# A Revision of the Chilodontidae (Gastropoda: Vetigastropoda: Seguenzioidea) of Southern Africa and the South-Western Indian Ocean

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# A revision of the Chilodontidae (Gastropoda: Vetigastropoda: Seguenzioidea) of southern Africa and the south-western Indian Ocean

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## ABSTRACT

All species of Chilodontidae known to occur in the south-western Indian Ocean are discussed (27 species, of which eight new, belonging to nine genera, of which three new). Keys to genera and species are provided. Observations on protoconch form, shell microsculpture, radula morphology, operculum shape and external anatomy are given, together with summary biological observations. The genus *Agathodonta* Cossmann, 1918 is not considered to be applicable to the extant species for which it has been recently used and a new genus is proposed for these living forms. Type specimens of a number of extralimital species examined for comparative purposes are illustrated.

New genera: *Ascetostoma*, *Clypeostoma* and *Pholidotrope*.

New species: *Clypeostoma reticulatum*, *Danilia boucheti*, *Danilia textilis*, *Herpetopoma serratocinctum*, *Herpetopoma stictum*, *Pholidotrope gloriosa*, *Vaceuchelus cretaceus* and *Vaceuchelus jayorum*.

New synonyms: *Cantharidus pliciferus* Schepman, 1908 = *Perrinia angulifera* (A. Adams, 1853); *Turcica* (*Perrinia*) *waiwailevensis* Ladd, 1982 and *Herpetopoma eboreum* Vilvens & Héros, 2003 = *Herpetopoma xeniolum* (Melvill, 1918); *Trochus alabastrum* Reeve, 1858 = *Euchelus asper* (Gmelin, 1791).

New combinations: *Agathodonta elongata* Vilvens, 2001, *A. meteorae* Neubert, 1998, *A. nortoni* McLean, 1984, *Euchelus townsendianus* Melvill & Standen, 1903 and *Turcica salpinx* Barnard, 1964 are transferred to *Clypeostoma* gen. n.; *Diloma verruca* Gould, 1861, *Euchelus seychellarum* G. & H. Nevill, 1869, *Euchelus xeniolum* Melvill, 1918, *Turcica helix* Barnard, 1964 and *T. waiwailevensis* Ladd, 1982 are transferred to *Herpetopoma*; *Euchelus gemmula* Turton, 1932 is transferred to *Vaceuchelus*; *Euchelus providentiae* Melvill, 1909 and *E. ringens* Schepman, 1908 are transferred to *Ascetostoma* gen. n.; *Stomatella cumingii* A. Adams, 1854 is transferred to *Granata*; *Turcica konos* Barnard, 1964 is transferred to *Perrinia*.

New records for the south-western Indian Ocean: *Clypeostoma meteorae* (Neubert, 1998); *Clypeostoma* cf. *nortoni* (McLean, 1984); *Granata cumingii* (A. Adams, 1854); *Herpetopoma instrictum* (Gould, 1849); *Herpetopoma ?naokoae* Poppe, Tagaro & Dekker, 2006; *Herpetopoma xeniolum* (Melvill, 1918); *Perrinia angulifera* (A. Adams, 1853).

New records for South Africa: *Ascetostoma providentiae* (Melvill, 1909); *Herpetopoma ?naokoae* Poppe, Tagaro & Dekker, 2006; *Perrinia angulifera* (A. Adams, 1853).

Lectotypes designated for: *Euchelus favosus* Melvill & Standen, 1896; *Euchelus gemmula* Turton, 1932; *Euchelus natalensis* Smith, 1906; *Euchelus seychellarum* G. & H. Nevill, 1869; *Euchelus townsendianus* Melvill & Standen, 1903; *Monodonta alveolata* A. Adams, 1853; *Monodonta angulifera* A. Adams, 1853; *Stomatella articulata* A. Adams, 1850; *Turbo semilugubris* Deshayes, 1863.

Type locality designations and emendations: Type locality for *Stomatella cumingii* Adams, 1854, designated to be tropical East Africa; type locality for *Turcica salpinx* Barnard, 1964, selected to be 'off Cape Morgan, 77 fath.' [-141 m]; type locality of *Turcica stellata* A. Adams, 1864, emended from 'China Seas' to Gulf of Suez, Red Sea.

*Danilia* Brusina, 1865 is deemed a *nomen protectum* and *Heliciella* O.G. Costa, 1861 a *nomen oblitum*.

KEY WORDS: Mollusca, Chilodontidae, Indian Ocean, taxonomic revision, new taxa, new synonyms.

## INTRODUCTION

The taxa discussed in this revision have traditionally been referred to the trochid subfamilies Margaritinae and Monodontinae (see for example Keen 1960). McLean (1981, 1982), however, identified certain lineages within these subfamilies that shared distinctive features of the shell, radula and epipodium. He proposed (McLean 1981) that

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these represented Recent descendents of Mesozoic lineages (Amberleyidae) previously thought to have become extinct in the Oligocene or earlier. He later suggested (McLean 1982, 1984) that they be recognised as separate tribes within the Margaritinae, but this idea was subsequently revised in the publication of Hickman and McLean (1990) in which a much modified trochoidean subfamily, the Eucyclinae, was employed for the taxa concerned, based on the extinct families Eucyclidae, Cirridae and Amberleyidae. This subfamily was further divided into three tribes, the Eucyclini, Calliotropini and Chilodontini (the latter two including extant taxa) on the grounds of differing shell morphology, radula form and external anatomy. Warén and Bouchet (1993), on account of uncertainties regarding the affinities of the exclusively fossil Eucyclini, subsequently chose to regard the other two tribes as subfamilies in their own right, although this was not followed by Hickman (1998).

A radically different position was subsequently proposed by Bouchet *et al*. (2005) in which the Calliotropinae and Chilodontinae were removed from the Trochoidea and referred instead to the Seguenzioidea, largely on the basis of molecular data (Warén *et al*. 2003). More recently, Kano (2008) has analysed the relationships of the Seguenzioidea using sequence data from a wider range of taxa and has confirmed that calliotropine and chilodontine species cluster together with seguenziids in a well supported clade, although no support was evident for the monophyly of either the Calliotropinae or Chilodontinae, nor for the two treated together as the Chilodontidae. He also highlighted potentially significant anatomical similarities including a peduncle posterior to the right eyestalk (distinct from the subocular tentacle) and hooded rachidian teeth in the radula, but pointed out that these may be plesiomorphic character states. Subsequently, Williams *et al*. (2008) recovered a monophyletic Chilodontidae, with monophyletic subfamilies Chilodontinae and Calliotropinae, but their study did not include other seguenzioid taxa. Most recently Kano *et al*. (2009), including additional seguenzioid taxa, recovered well supported Chilodontinae and Calliotropinae clades, but found no support for the combined Chilodontinae + Calliotropinae clade. Consequently, they proposed that the two groups be recognised as separate families within the Seguenzioidea. Further support for the seguenzioid affinities of these families was recently provided by Aktipis and Giribet (2012). Kano *et al*. (2009) also demonstrated that *Turcica* H. & A. Adams, 1854, traditionally grouped with chilodontid taxa (Hickman & McLean 1990), belongs within the Calliotropidae. For the purposes of this revision, I follow the recommendations of Kano *et al*. (2009); however, it should be noted that Bandel (2010) has proposed a very different classification for the taxa discussed here, in which he recognised a superfamily Eucycloidea and proposed several new families.

Since chilodontids have only recently been recognised as a distinct entity, there has been no previous collective analysis of the group in this region. In many cases little information over and above that contained in the original descriptions is available. Hickman and McLean (1990) considered the genus *Synaptocochlea* Pilsbry, 1890 to belong to this group, but although it occurs in the south-western Indian Ocean, it is not treated here. Morphological and molecular evidence now indicates that *Synaptocochlea* belongs within the Trochidae (Herbert 1998; Williams *et al*. 2008, 2010), in the subfamily Fossarininae Bandel, 2009. Another western Indian Ocean genus which Bandel (2010) referred to the Eucycloidea is *Pagodatrochus* Herbert, 1989, creating for it a new family, the Pagodatrochidae. Whilst this taxon shares some features of early teleoconch ribbing and microsculpture with chilodontids and has a radula somewhat atypical of trochids, the proposal of a new family in the absence of corroborating evidence from soft-part anatomy and molecular data seems premature. In terms of its external morphology there are no cephalic lappets or laterally expanded snout flanges, nor is a right post-ocular peduncle evident, and the ctenidium is monopectinate (Herbert unpubl. observ. on the type species *Pagodatrochus variabilis* (H. Adams, 1873)). None of these character states suggests a closer relationship with the Chilodontidae than with the Trochidae. It is evidently one of many small, anomalous vetigastropod taxa for which molecular sequence data could provide valuable phylogenetic insights.

## MATERIAL AND METHODS

The material studied is kept in the following institutions:

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| AMS | – | Australian Museum, Sydney, Australia; |
| MCSNG | – | Museo Civico di Storia Naturale "Giacomo Doria", Genova, Italy; |
| MHNB | – | Muséum d'Histoire Naturelle, Bordeaux, France; |
| MHNG | – | Muséum d'Histoire Naturelle, Geneva, Switzerland; |
| MMUM | – | Manchester Museum, University of Manchester, UK; |
| MNHN | – | Muséum National d'Histoire Naturelle, Paris, France; |
| NHMUK | – | Natural History Museum, London, UK; |
| NMSA | – | KwaZulu-Natal Museum, Pietermaritzburg, South Africa; |
| NMW | – | National Museum of Wales, Cardiff, UK; |
| OXUM | – | Oxford University Museum, Oxford, UK; |
| SAMC | – | Iziko South African Museum, Cape Town, South Africa; |
| UCBL | – | Université Claude Bernard (Centre des Sciences de la Terre), Lyon, France; |
| USNM | – | United States National Museum, Smithsonian Institution, Washington, USA; |
| WAM | – | Western Australian Museum, Perth, Australia; |
| ZMAN | – | Zoölogisch Museum Amsterdam, The Netherlands. |

The bulk of the material discussed in this work was obtained during the Natal Museum Dredging Programme (1981–1997) off the east coast of South Africa, on board the RV *Meiring Naude* and RV *Sardinops*. This has been augmented by additional material from Madagascar, Mozambique and Réunion obtained during the BENTHEDI (1977), MAINBAZA (2009), *Miriky* (2009) and ATIMO VATAE (2010) campaigns (MNHN) (see acknowledgements). Littoral and shallow water material has also been accumulated over many years and from throughout the region, during the course of on-going field research and through the collecting activities of amateur malacologists.

Shell length and diameter measurements were made with the shell held in apertural view with the axis of coiling vertical. Immature shells were excluded from the data used to calculate length : diameter ratios. The dimensions of the protoconch were measured according to the method set out previously (Herbert 1987). Photographs of shells were taken with a Nikon F4 or Nikon D70 camera. Radulae were extracted by maceration of the buccal mass in dilute NaOH and then thoroughly rinsed in distilled water. For light microscopy radulae were stained in Shirlastain A [SDL Atlas] and for SEM they were dehydrated in ethanol, placed on stubs with double-sided carbon tape and manipulated into position using fine entomological pins whilst air-drying. Shells and radulae for SEM examination were coated with gold-palladium and examined at low accelerating voltage (5–10 kv) in Jeol T/200, Hitachi S–570 SEM, Philips XL30 ESEM and Zeiss EVO 10LS scanning electron microscopes.

The following acronyms and abbreviations are used in this paper:

CSIR – Council for Scientific and Industrial Research, South Africa;
Coll'n – Collection;
Exped'n – Expedition;
IIOE – International Indian Ocean Expedition;
KZN – KwaZulu-Natal;
L/D – length: diameter ratio;
L(S)T – low (spring) tide;
NMDP – Natal Museum Dredging Programme;
NPB – Natal Parks Board [now Ezemvelo KZN Wildlife];
s.d. – subsequent designation;
st'n – station.

New taxa have been registered with ZooBank (Appendix I, p. 502).

