae: Gibbulini).

*Fenioniana* Kolesnikov, 1939 (*Trochus fenionianus* d'Orbigny, 1845) (as subgenus of *Calliostoma*). Judging from illustrations (D'ORBIGNY, 1844: pl. 2, figs 13-15; KOLESNIKOV, 1935: pl.19, figs 49-51), the type species is probably a trochid, perhaps a solarielline.

*Kishinewia* Kolesnikov, 1935 (*Phasianella bessarabica* d'Orbigny, 1844). Judging from illustrations (D'ORBIGNY, 1844: pl. 3, figs 4-6; KOLESNIKOV, 1935: pl. 26, figs 37-39; WENZ, 1943: fig. 4196; KOJUMDGIEVA 1969: pl. 29, figs 10-13) the narrowly attenuate type species is quite unlike any known calliostomatid. It is probably a trochid related to *Cantharidus*.

*Manotrochus* Fischer, 1885 (*Trochus unidentatus* Philippi, 1844). Although placed as a synonym of *Calliostoma* (*s. str.*) by CLENCH & TURNER (1960), the type species is clearly referable to *Jujubinus* Monterosato, 1884 (KEEN, 1960) (Trochinae: Cantharidini).

*Mazastele* Iredale, 1936 (*Trochus glypta* Watson, 1886). *Mazastele* was regarded as a calliostomatine genus by IREDALE (1936) and KEEN (1960), but placed as a synonym of *Calliotropis* Seguenza, 1903 (Trochidae, Eucyclinae) by MARSHALL (1979).

*Meticonulus* Cossmann, 1918 (*Trochus princeps* Deshayes, 1863). Judging from examination of actual specimens (J. LE RENARD collection, France), the type species is a turbinid.

*Montagua* Leach in Gray, 1852 (*Montagua dammoniensis* Leach, 1852) (not *Montagua* Fleming, 1828). Although placed as a synonym of *Calliostoma* (*s. str.*) by KEEN (1960), according to JEFFREYS (1865: 322) the type species is a synonym of *Jujubinus montagni* (Wood, 1828) (Trochidae). Type material (never illustrated) of *M. dammoniensis* could not be located and since there is nothing in LEACH's (1852) description that would contradict JEFFREYS' (1865) opinion, I regard *Montagua* as a synonym of *Jujubinus*.

*Pulchrastele* Iredale, 1929 (*Calliostoma (Eutrochus) septemvirium* Melvill & Standen, 1899). From examination of type (BMNH 1899.2.23.13) and additional material (AMS) of *C. septemvirium*, *Pulchrastele* is related to *Clanculus* Montfort, 1810 (Trochidae, Trochinae).

*Putzeysia* Sullioti, 1889 (*Trochus clathratus* Aradas, 1847). Long regarded as a genus of the Calliostomatinae, *Putzeysia* has been conclusively shown to be related to *Danilia* Brusina, 1865 (GUTDASTRI *et al.*, 1984) and it thus belongs in Trochidae, subfamily Eucyclinae.

*Sarmates* Kolesnikov, 1939 (*Trochus sarmates* Eichwald, 1850). Judging from illustrations (EICHWALD, 1853: pl. 9, fig. 10; KOLESNIKOV, 1935: pl. 23, figs 24-27; KOJUMDGIEVA, 1969: pl. 23, figs 9-10), *T. sarmates* seems most unlikely to be a calliostomatid. Although it is probably a trochid, its relationships within the family are uncertain.

*Scrobiculinus* Monterosato, 1889 (*Trochus strigosus* Gmelin, 1791). Although *Scrobiculinus* was placed as a subgenus of *Astele* by KEEN (1960), the type species belongs in the trochid genus *Gibbula* (Trochinae: Gibbulini). Incidentally, *Strigosella* Saeco, 1896 has the same type species and is thus an objective synonym.

*Sinzowia* Kolesnikov, 1935 (*Trochus elatior* d'Orbigny, 1845). The type species (KOLESNIKOV, 1935: pl. 25, figs 31-33; WENZ, 1943: fig. 4197) has an extremely attenuate turriculate spire and, like *Kishinewia*, exhibits no character that would indicate relationship with Calliostomatidae. It is presumably related to *Jujubinus* (Trochidae, Trochinae).

*Stylotrochus* Seguenza, 1876 (not Haekel, 1862). Regarded as a synonym of *Calliostoma* (*s. str.*) by KEEN (1960). SEGUENZA (1876) introduced *Stylotrochus* with descriptions of four new species, none of which were ever illustrated. The shell was described as being conic-trochiform, with an axially ribbed, styliform, cylindrical apex, a description alien to an archaeogastropod. A search of the European literature for a gastropod fitting the generic diagnosis led to JEFFREYS' (1883: 113) discussion of the type species of his new genus *Iphitus* (*I. tuberatus* Jeffreys, 1883), in which he stated that he had received a similar shell from SEGUENZA from the Lower Pliocene of Messina under the manuscript name *Gemmula asperata*. This is probably the specimen so-labelled in the JEFFREYS' collection (USNM 186200), and clearly represents *Stylotrochus asperatus* Seguenza, 1876. Since this specimen is a species of *Iphitus*, *Stylotrochus* is a hitherto overlooked senior synonym of *Iphitus*, though a homonym. Incidentally, since the USNM specimen of *S. asperatus* is presumably a syntype it represents a potential lectotype by which the identity of the specific name can be stabilised. *Iphitus* is a genus of the Epitonidae.

[The present paper was in press when BERTOLASO & PALAZZI (1994) independently published the same results. They failed to indicate, however, that *Stylotrochus* Seguenza, 1876 is preoccupied by *Stylotrochus* Haekel, 1862].