## MORPHOLOGY

### *Protoconch* (Fig. 1)

SEM illustrations of chilodontid protoconchs have been given by Marshall (1979), Bandel (1982, 2010), Guidastri *et al*. (1984), Moolenbeek & Faber (1989), Sasaki (1998) and Engl & Rolán (2009). These together with the illustrations given here reveal considerable variation in protoconch morphology and sculpture. Although the paucispiral form (*ca* 1.25 whorls) is typical of vetigastropods and the apical beak consistently absent or only weakly developed, features associated with the terminal lip and superficial sculpture vary significantly.

In some species the terminal lip is straight or very slightly curved, but a number have developed a strong beak or sinusigera-like projection (Fig. 1B, C). This is only visible in the most well preserved protoconchs, but the strong angulation in the somewhat worn protoconchs of a number of other taxa is perhaps evidence of the occurrence of a similar structure (e.g. *Ascetostoma providentiae*, *Perrinia angulifera* and *Vaceuchelus cretaceus*). I am not aware of any prior reports of such a projection on the protoconch lip in the Vetigastropoda, although some seguenziids have a protoconch with a strongly convex lip (Marshall 1991). A beak or sinusigera-lip is found in the pelagic larvae of a wide variety of caenogastropods and is thought to be indicative of relatively long-lived, planktotrophic larvae (Lima & Lutz 1990; Fretter & Graham 1994). Its presence in lecithotrophic vetigastropods is less easy to explain, but could perhaps indicate a larger velum and a longer, more active swimming phase than is typical for vetigastropods. None of the species examined show any kind of varix (terminal or subterminal) associated with the protoconch lip.

The different patterns evident in the superficial sculpture of the chilodontid protoconch can be grouped as follows:

- almost totally smooth, usually exsert and rather globose [*Perrinia konos, Pholidotrope gloriosa*] (Fig. 1A).

- finely granular, sometimes with traces of spiral lines, exsert and sometimes globose [*Clypeostoma salpinx, Granata sulcifera* and *Putzeysia* spp. (Engl & Rolán 2009)] (Fig. 1B, C).
- widely spaced spiral threads with close-set axial or oblique lines in the intervals; rather globose [*Ascetostoma providentiae*] (Fig. 1D). Similar sculpture has been illustrated in some seguenziids (Marshall 1983, 1991).
- strong irregular axial ridges with little or no spiral sculpture; not obviously globose, more or less level with first teleoconch whorl or at most weakly exsert [*Herpetopoma* (s.s.), most species of *Vaceuchelus* and '*Euchelus*' *guttarosea* Dall, 1889 (Moolenbeek & Faber 1989)] (Fig. 1E, F).

This degree of variation is considerable when compared with that seen in some other vetigastropod groups, e.g. Calliostomatidae, Solariellidae, Trochinae, Umboniinae (Herbert 1987, 1992, 1993; Marshall 1995), but is no more diverse than that evident in others, e.g. Scissurellidae and Fissurellidae (Sasaki 1998; Geiger & Jansen 2004). Although care needs to be taken in drawing conclusions of a phylogenetic nature based on vetigastropod protoconch microsculptural patterns, due to frequent homoplasy (Sasaki 1998), it seems that in some instances the sculptural patterns evident in the taxa studied here are broadly consistent within some genera (e.g. *Herpetopoma* (s.s.) and

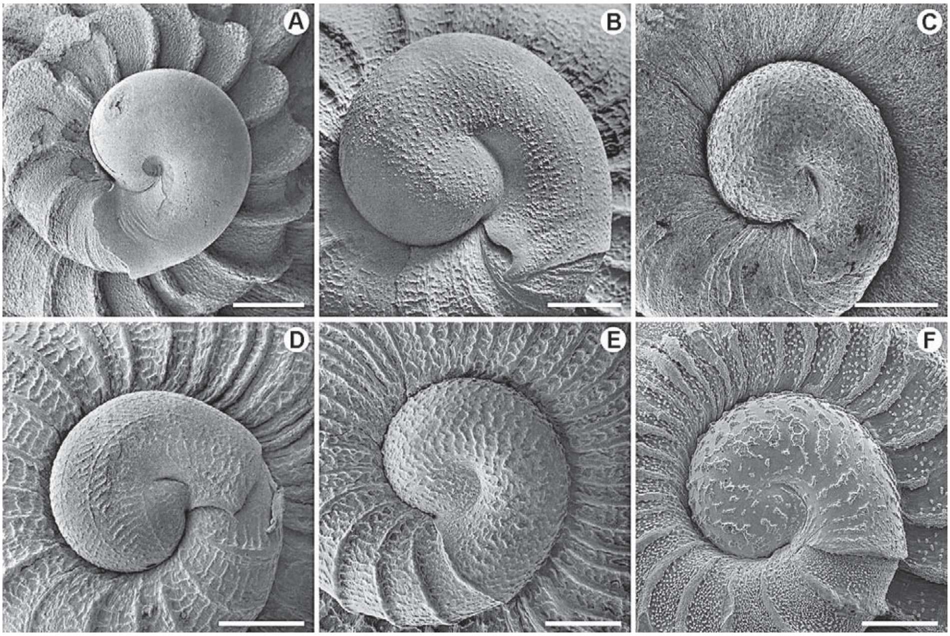

Fig. 1. Protoconch morphology in the Chilodontidae: (A) *Perrinia konos* (Barnard, 1964), exsert protoconch with little superficial sculpture, off Umzinto, KZN (NMSA D5426); (B) *Clypeostoma salpinx* (Barnard, 1964), exsert protoconch with beak-like projection on terminal lip, off Whale Rock, Eastern Cape (NMSA E289); (C) *Granata sulcifera* (Lamarck, 1822), protoconch with beak-like projection on terminal lip, Mtwalume, KZN (NMSA B8666); (D) *Ascetostoma providentiae* (Melvill, 1909), protoconch with widely spaced spiral threads and oblique axial lines in the intervals, off Dog Point, KZN (NMSA E1743); (E) *Herpetopoma serratocinctum* sp. n., protoconch with close-set axial sculpture, Kilifi, Kenya (paratype, NMSA L8270/T2641); (F) *Vaceuchelus jayorum* sp. n., protoconch with coarse axial sculpture, Réunion (paratype, M. Jay coll'n, MNHN 24810). All bars = 100 µm.

*Vaceuchelus*), in others less so (e.g. *Perrinia*). For the majority of genera, however, data on protoconch microsculpture are available for too few species to assess its intrageneric consistency.

Similarly, there is also variation in the size of the protoconch and its elevation above the first teleoconch whorl. In most species protoconch diameter lies between 200–300 µm; however, in *Clypeostoma salpinx*, *Danilia textilis* and *Vaceuchelus gemmula*, protoconch diameter may reach 340–380 µm. This appears to be more of a species character than a generic one, as other species in these genera have protoconchs within the 200–300 µm range. Mostly the protoconch projects a little above the first teleoconch whorl and is slightly down-tilted, but in some species it is strongly exsert (*Clypeostoma salpinx*, *Pholidotrope gloriosa, Perrinia konos*) or slightly sunken below the level of the first teleoconch whorl rendering the apex truncated (*Danilia* spp., *Perrinia angulifera*, *Vaceuchelus cretaceus*).

*Microsculpture* (Fig. 2)

Teleoconch microsculpture within the Chilodontidae appears to show distinct juvenile and adult facies, both of which reveal commonly occurring features that warrant further study as characters of potential phylogenetic significance. The spiral cords of most chilodontid taxa develop only during the second and third teleoconch whorls, and the first whorl is for the most part sculptured only by axial pliculae. Between these there is often an unusual vermiform microsculpture of fine, broken, wavy and frequently bifurcating, spiral threads which continues onto the second and sometimes subsequent whorls (Fig. 2A). Although this is cannot be said to be a ubiquitous feature in the Chilodontidae, it is nonetheless common within local representatives of the group, occurring in species belonging to *Ascetostoma*, *Clypeostoma*, *Danilia* and *Herpetopoma* and has been illustrated in other chilodontids by Marshall (1979: fig. 2h), Moolenbeek & Faber (1989: figs 12, 13) and Engl & Rolán (2009: figs 6, 11). Hickman (1998) indicted that this microsculpture is present from the first appearance of the group in the fossil record (Early Mesozoic).

The microsculpture of later teleoconch whorls is generally of a completely different nature, comprising densely crowded, collabral, scratch-like marks (Fig. 2B). In living

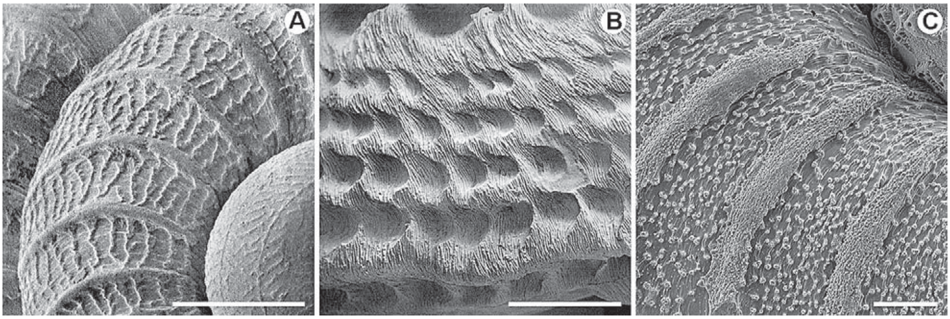

Fig. 2. Shell microsculpture in the Chilodontidae: (A) vermiform spiral threads between axial pliculae on first teleoconch whorl of *Ascetostoma providentiae* (Melvill, 1909), off Dog Point, KZN, bar = 100 µm (NMSA E1743); (B) scratch-like adult microsculpture of *Perrinia angulifera* (A. Adams, 1853), off Boteler Point, KZN, bar = 50 µm (NMSA E1762); (C) crisp, granular microsculpture between axial pliculae on first teleoconch whorl of *Vaceuchelus jayorum* sp. n., Réunion, bar = 25 µm (paratype, M. Jay coll'n, MNHN 24810).

or fresh shells these are filled with a chalky, white, dirty-brown or ash-grey intritacalx, deposited as elongate grains which fill the scratch-like marks. Such a sculpture is evident also in many members of the Calliotropidae (Marshall 1979: fig. 3g, k, o, and pers. observ.).

Although the two types of microsculpture described above are by far the most common, they are not the only ones evident in family. Marshall (1979) and Moolenbeek & Faber (1989) have illustrated a microsculpture of crisp granules in other chilodontid species. Similar sculpture is evident on the early teleoconch whorls in *Perrinia* spp., *Herpetopoma helix*, *Pholidotrope gloriosa* and *Vaceuchelus jayorum*, in place of the more common vermiform spiral threads (Fig. 2C).

Microsculptural details are not always evident and may be effected by a number of parameters. Firstly, wear, which removes fine sculptural details, although in live-collected shells this usually only effects the apical whorls (and thus the juvenile microsculpture), and some part of the adult shell generally remains unworn. Secondly, encrustations can also obscure superficial details and this is particularly so in chilodontids, which are frequently encrusted with sponges or coralline algal growths, in the case of sponges sometimes almost completely so (e.g. *Ascetostoma providentiae* and *Clypeostoma salpinx*). Thirdly, several taxa have a particularly well developed intritacalx, which instead of being grain-like, occurs as a thick chalky layer obscuring all microsculptural details (e.g. *Herpetopoma helix* and *Vaceuchelus cretaceus*). In such cases microsculpture is evident only after ultrasonic cleaning, although the extent to which such treatment might also effect the microsculpture itself is not clear.

*Radula* (Fig. 3)

The chilodontid radula is not simple to interpret. Unlike that of many other vetigastropod groups such as the Fissurellidae, Solariellidae and Trochidae, it is difficult to prepare for SEM. The marginal teeth are long and fine, and naturally tend to fold inwards, overlapping each other and the central radula field, and thus obscuring the rachidian and lateral teeth. Careful micro-manipulation of the radula is needed during the final drying stages in order to splay the marginal teeth outward. A further complication is that the differentiation between the lateral and marginal series is not always clear, the transition from one to the other being somewhat gradual.

Illustrations of chilodontid radulae were given by Troschel (1879, *Euchelus*), Hutton (1883, *Herpetopoma*), Odhner (1917, *Hybochelus*), Thiele (1924, *Euchelus*, *Danilia* and *Granata*), Cotton (1946, 1959, *Granata* and *Herpetopoma*), McLean (1970, *Mirachelus*), Olsson (1971, *Turcica*), Beu & Climo (1974, *Danilia*), Quinn (1979, *Mirachelus*) and Guidastri *et al*. (1984, *Danilia* and *Putzeysia*). More recently, radula morphology within the group as a whole was discussed and summarised by Hickman and McLean (1990) who used radula characters exclusively in their diagnosis of the subfamily Eucyclinae. Amongst the most significant features noted were the so-called ‘hooded’ rachidian, complexly interlocking lateral tooth bases, rectangular latero-marginal plate and broad, mitten-shaped outermost marginal tooth. The expanded lateral flanges on the rachidian shaft (the ‘hood’) and the interlocking of lateral tooth bases are clearly evident in the taxa examined here (Fig. 3A, D). A broad outermost marginal tooth is also present in many of the local species (Fig. 3B), but it seems not to be as large as that illustrated for *Turcica* (Olsson 1971; Hickman & McLean 1990) and *Bathybembix* (Hickman 1981). These teeth are generally difficult to see, often being obscured by the reflected underlying lingual membrane. In contrast, I have been unable to identify a rectangular latero-marginal plate in any of the species examined in this revision, and such has not been mentioned by the earlier authors cited above. Odhner (1917) considered the fourth lateral tooth of *Hybochelus mysticus* to be vestigial and transitional, but in his drawing this tooth is far from vestigial and retains a serrated cusp. In reality, Hickman and McLean (1990) illustrated latero-marginal plates in a species of *Calliotropis* and in view of our enhanced understanding of the classification of their 'Eucyclinae' it may be that latero-marginal plates are restricted to the Calliotropidae. Similarly, since *Turcica* is also now thought to belong to the Calliotropidae (Kano *et*

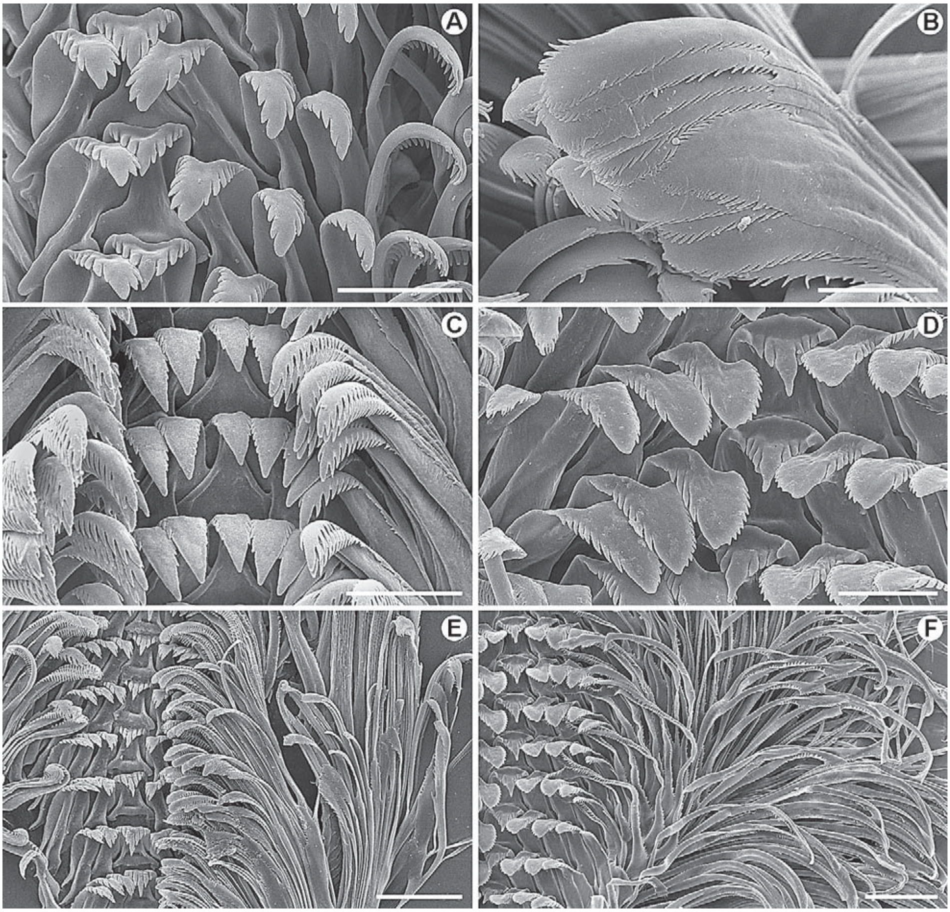

Fig. 3. Radula morphology in the Chilodontidae: (A, B) *Herpetopoma scabriusculum* (Adams & Angas in Angas, 1867), Bradleys Head, Sydney Harbour, NSW, Australia (AMS C304695): (A) rachidian and right lateral teeth, bar = 20 µm; (B) outer marginal teeth, bar = 10 µm; (C) *Granata sulcifera* (Lamarck, 1822), central field, Santa Carolina Is., central Mozambique, bar = 50 µm (NMSA K3084); (D) *Danilia textilis*, rachidian and left lateral teeth, off Rame Head, Eastern Cape, bar = 25 µm (paratype, NMSA S9912/T2594); (E) *Herpetopoma helix* (Barnard, 1964), half row of radula, SE of Green Point, KZN, bar = 25 µm (D5990); (F) *Danilia textilis*, half row of radula showing the mop-like marginal series, off Rame Head, Eastern Cape, bar = 50 µm (paratype, NMSA S9912/T2594).

*al*. 2009), the extremely large, mitten-shaped outermost marginal tooth may also be a character more distinctive of the Calliotropidae than the Chilodontidae, in which the distal portion of the outermost marginal, though broadened, is not as massively enlarged. A similar expansion of this tooth is evident in some Scissurelloidea (Høisæter & Geiger 2011; Luque *et al*. 2001), suggesting that it may be a more widespread, but seldom recorded feature in the Vetigastropoda.

Where possible I have examined the radula of at least one species in each genus to provide information on intergeneric variation in radula form. The rachidian cusp is generally well developed and the lateral flanges on its upper shaft expanded to create a hood of variable extent. In most genera there is also a conspicuous raised transverse ridge at the base of the rachidian cusp, giving the tooth a distinctly hunched appearance (Fig. 3A, D) (e.g. *Ascetostoma*, *Clypeostoma*, *Danilia*, *Herpetopoma*, *Perrinia* and *Vaceuchelus*). Guidastri *et al*. (1984) reported the same structure in *Putzeysia* Sulliotti, 1889, and it is also evident in some calliotropids (Hickman & McLean 1990). This articulates with the similarly shaped posterior border of the base-plate of the tooth in front. Commonly, the rachidian cusp is relatively coarsely dentate with a strong, lanceolate or acuminate central denticle and 3–5 smaller, also lanceolate, lateral denticles on each side (Fig. 3A, D, E) (e.g. *Ascetostoma*, *Clypeostoma*, *Danilia*, *Herpetopoma*, *Perrinia*, *Vaceuchelus* herein, and *Mirachelus* (McLean 1970; Quinn 1979)), but in *Granata* (Fig. 3C) the rachidian cusp is narrowly triangular and its lateral margins finely serrate toward the base (also illustrated by Thiele 1924 and Hickman & McLean 1990). A coarsely dentate rachidian cusp morphology is also found in some seguenziids (Marshall 1991, subfamily Asthelysinae and tribe Fluxinellini), suggesting that this commonly occurring character state in the Chilodontidae may be the ancestral condition.

Within row interaction of the tooth bases is complex in the central field, with extensive tooth overlap (Fig. 3A, C, D). The cusp of the innermost lateral is usually similar in size or slightly larger than that of the rachidian, with those of the remaining laterals being similar in size or progressively decreasing slightly in size (rarely the reverse). The shaft of the lateral teeth comprises a thickened median pillar, usually straight, but set at an angle to the long axis of the radula, with an alate flange on both margins, that on the inner margin slotting behind the median pillar of its inner neighbour, that on the outer margin lying behind the inner flange of its outer neighbour (Fig. 3A). The cusp of these teeth is generally obliquely trigonal and rather coarsely dentate, with the central denticle often spathulate, but in *Granata* the cusps are less oblique and, like the rachidian, finely serrate (Fig. 3C). In *Danilia* (Fig. 3D) the lateral tooth cusps are strongly asymmetrical, finely serrate on the inner margin and more coarsely dentate on the outer margin (also illustrated by Thiele 1924 and Beu & Climo 1974). The transition from the lateral series to the marginal series is moderately clear in some genera (e.g. *Herpetopoma* and *Vaceuchelus*, though not in all species), but in others (e.g. *Clypeostoma* and *Granata*) there is no clear-cut boundary and determining the number of lateral teeth is therefore difficult. Whether the fourth tooth is considered a lateral or a marginal is open to question in these genera. Many authors have cited the number of pairs of lateral teeth in chilodontid taxa as four (e.g. Odhner 1917; Thiele 1924, 1929; Cotton 1946; Beu & Climo 1974; Quinn 1979; Guidastri *et al*. 1984), but others have cited three (e.g. McLean 1970; Bandel 2010) and some *Vaceuchelus* species evidently have only two (see below). However, I am not inclined to put much emphasis on this character for several reasons. Firstly, because it is often somewhat subjective to determine; secondly, because it is likely to be influenced by the size of the species (hence some small *Vaceuchelus* species with only two pairs of laterals); and thirdly, in one species where the transition is clear (*Herpetopoma scabriusculum*), I observed one individual with three pairs of laterals and another with four. The character is thus also individually variable.

The marginal teeth are numerous, but the precise number is difficult to establish. In *Herpetopoma* and *Vaceuchelus*, though long and slender, they remain relatively robust (Fig. 3E), but in some other genera the marginals are even more elongate and fine, particularly so in *Danilia* in which all the marginal teeth are extremely slender and delicate (Fig. 3F), appearing as a mop-like mass along the radula margin (described as a 'hairy rope' by Beu & Climo 1974). The inner marginals are coarsely dentate or pectinate along their outer margin in most genera, particularly *Herpetopoma* and *Vaceuchelus*, and the denticles may extend some way down the shaft. However, in *Clypeostoma* and more so *Danilia*, the dentition on these teeth is finer. As mentioned above, the marginal teeth at the end of the series, particularly the outermost one, have a broader, more spathulate cusp with a finely dentate, almost feathered margin (Fig. 3B). Another unusual feature of the *Danilia* radula is the buttressed outer shaft base of the inner marginals and its raggedly dentate edge (Fig. 3F). There is also some evidence of this in *Perrinia*, and it may be a more widely occurring, but seldom visible feature.

In calliotropid taxa, judging by the illustrations given by Hickman and McLean (1990), the rachidian is narrower and has a smaller cusp relative to the laterals, but it retains a well-developed hood and has a particularly strong transverse ridge at the cusp base. Only three pairs of lateral teeth are present and they increase markedly in size from first to third (something not seen on chilodontids). The marginal series is clearly distinct from the lateral one and there is an intervening latero-marginal plate. By comparison with chilodontids, the marginals are considerably less numerous. However, Hickman and McLean (1990) only illustrated the radula of *Calliotropis* species and how reflective these are of other calliotropid taxa is unclear. If, as molecular data suggests, genera such as *Turcica* are calliotropid rather than chilodontid (Kano *et al*. 2009), then radula form in calliotropids is certainly more diverse than is evident from *Calliotropis* species alone.

### *Operculum* (Fig. 4)

The chilodontid operculum is thin, corneous and generally multispiral. In *Euchelus*, however, Pilsbry (1890 in 1889–1890) noted that the operculum is of few whorls and he likened it to that of *Littorina*, using this as a character separating *Euchelus* from *Herpetopoma*, which he stated possessed a conventionally multispiral operculum. Beu and Climo (1974) discussed the matter further in relation to the genus *Danilia* and confirmed that the *Euchelus* operculum is indeed paucispiral like that of *Littorina*. This, however, is an oversimplification, for whilst the operculum of *Euchelus* has a long growing margin and thus relatively few whorls, it is not as paucispiral as that of littorinids and has a noticeably less eccentric nucleus (compare Figs 4A and 4B). In reality, the *Euchelus* operculum represents a well-developed example of a trend, common in chilodontids, towards the reduction in the number of opercular whorls, particularly in comparison to trochoidean taxa (Hickman & McLean 1990). This trend is also evident in the Seguenziidae (Marshall 1983; Quinn 1983).

The coiling of the operculum is usually tight initially, but the outermost whorls expand somewhat more rapidly and the growing margin is correspondingly broader. Ultimately, as in *Euchelus*, the angle of accretion becomes almost tangential to the preceding opercular whorl and the growing edge is long. Operculum form in the taxa

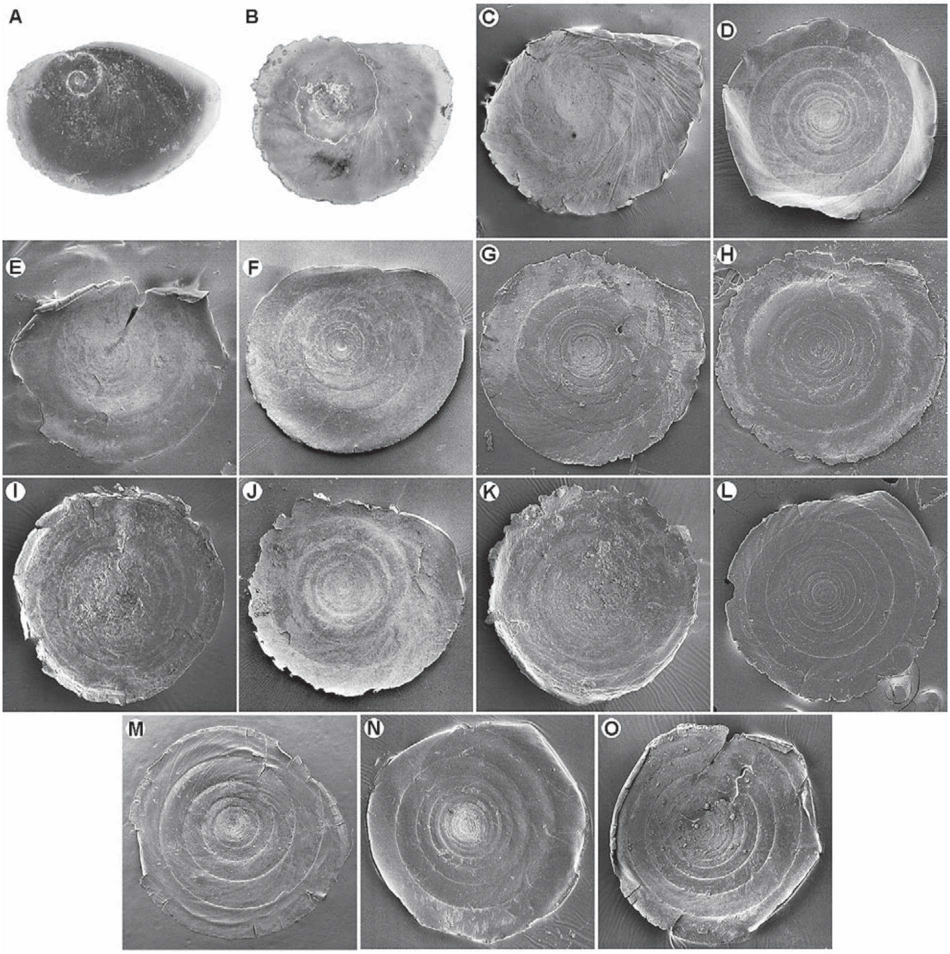

Fig. 4. Operculum morphology in the Chilodontidae: (A) *Littorina littorea* (Linnaeus, 1758), Cancale, Brittany, France, max. diameter 10.2 mm (NMSA G778); (B) *Euchelus asper* (Gmelin, 1791), Bombay, India, max. diameter 9.0 mm (NMSA J8066); (C) *Granata sulcifera*, Mtwalume, KZN, max. diameter 3.58 mm (NMSA V3927); (D) *Clypeostoma salpinx*, off Whale Rock, Eastern Cape, max. diameter 2.59 mm (NMSA C9502); (E) *Danilia textilis*, max. diameter 2.97 mm (holotype, NMSA E7756/T2595); (F) *Ascetostoma providentiae*, off Boteler Point, KZN, max. diameter 2.52 mm (NMSA S4904); (G) *Herpetopoma* (s.s.) *instrictum*, Low Isles, Great Barrier Reef, Queensland, max. diameter 3.17 mm (AMS C.304699); (H) *H.* (s.s.) *scabriusculum*, Bradleys Head, Sydney Harbour, Australia, max. diameter 1.78 mm (AMS C.30695); (I) *H.* (s.l.) *helix*, off Umzinto, KZN, max. diameter 1.01 mm (NMSA D5427); (J) *Vaceuchelus cretaceus*, SE of Kosi Bay, KZN, max. diameter 2.52 mm (paratype, NMSA S4006/T2638); (K) *V. natalensis*, off Umzinto, KZN, max. diameter 0.99 mm (NMSA D5428); (L) *V. semilugubris*, Réunion, max. diameter 1.28 mm (M. Jay coll'n MNHN); (M) *Perrinia angulifera*, off Boteler Point, KZN, max. diameter 4.44 mm (NMSA D9209); (N) *P. konos*, off Port Grosvenor, Eastern Cape, max. diameter 1.23 mm (NMSA E177); (O) *P. stellata*, Kosi Bay main coral reef, KZN, max. diameter 1.14 mm (NMSA S1985).

examined herein ranges from relatively tightly multispiral (e.g. *Herpetopoma helix*, *Perrinia stellata* and *Vaceuchelus semilugubris*, Fig. 4I, L, O), to more openly multispiral (e.g. *Ascetostoma*, *Clypeostoma* and *Danilia* species, as well as *Herpetopoma* s.s., Fig. 4D–H), to oligospiral (*Euchelus*-like) in *Granata* species (Fig. 4C), but the gradations are relative rather than categorical. Of necessity, as the rate of whorl expansion increases, the nucleus of the operculum becomes increasingly eccentric.

Hickman and McLean (1990) observed that opercular development in chilodontids does not always keep pace with growth of the shell (aperture), noting that the operculum in *Granata* it is vestigial. My own observations on *Granata sulcifera* indicate that its operculum, though it does not completely close the shell aperture, is not truly vestigial, its diameter equalling approximately half that of the aperture. In *G. imbricata* it is considerably smaller, relative to the aperture, but still not vestigial when compared to the miniature operculum of the similarly shaped stomatelline trochid genus *Pseudostomatella* (Herbert 1998).

*External anatomy* (Figs 5, 6)

Hickman & McLean (1990) and Hickman (1998) have summarised the basic features of the external anatomy of chilodontid taxa, building upon earlier descriptions provided by Beu & Climo (1974) and Guidastri *et al*. (1984). Judging from the species examined in this study, although the basic ground plan is similar, there is considerable variation in detail. However, since these details are largely available for only one species in each genus, it is not possible to establish whether the features reported here are broadly characteristic for the respective genera as a whole.

Cephalic lappets are present, the free margin ranging from finely digitate to microscopically fimbriate. The cephalic tentacles are well developed and micropapillate. The eyes are prominent, on short stalks not fused to the cephalic tentacles; the eye itself is subterminal and black. Immediately behind the right eyestalk, sometimes appearing to arise from its base, is a post-ocular peduncle. This may be nearly as long or longer than the eyestalk and is not micropapillate, but it is often slightly expanded and flattened distally, and a dorsal longitudinal groove is frequently evident. It is present in both

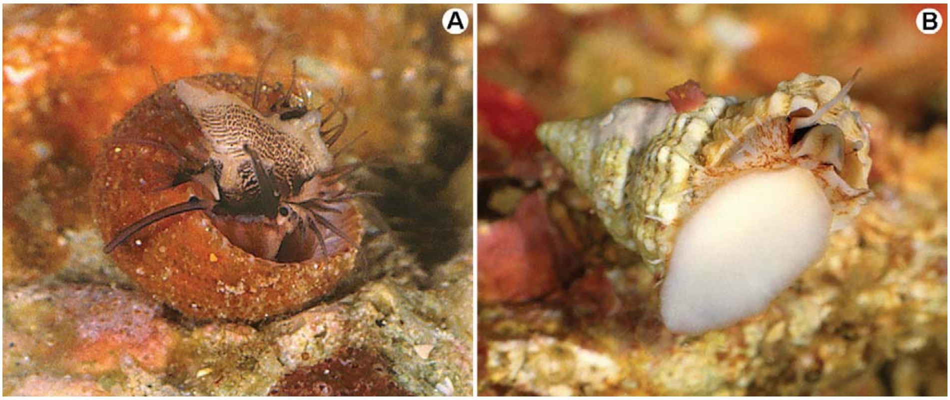

Fig. 5. Living animals: (A) *Ascetostoma providentiae* (Melvill, 1909), off Boteler Point, KZN, shell diameter 7.3 mm (NMSA S8961); (B) *Perrinia angulifera* (A. Adams, 1853), NE of Liefeldt's Rocks, KZN, shell length 12.8 mm, left cephalic tentacle damaged (NMSA E4344).

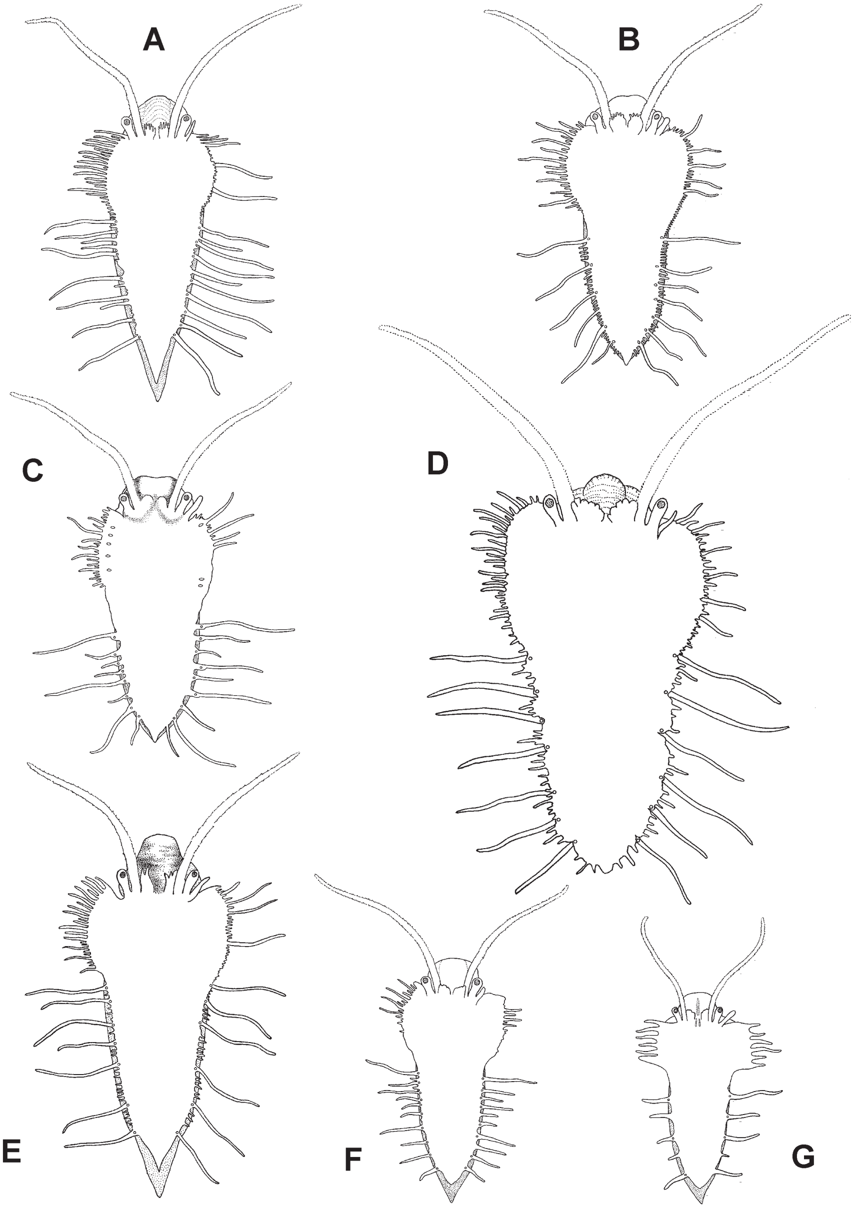

Fig. 6. External anatomy of Chilodontidae. Schematic illustrations of the external features of the head-foot, viewed from above: (A) *Ascetostoma providentiae* (Melvill, 1909); (B) *Clypeostoma salpinx* (Barnard, 1964); (C) *Danilia textilis* sp. n.; (D) *Granata sulcifera* (Lamarck, 1822); (E) *Perrinia angulifera* (A. Adams, 1853); (F) *Vaceuchelus cretaceus* sp. n.; (G) *V. natalensis* (Smith, 1906).

sexes. An additional very small process, the subocular tentacle is occasionally present projecting from beneath the base of the right eyestalk (e.g. in *Granata*, see below and Kano 2008). The snout is often pigmented, has extensive ventro-lateral flanges and the ventral lip is deeply split in the mid-line.

The neck lobes are not fused to the eyestalks, arising instead adjacent to and overlapping the snout flanges, below the cephalic tentacles. Both neck lobes are well developed, the free margin microscopically fimbriate and bearing a series of micropapillate tentacles often of two or three size ranks. There is considerable variation in the number and arrangement of the neck lobe tentacles between genera. Commonly these arise from just under the lobe margin. Similar tentacles occur posteriorly along the length of the epipodial fold, the number depending on the size of the species and the individual. Again there are two or three size ranks. In *Ascetostoma*, *Clypeostoma*, *Granata* and *Perrinia* there are minute tentacles between the larger tentacles, but these are absent in *Danilia* and *Vaceuchelus*. Free-standing, mushroom-like epipodial sense organs such as occur in many trochiodean genera are not evident, even beneath neck lobes, but most of the larger epipodial tentacles have a basal swelling on the ventral side which probably represents an epipodial sense organ. Similar swellings are sometimes evident at the base of the larger neck lobe tentacles and *Danilia* possesses several distinct sense organs on the underside of its neck lobes.

The ctenidium is bipectinate with a short afferent membrane and thus the free portion is long. The right hypobranchial gland is well developed and trigonal in shape, surrounded on two sides by the rectum which loops around its left margin. In *Granata* the gland is particularly large, ovate to kidney-shaped, with the rectum curving around the left side. It is responsible for producing the foul-smelling, milky secretion that is emitted when animals of this genus are disturbed (Hickman 1998, and pers. observ.). The rectum is generally turgid, filled with a longitudinally ridged faecal string composed of amorphous microscopically particulate faecal material. It extends further forward than is the case in trochoidean taxa, almost reaching the anterior right extremity of the mantle edge. Distally it is free of the mantle cavity wall and tapers to form a nozzle, the tip of which frequently possesses a minute tentacle-like appendage.

The presence of a post-ocular peduncle in chilodontids is a significant feature and one reflective of their seguenzioidean affinity (Kano 2008). This is distinct from, and should not be confused with, the subocular tentacle, a structure found also in many Trochoidea. The function of the post-ocular peduncle is unclear, though a penis-like role as a conduit for sperm transfer during pseudo-copulation has been suggested for a similar structure found in calliotropids (Dall 1889). If such is the case, then its presence in both sexes is puzzling and requires an explanation – something that has not yet been provided. Similar structures are evident in other vetigastropods, some present only in males, but care needs to be taken before inferences relating to the function of these structure and the phylogenetic implications of their presence are drawn, since their structure has not been investigated in detail and their homology has not been demonstrated.

## BIOLOGY, ECOLOGY AND ZOOGEOGRAPHY

Chilodontid gastropods inhabit a considerable depth range, from the intertidal zone (e.g. *Euchelus*, *Granata*, *Herpetopoma* and *Vaceuchelus*) to depths of 2000 m (*Danilia*) or more (*Putzeysia*). However, despite the fact that some species are intertidal and may even be common, the biology of the family as a whole is poorly known. The group is thought to have arisen in the Early Mesozoic of Europe, and to have subsequently radiated in the Cretaceous, both in terms of diversity and geographic range (Hickman & McLean 1990), in association with the contemporaneous expansion of the carbonate-based habitats on which they lived. Today the greatest diversity, at both genus and species level, remains associated with warm water and hard, carbonate-based substrata, as evidenced by the rich chilodontid fauna of the Philippines (Poppe *et al*. 2006; Poppe & Tagaro 2008) and the central Indo-West Pacific in general. Mostly this fauna occurs in near-shore and continental shelf ecosystems (<200 m). The greatest depth at which living specimens have been found in the south-western Indian Ocean is 277 m (*Clypeostoma salpinx*; Table 1). Such is in marked contrast to the Calliotropidae, which are largely bathyal (>200 m), and are associated with unconsolidated substrata and colder water (including the Antarctic).

Consistent with the above, the Chilodontidae is clearly a tropical element within the fauna of the south-western Indian Ocean. Only one species, *Vaceuchelus gemmula*, ranges beyond the subtropical waters of the east coast of South Africa in to the warm-temperate waters of the southern Cape. This is also the only chilodontid endemic to South Africa. A considerable portion of the regional chilodontid fauna (14 out of 27 recorded species, 51.9 %); however, is endemic to the south-western Indian Ocean (Table 1), indicating a significant focus of endemism in this part of the Indo-West Pacific. This may be due to the prevailing south-westerly current regime, which would tend to restrict nascent taxa to this region. A further five species (18.5 %) are endemic to the western Indian Ocean and eight (29.6 %) are more widespread Indo-West Pacific taxa ranging east to south-east Asia. Interestingly, for some of the regionally endemic species there is a closely similar species occurring in the central Indo-West Pacific, suggestive of a sister taxon relationship spanning the Indian Ocean (e.g. *Ascetostoma providentiae* and *A. ringens*, and *Vaceuchelus cretaceus* and *V. pagoboorum*).

Almost without exception, the chilodontids of the south-western Indian Ocean are associated with hard substrata (Table 1). Commonly these are carbonate-based, but some species occur in habitats lacking and obvious carbonate facies, such as the rocky shore of KwaZulu-Natal and Eastern Cape (*Vaceuchelus natalensis* and *V. gemmula*), and the sponge-dominated communities on the edge of the continental shelf in the same region (*Clypeostoma salpinx* and *Danilia textilis*). The latter communities, however, often contain a significant octocoral and scleractinian component. Only one species, *Granata sulcifera*, occurs in habitats dominated by soft substrata, and can be found in sheltered bays with muddy sand, but even here it lives attached to hard objects. This species evinces a somewhat limpet-like mode of life that is taken further by the Australian *G. imbricata*, which clings tenaciously to the rocks on which it lives and is unable to right itself once dislodged (Hickman 1998). Both species are negatively phototropic and secrete a foul-smelling, milky mucus when disturbed (see external anatomy above), as evidently does *G. lyrata* (Kano 2008). Unlike *G. imbricata*, however, *G. sulcifera* has no difficulty righting itself if upturned, using the highly mobile and extendable anterior portion of the foot.

Almost nothing is known of their diet, though one may speculate, given the robust interlocking of the teeth in the central field of the radula, and the generally strong dentition of the rachidian and lateral tooth cusps, that they graze superficially on the hard substrata on which they occur and on the organisms growing thereon, the long marginal teeth being used to gather up dislodged material. The unusual marginal teeth of *Danilia* species, however, are suggestive of a more specialised diet, perhaps associated with the deep-water corals with which they commonly co-occur.

TABLE 1

Chilodontidae of the south-western Indian Ocean: geographical distribution, bathymetric range and principle habitat preferences. Where possible, bathymetric data are given only for live collected samples. Distribution: IWP – Indo-West Pacific; MI – Mascarene Islands; RSA – South Africa; SWIO – south-western Indian Ocean; WIO – western Indian Ocean.

| | **Species** | **Distribution** | **Depth range in SWIO** | **Principle habitat in SWIO** |
|---|---|---|---|---|
| 1 | *Clypeostoma reticulatum* | SWIO | 228–230 m, dead shells | no data |
| 2 | *Clypeostoma salpinx* | SWIO | 60–277 m, living | sponge communities |
| 3 | *Clypeostoma meteorae* | WIO | 80–257 m, dead shells | no data |
| 4 | *Clypeostoma nortoni* | IWP | 90–333 m, dead shells | no data |
| 5 | *Danilia boucheti* | SWIO | 238–249 m, dead shells | no data |
| 6 | *Danilia textilis* | SWIO | 150–250 m, living | sponge communities |
| 7 | *Ascetostoma providentiae* | SWIO | 50–85 m, living | sandstone and coral rubble |
| 8 | *Euchelus asper* | IWP | no data | no data |
| 9 | *Euchelus atratus* | IWP | no data | no data |
| 10 | *Herpetopoma* (s.s.) *instrictum* | IWP | near shore, living | coral rubble |
| 11 | *Herpetopoma* (s.s.) *serratocinctum* | WIO | near shore, living | coral rubble |
| 12 | *Herpetopoma* (s.s.) *seychellarum* | WIO | no data | no data |
| 13 | *Herpetopoma* (s.s.) *stictum* | MI | near shore, living | fringing reef systems |
| 14 | *Herpetopoma* (s.l.) *helix* | SWIO | 70–180 m, living | varied hard substrata |
| 15 | *Herpetopoma* (s.l.) ?*naokoae* | IWP | 280–375 m, dead shells | no data |
| 16 | *Herpetopoma* (s.l.) *xeniolum* | IWP | near shore to 247 m, dead shells | no data |
| 17 | *Perrinia angulifera* | IWP | 50–65 m, living | coral rubble and lithothamnion pebbles |
| 18 | *Perrinia konos* | SWIO | 55–110 m, living | sponge and coral rubble |
| 19 | *Perrinia stellata* | WIO | 18–50 m, living | inconclusive |
| 20 | *Pholidotrope gloriosa* | SWIO | 35–250 m, dead shells | rocky substrata |
| 21 | *Vaceuchelus cretaceus* | SWIO | near shore to 70 m, living | coral rubble |
| 22 | *Vaceuchelus jayorum* | SWIO | near shore, living | rocky substrata |
| 23 | *Vaceuchelus gemmula* | RSA | low shore to 115 m, living | rocky substrata |
| 24 | *Vaceuchelus natalensis* | SWIO | low shore to 84 m, living | rocky substrata |
| 25 | *Vaceuchelus semilugubris* | MI | near shore, living | rocky substrata |
| 26 | *Granata cumingii* | WIO | low shore, living | under rocks |
| 27 | *Granata sulcifera* | IWP | low shore to 18 m, living | under rocks and coral blocks |

As is to be expected in vetigastropods the sexes are separate in chilodontids, but little is known of their reproductive biology. Duch (1969) recorded that in the littoral *Euchelus gemmatus* (Gould, 1845) (probably a species of *Herpetopoma*) spawning is associated with the spring equinox and is initiated by pair formation, subsequent to which gelatinous egg masses are deposited on hard surfaces, inside which the embryo grows into a fully developed veliger that hatches as a 'semi-crawling larva' after 1–2 weeks. One may assume, therefore, that, in this species at least, a free-swimming stage, if such exists at all, is at most brief. Such may not be the case in other species, particularly those that possess a prominent beak on the protoconch lip (e.g. *Clypeostoma salpinx* and *Granata sulcifera*), suggesting, as mentioned above, a longer, more active swimming phase.

In life, the shell of many species is covered, often entirely so, with a living encrusting sponge, particularly in *Euchelus* and *Herpetopoma* (Odhner 1917; Gardner 1975; Walsby & Morton 1982; Hickman & McLean 1990; Wilson 1993; Poppe *et al*. 2006; Poppe & Tagaro 2008). Others commonly have superficial growths of white or pink encrusting coralline algae.

## TAXONOMY

### Family Chilodontidae[1] Wenz, 1938

The use of generic names now considered to belong to the Chilodontidae has been complicated by a lack of precision. Doubtlessly, in many cases this is due to the fact that the type species are poorly known and thus the diagnostic characters of the genera are not clearly identified. Genera such as *Turcica* (*sensu stricto*, a calliotropid genus) and *Euchelus* have been employed as hold-all taxa that in reality represent ill-defined assemblages of dubiously related species. Some clarity is beginning to emerge as more material is studied, but there remain problematic areas where shell characters, when considered across a range of taxa, seem to intergrade between genera, as for example between *Euchelus* and *Herpetopoma*. Even within *Herpetopoma* there is a puzzling diversity of shell form, which suggests that it may be a composite taxon (see below). I propose two new genera for taxa which exhibit distinctive combinations of characters not present in the existing genera. A third new genus is proposed for extant species currently referred to *Agathodonta*, a fossil genus that I consider is not appropriate for these Recent forms.

The genera are not treated alphabetical order, but are grouped loosely in terms of similarity in shell form. However, this should not be taken to indicate any suggestion of phylogenetic relationship. Such inferences must await analysis of molecular data and a more complete dataset of morphological characters. Species treatments do not contain diagnoses as these tend to be repetitive of information given in the description. Instead, I provide keys to species which summarise the characters important for species discrimination and represent a more useful tool for identification. Further discussion of distinctive features and comparison with similar extralimital species is provided under 'Remarks'. In addition to the Recent species discussed, I draw attention to a fossil taxon *Chilodonta* (*Agathodonta*) *africana* described by Rennie (1930) from Upper Cretaceous deposits on the Pondoland coast, Eastern Cape. The holotype (SAMC 8630) somewhat resembles *Ascetosotoma providentiae* (see below) and it seems correctly referred to the Chilodontidae.

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[1] Chilodontinae Wenz, 1938 (Mollusca) is homonymous with Chilodontidae Macalister, 1876 (Ciliophora) and Chilodontinae Eigenmann, 1910 (Pisces). An application has been submitted to the International Commission on Zoological Nomenclature (Case 3555) to emend the spelling of Chilodontidae Wenz, 1938 to Chilodontaidae (Herbert & Bouchet 2011). While such a case is under consideration by the Commission, prevailing usage is to be retained (ICZN 1999: Art. 82.1).

*Excluded taxa*

*Leptothyra alfredensis* Bartsch, 1915, and *Cyclostremella alfredensis* Bartsch, 1915, both from Port Alfred, Eastern Cape, superficially resemble *Vaceuchelus*, but show much greater similarity to the skeneid genus *Parviturbo* Pilsbry & McGinty, 1945 (Hickman & McLean 1990; Warén 1991). Unfortunately, this cannot be confirmed by examination of the radula, as neither species has ever been found alive. Both names may quite possibly apply to the same species. Likewise *Vitrinella agulhasensis* Thiele, 1925, from the Agulhas Bank, resembles *Vaceuchelus*, but is also probably a species of *Parviturbo*.

*Stomatella cancellata* Krauss, 1848, the type species of *Hybochelus* Pilsbry, 1890, was erroneously described from Table Bay, Cape Town. The species is not part of the southern African fauna and occurs instead in the central Indo-West Pacific (Wilson 1993; Herbert 1996; Herbert & Warén 1999; Poppe *et al*. 2006; Poppe & Tagaro 2008).

Material referable to *Tibatrochus* Nomura, 1940 has been dredged off southern Mozambique and north-eastern South Africa, but is not included in this review as I strongly suspect the genus belongs in the Calliotropidae.

Key to genera of Chilodontidae in the south-western Indian Ocean
(applies only to specimens with mature apertural dentition)

1 Columella lacking any form of dentition or with at most a low rounded bulge at its base ........................................ 2
– Columella with one or more denticles (mature specimens) ........................................ 3

2 Shell small (adult diameter <10 mm) and predominantly white, turbiniform; sculpture cancellate or foveolate ........................................ **Vaceuchelus**
– Shell larger, depressed turbiniform to ear-shaped, last whorl expanding rapidly and aperture consequently large; interior highly nacreous ........................................ **Granata**

3 Aperture lacking a U-shaped notch at junction of basal and columella lips ........................................ 4
– Aperture with a distinct U-shaped notch at junction of basal and columella lips .. 6

4 Periphery angled and marked by a well-developed, often keel-like, spiral cord, sometimes stellate; suture strongly channelled; spiral sculpture inside outer lip extending deep within aperture ........................................ **Perrinia**
– Periphery more or less rounded ........................................ 5

5 Adult shell generally exceeding 10 mm in length; operculum oligospiral ........................................ **Euchelus**
– Adult shell less than 10 mm in length; operculum multispiral ........................................ **Herpetopoma** (part)

6 Columella with a single tooth above U-shaped basal notch ........................................ 7
– Columella with 2 teeth above U-shaped basal notch ........................................ 8

7 Shell trochiform and with coarsely cancellate sculpture; periphery almost stellate; outer lip with subterminal external varix; parietal callus expanded beyond aperture ........................................ **Pholidotrope**
– Shell turbiniform-conical and with finely cancellate or beaded sculpture; periphery more or less evenly rounded; outer lip lacking external varix; parietal callus not expanded ........................................ **Herpetopoma** (part)

8 Exterior of outer lip with a strong, rib-like, subterminal varix; apex truncate and protoconch sunken ........................................................................... **Danilia**

– Exterior of outer lip lacking such a varix, at most with a broad, low thickening behind outer lip; apex not truncate and protoconch exsert ....................................9

9 Umbilicus present, lined and apically plugged with callus................ **Ascetostoma**

– Umbilicus absent.......................................................................... **Clypeostoma**

## Genus **Clypeostoma** gen. n.

Etymology: From Latin *clypeus* (a shield) and Greek *stoma* (a mouth); in reference to the shield-like inductural callus. Gender neuter.

Type species: *Turcica salpinx* Barnard, 1964.

Diagnosis: Shell moderately elevated; spire whorls flat-sided to weakly convex; suture indented, level with subperipheral cord; sculpture of spiral cords and axial pliculae, cords ornamented with squamose beads where crossed by pliculae; aperture subcircular to obliquely D-shaped; outer lip conspicuously flaring beyond an internal collabral thickening; columella stout and bearing 2 rounded teeth when mature; thickened interior of outer lip with ridge-like denticles, that nearest columella largest and separated from basal columella tooth by deep U-shaped notch; umbilical and parietal region covered by glossy inductural callus shield; shield raised and flaring basally where it joins basal lip; umbilicus absent; circumference of aperture and inductural shield more or less in one plane, obliquely tangential to base of last adult whorl; outer lip not thickened externally; protoconch exsert and with a distinct sinusigera-like projection on terminal lip.

Remarks: Extant species belonging to this genus have previously been referred to *Agathodonta* Cossmann, 1918 (McLean 1984; Neubert 1998; Vilvens 2001; Vilvens & Héros 2003; Poppe *et al*. 2006). The type species of *Agathodonta*, by original designation, is *Trochus dentiger* d'Orbigny, 1843 (an unjustified emendation of *Trochus dentigerus* d'Orbigny, 1843) from the Lower Cretaceous (Neocomian) of north-eastern France, which has recently been shown to be a junior synonym of *Littorina elegans* Deshayes in Leymerie, 1842 (Kollmann 2005). Whilst extant species undoubtedly exhibit some similarity with *Agathodonta*, examination of the lectotype (designated by Kollmann 2005: 70, pl. 9, fig. 6) and topotypic material of *Trochus dentigerus* (UCBL, Fig. 7A, B and MNHN, Fig. 7C, respectively) indicates that its shell has more strongly convex whorls, does not develop a flaring aperture or expanded inductural callus shield, has a broad, thickened external varix behind the outer lip, with additional varices on the spire whorls (arrowed in Fig. 7A, C), shows little evidence of any denticles or ridges inside the outer lip, and the columella teeth, instead of being discrete teeth (which develop only at maturity), appear to be the ends of ridges spiralling up the columella. In addition, the sculpture is considerably less coarse, the spiral cords being finely and regularly beaded, and without axial pliculae in their intervals. Since these characters are at variance with those of Recent species, I have chosen not to refer extant material to *Agathodonta*. The original figure of *Trochus dentigerus* provided by d'Orbigny (1843) is misleading in not showing the varices (Fig. 7D), but Cossmann's figures clearly do so, though strangely he does not mention them in his description of the genus (Cossmann 1918: pl. vii, fig. 9). Such varices also occur in *Calliovarica* Vokes, 1939, which is also probably referable to the Chilodontidae (Beu & Raine 2009).

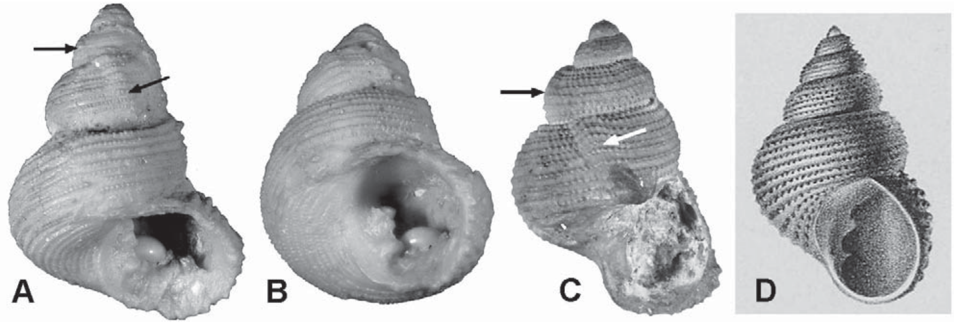

Fig. 7. *Agathodonta* Cossmann, 1918: (A, B) cast of lectotype of *Trochus dentigerus* d'Orbigny, 1843 (Dupin coll'n, UCBL, EM-32041-1, originally in l'École des Mines de Paris), designated lectotype by Kollmann (2005: 70, pl. 9, fig. 6), specimen also illustrated by Cossmann (1918: pl. vii, fig. 9), Neocomian, Marolles, Aube, France, length 18.3 mm (cast in NMSA L2816); (C) topotype of *T. dentigerus* d'Orbigny, 1843, Neocomian, Aube, Marolles, length 11.7 mm, diameter 8.1 mm, (d'Orbigny coll'n, MNHN 4927); (D) original figure of *T. dentigerus* provided by d'Orbigny (1843: pl. 177, fig. 9). Arrows indicate varices on spire whorls.

Since no other genus-rank name is available for these extant species, I propose the new genus *Clypeostoma*, with *Turcica salpinx* Barnard, 1964, as type species. Other described taxa referable here are *Agathodonta elongata* Vilvens, 2001, *A. meteorae* Neubert, 1998, *A. nortoni* McLean, 1984, *Euchelus townsendianus* Melvill & Standen, 1903 and perhaps *Perrinia cecileae*, *P. docili* and *Herpetopoma barbieri* all of Poppe, Tagaro & Dekker (2006). Whereas *Clypeostoma elongatum, C. reticulatum* and *C. salpinx* are distinctive, the others are confusingly similar and exhibit intergrading variability, suggesting that some at least may prove to be synonyms (see below). When a good series of samples is available for one taxon, e.g. *C. salpinx*, it is clear that allowance must be made for some individual variation in size at maturity, L/D ratio, spiral cord number and strength of apertural dentition. In the absence of such information for the other taxa, it is not possible to make informed comment on potential synonymies within the genus. In some cases the differences evident between the species are small and perhaps of limited significance. *C. meteorae* and *C. townsendianum* were both described from the mid to outer continental shelf of the north-western Indian Ocean and may well be synonyms, even though the holotype of former is smaller than the figured syntype of *Euchelus townsendianus* (length 7.5 *vs* 10.4 mm), which I here refigure and designate as lectotype (Fig. 12F, G).

*Clypeostoma* differs from *Danilia* in lacking an external varix behind the outer lip and in not having a sunken region median to the thickened edge of the columella pillar. In *Danilia* the shell apex is also truncate and the protoconch flat or a little sunken. In *Ascetostoma* gen. n. the apertural dentition is more complex and the umbilicus is retained and lined with callus. Some species referred to *Herpetopoma* Pilsbry, 1890, also have a strong U-shaped notch at the base of the columella, but such species have only one distinct columella tooth, lack an expanded inductural callus and often retain an open umbilicus.

### Key to species of *Clypeostoma* in the south-western Indian Ocean

1 Columella teeth well developed, of more or less equal size (though not necessarily the same shape) ........................................................................................2

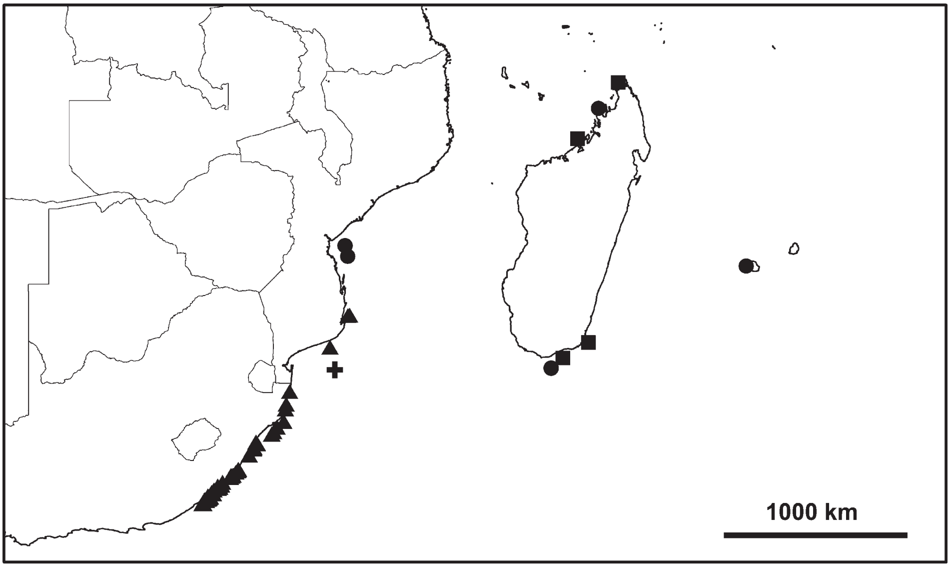

Fig. 8. Distribution of *Clypeostoma* species in the south-western Indian Ocean. *C. meteorae* (squares), *C.* cf. *nortoni* (circles), *C. reticulatum* (cross) and *C. salpinx* (triangles). Each symbol represents one or more records.

– Columella teeth relatively weak, the lower one usually stronger; basal callus shield extensive, smooth and glossy; South Africa and southern Mozambique.... **salpinx**

2 Adult shell relatively large (length >16 mm); sculpture coarsely reticulate; currently known only from Almirante Leite Knolls ........................................... **reticulatum**

– Adult shell smaller (length <15 mm); sculpture relatively fine .............................3

3 Adult shell <8.0 mm in length; protoconch diameter 220–240 µm; basal callus shield not extensive; dentition of aperture and callus shield well developed .......... ........................................................................................................... **meteorae**

– Adult shell >9.0 mm in length; protoconch diameter 310–320 µm; basal callus shield extensive, but with weak superficial ridging (except inside aperture) .......... ........................................................................................................ cf. **nortoni**

## **Clypeostoma reticulatum** sp. n.

Figs 8, 9

Etymology: From Latin *reticulatus* (netted); in reference to the cancellate, net-like sculpture.

Description:

*Shell*: Large for the genus (length up to 16.7 mm), trochoid-turbiniform, with conical spire and relatively deep, globose last adult whorl (L/D=1.38–1.44, last adult whorl 0.70–0.74 of shell length); teleoconch of up to 6 whorls; first two whorls rounded, whorls 3–4 more or less flat-sided, subsequent whorls convex; apical angle 69–74°; suture of spire whorls level with and mostly covering subperipheral cord of preceding whorl, demarcated by a well-developed channel below peripheral cord; shell periphery

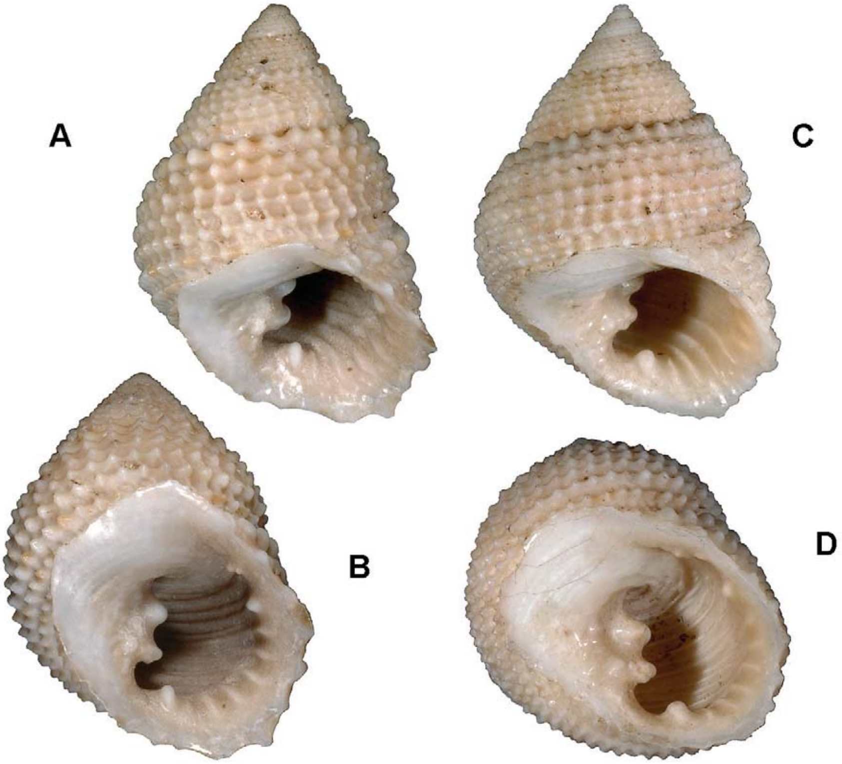

Fig. 9. *Clypeostoma reticulatum* sp. n., Almirante Leite Knolls, Mozambique Channel: (A, B) holotype, length 16. 4 mm (MNHN); (C, D) paratype, length 16. 3 mm (MNHN).

rounded. First teleoconch whorl worn in all available specimens, but traces of curved axial pliculae remaining; 3 spiral cords arise during second whorl, with a fourth appearing below adapical suture toward end of whorl; abapical (peripheral) cord strongest; cords crossed by axial pliculae and beaded at intersections; a fifth cord arising below subsutural cord during third whorl (sometimes a sixth during fourth whorl), penultimate whorl thus with 5–6 spiral cords, an additional cord becoming evident level with abapical suture; sculpture remaining similar but strengthening on fourth and subsequent whorls; beads on subsutural cord developing in to angular nodules (25–30 on last adult whorl); intervals between cords slightly wider than cords themselves (that below peripheral cord widest) and crossed by axial pliculae creating quadrate interstices; alignment of pliculae from interval to interval somewhat variable and irregular due to intercalation of additional pliculae, but general pattern of sculpture clearly reticulate, particularly on spire whorls; beads stronger and axially elongated on latter part of last adult whorl; sutural cord of spire whorls may emerge above suture toward end of last adult whorl. Base rounded with 4–6 spiral cords, the last small and partly concealed by reflected lip of aperture; basal cords somewhat more finely beaded than those above periphery. Peristome markedly oblique, more or less in one tangential plane; aperture subcircular to roundly quadrate; columella lip robust, with 2 relatively massive teeth, the upper one slightly more robust, the lower one somewhat narrower and with a small denticle on its lower margin; parietal and umbilical region covered with well-developed, glossy callus which flares outward over base; callus porcelaneous and mostly smooth, but with some beads of unequal size in region adjacent to columella teeth; one particularly strong bead at base of lower columella tooth; edge of callus raised and flaring where it joins flared margin of outer lip. Outer lip lacking an external varix, but somewhat thickened internally and strongly flaring, with 9 labral denticles; denticle nearest base of columella largest and peg-like, separated from basal columella tooth by a U-shaped notch; remaining labral denticles representing the ends of in-running spiral ridges extending deep into aperture, where there may be additional intermediary ridges; similar ridges present inside parietal portion of aperture; denticle at end of uppermost labral spiral ridge comprises a somewhat disjunct swelling, itself with 2 or 3 smaller granules; ridge below this ending in a single large elongate denticle.

Microsculpture: No fresh material available; all traces of intritacalx lost, but some evidence of scratch-like microsculpture present on later whorls.

Protoconch: Missing in all available specimens.

Colour: Shell mostly uniform cream-white to dirty buff, with some pale orange-brown spotting, particularly on subsutural and basal cords.

Dimensions: Holotype, length 16.4 mm, diameter, 11.4 mm; largest specimen, length 16.7 mm.

*Operculum, radula and external anatomy*: Unknown.

Holotype (Fig. 9A, B): MOZAMBIQUE: Mozambique Channel, Almirante Leite Knolls (26.200°S 35.033°E), -228–230 m, Campagne Mainbaza, st'n DW3167, dredged RV *Vizconde de Eza*, 16.iv.2009 (MNHN 24646).

Paratypes: Same data as holotype (MNHN 24647, 4 specimens, of which 3 adult, 1 juvenile).

Distribution and habitat (Fig. 8): Known only from Almirante Leite Knolls, approx. 250 km due east of Maputo, Mozambique, -228–230 m; rocky substrata with corals, sponges and gorgonians (Fraussen & Rosado 2011).

Remarks: This species is distinctive amongst south-western Indian Ocean chilodontids on account of its relatively large size, coarse sculpture and well-developed apertural dentition. The most similar species is *Clypeostoma elongata* (Vilvens, 2001) from Indonesia and the Philippines, but that species is still larger (adult length over 19 mm), has a more acute apical angle (<60°), a less rounded last adult whorl and only four spiral cords on the spire whorls. In addition, the aperture is transversely elongate and the lower columella tooth is larger than the upper one and bears additional denticles. *C. reticulatum* shows some variation in the strength of the sculpture (coarseness of reticulation), but this may in part be caused by damage to the outer lip during growth and the subsequent intercalation of additional spiral cords.

That this species has not been found off the Zululand coast of South Africa, a relatively well sampled area not far removed from the type locality, indicates that the isolated Almirante Leite Knolls (a volcanic seamount with numerous craters, rising from -1100 to -80 m) provide habitats of a different nature to those occurring on the continental shelf and upper slope. The station from which this material was obtained also contained an undescribed species of *Bolma* (Alf *et al*. 2010) and two new buccinid species (Fraussen & Rosado 2011), and many other new species of benthic invertebrates have been obtained from the locality as a whole (Bouchet pers. comm.), some of which have already been named (Cabezas *et al*. 2010; Komai & Chan 2010; Richer de Forges 2010).

### *Clypeostoma salpinx* (Barnard, 1964) **comb. n.**

Figs 4D, 6B, 10, 11

*Turcica salpinx*: Barnard 1964: 19, fig. 3a–d; Kensley 1973: 44, fig. 112. Type loc. (here designated, see below): off Cape Morgan, Eastern Cape, South Africa, 77 fath. [-141 m].

Description:

*Shell*: Trochoid-turbiniform, moderately elevated (L/D=1.25–1.50); teleoconch of 6–7 whorls; apical whorls convex, later ones more flat-sided; apical angle 60–70°; suture level with subperipheral cord, not itself channelled, but appearing so due to presence of a narrow sulcus below peripheral cord of preceding whorl, particularly pronounced on spire whorls; shell periphery rounded. First teleoconch whorl sculptured by somewhat sinuous axial pliculae; 3 spiral cords arise during second whorl and a fourth, beneath the adapical suture, during whorl three; sculpture of subsequent whorls comprising 4 (rarely five) spiral cords (not counting that level with abapical suture), these crossed by somewhat irregular, prosocline axial pliculae (30–40 on last adult whorl); cords with

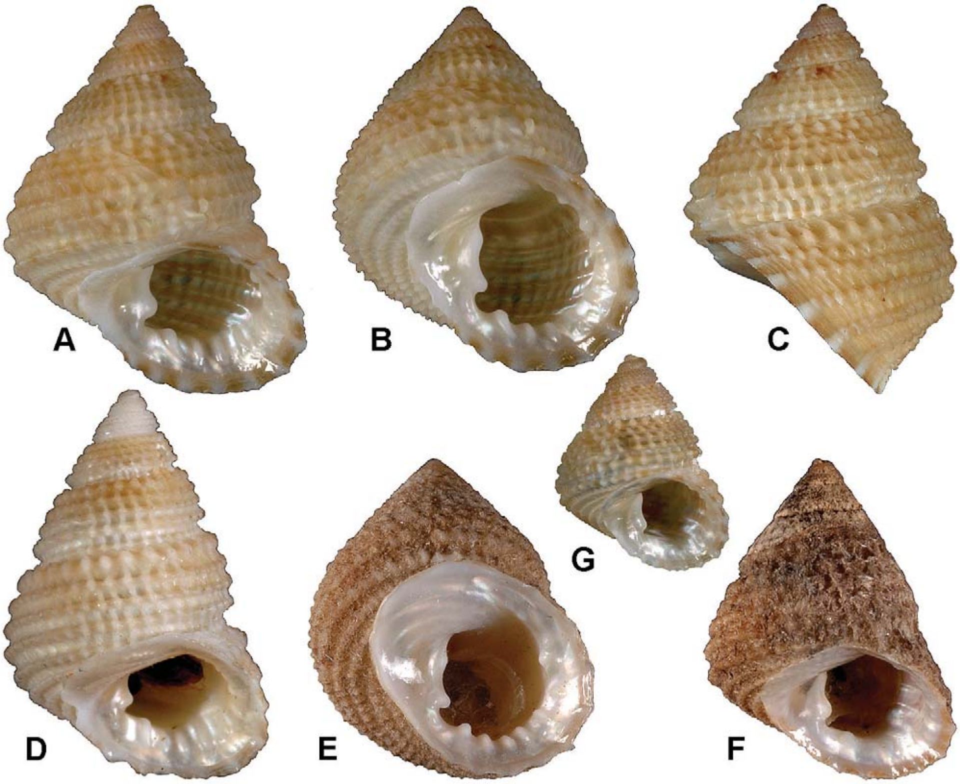

Fig. 10. *Clypeostoma salpinx* (Barnard, 1964): (A–C) live-collected adult specimen cleaned of superficial encrustations, north of Port Edward, KZN, length 11.3 mm (NMSA D1402); (D) elevated specimen, off Nthlonyane River, Eastern Cape, length 11.3 mm (NMSA C3300); (E) basal view of specimen with well-developed apertural dentition and callus shield, off Nthlonyane River, Eastern Cape, diameter 8.25 mm (NMSA C3300); (F) live-collected specimen covered with encrusting sponge, off Nthlonyane River, Eastern Cape, length 9.8 mm (NMSA C2565); (G) dwarf adult specimen (apex missing), Inhambane, Mozambique, length 6.25 mm (MNHN).

scale-like nodules where crossed by pliculae, those on uppermost (subsutural) cord frequently larger; intervals between cords slightly wider than cords themselves; cord intervals on last adult whorl occasionally with a weak intermediary cord. Base rounded, sculptured with ±6 spiral cords; cords somewhat weaker than those on apical surface, but similarly nodose; umbilicus closed in all but small juveniles (<4 whorls). Peristome markedly oblique, more or less in one tangential plane; aperture subcircular to D-shaped, flattened in the parietal region; columella lip with 2 teeth, the lower one well developed, the upper one less so; teeth bluntly rounded, separated by shallow concavity; parietal and umbilical region covered with well-developed, translucent, smooth, glossy callus; margin of callus raised and flaring basally, running smoothly into basal lip; callus with 1 or 2 small tubercles near base of lower columella tooth. Outer lip lacking external varix, but thickened internally and bearing up to 15 denticles; denticles ridge-like, more or less in a single row and usually alternating in strength, that nearest columella usually strongest and separated from basal columella tooth by a U-shaped notch; edge of outer lip flaring; interior highly nacreous, not spirally lirate (except at apertural thickening), but somewhat angled beneath cords of external surface.

Microsculpture (Fig. 11B, C): Early teleoconch whorls with vermiform spiral threads in intervals between axial pliculae; adult microsculpture of scratch-like marks, filled with intritacalx in fresh specimens, but this seldom well developed and usually obscured by superficial encrustations.

Protoconch (Fig. 11A, C): Translucent white to pale buff; diameter 360–380 µm; globose, strongly exsert and somewhat tilted; terminal lip convex with sinusigera-like beak in mid region; surface sculptured with a fine irregular granulation and a faint spiral thread midway between sutures.

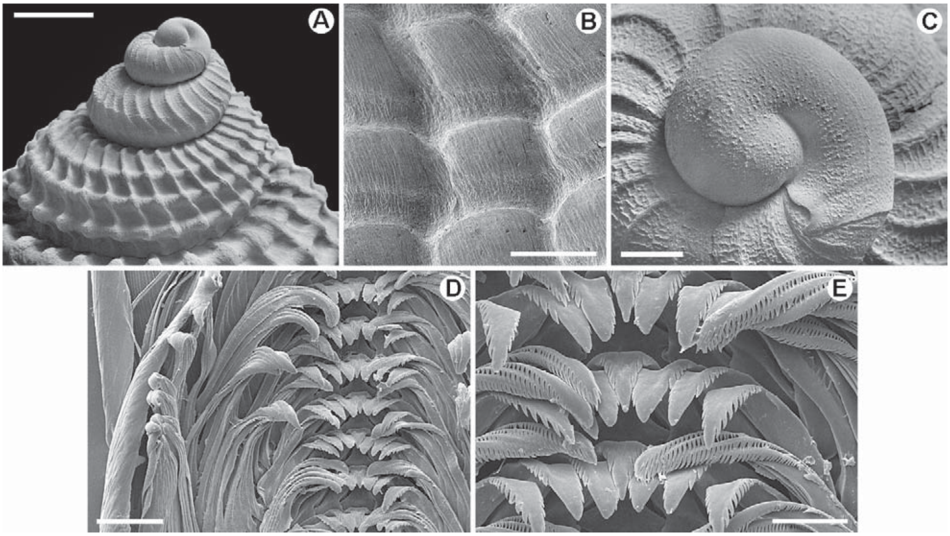

Fig. 11. *Clypeostoma salpinx* (Barnard, 1964): (A) apical whorls showing exsert protoconch, bar = 500 µm (NMSA E289); (B) adult microsculpture, bar = 50 µm (NMSA E289); (C) protoconch with sinusigera-like projection on terminal lip, bar = 100 µm (NMSA E289); (D) radula, central field and left marginals, bar = 50 µm (NMSA C2313); (E) radula, rachidian and lateral teeth, bar = 25 µm (NMSA C2313). All dredged off Whale Rock, Eastern Cape, South Africa.

Colour: Shell mostly uniform buff to pale orange-brown, occasionally nearly white; cord intervals with slight pink/green iridescence; some specimens with occasional slightly darker spots and blotches beneath suture and at edge of outer lip; live-collected specimens nearly always over-grown with a thin encrusting sponge (Fig. 10E, F).

Dimensions: Largest specimen (NMSA D4231), length 12.6 mm, diameter 9.0 mm; adult length mostly 11.0–12.5 mm, but at the northern limit of the distribution specimens are considerably smaller (adult length 6–7 mm) (Fig. 10G).

*Operculum* (Fig. 4D): Initially tightly multispiral, but whorls broadening with growth and becoming more openly multispiral.

*Radula* (Fig. 11D, E): Formula ∞+3+1+3+∞, with *ca* 80 transverse rows of teeth; transition from lateral to marginal series not clearly defined. Rachidian shaft with well-developed lateral flanges creating a distinct hood, base of cusp with raised, transverse basal ridge, cusp apex acutely trigonal with a narrow median denticle and 3–5 smaller denticles on each side. Lateral teeth overlapping extensively, their cusps asymmetrically trigonal; central denticle large on first lateral, progressively decreasing in size on second and third; side denticles few on first lateral, but progressively more numerous on laterals 2 and 3. Marginals numerous, the inner ones slightly longer than the laterals, their tips relatively narrow and finely pectinate laterally; marginals progressively longer and more slender in middle of series then shorter with proportionately broader tips at radula margin.

*External anatomy* (Fig. 6B): Body uniformly yellowish white, no skin pigmentation evident in preserved specimens. Cephalic lappets well developed, almost meeting in mid-line, free margin with fine projections; right post-ocular peduncle present in both sexes, nearly as long or longer than eyestalk, with a faint dorsal groove, peduncle tip often flattened and expanded; no right subocular tentacle evident; snout with extensive ventro-lateral flanges extending well beneath neck lobes, mouth deeply split mid-ventrally; neck lobes broad, anterior two-thirds of right lobe with approx. 5 first-order tentacles with many smaller intermediaries, posterior third minutely fimbriate; anterior three-quarters of left lobe with approx. 10 tentacles in a variety of sizes, posterior quarter more or less smooth; epipodium bearing approx. 7 relatively large, first-order tentacles (not all the same size) with many, very much smaller intermediaries; larger epipodial tentacles usually with an indistinct basal sense organ; no epipodial sense organs evident beneath neck lobes.

Type material: Two syntype lots of *Turcica salpinx* Barnard, 1964 (SAMC): SOUTH AFRICA: off Cape Morgan, 77 fath. [-141 m], 1 broken adult (A9252); off Hood Point, 49 fath. [-90 m], 2 juvenile, 1 immature, 3 fragments (A9253).

Material examined (all NMSA unless indicated otherwise): MOZAMBIQUE: Inhambane transect, Campagne Mainbaza, dredged RV *Vizconde de Eza*, st'n CP3143 (23.533°S 35.767°E), living, -264–277 m, 11.iv.2009 (MNHN); ditto, st'n CP3144 (23.55°S 35.68°E), living, -171–180 m, 16.iv.2009 (MNHN); between Inhaca and Inhambane (approx. 25.1°S 34.8°E), -225–300 m, lobster traps, J. Rosado, v.1996 (L8399); southern Mozambique [not further localized], living, -250 m, don. F. Amorim, v.1990 (K7361). SOUTH ARICA: *KwaZulu-Natal*: off Island Rock (27.2800°S 32.8233°E), -400 m, sandstone boulders, dredged NMDP, RV *Meiring Naude*, st'n ZE5, 5.vi.1987 (D6150); NE of Leven Point (27.8983°S 32.6567°E), -260 m, sponges, stones, dredged NMDP, RV *Meiring Naude*, st'n ZL6, 9.vi.1988 (E4447); off Cape Vidal off (28.1383°S 32.6150°E), -200 m, sponge rubble, dredged NMDP, RV *Meiring Naude*, st'n ZM9, 11.vi.1988 (E3941); SE of Neill Peak [Cunge Hill] (28.7400°S 32.5367°E), -320–340 m, sandy mud, dredged NMDP, RV *Meiring Naude*, st'n ZP5, 12.vi.1988 (E3979); SE of Port Durnford (29.0150°S 32.2017°E), -215 m, glutinous sandy mud, dredged NMDP, RV *Meiring Naude*, st'n ZQ8, 13.vi.1988 (E3123); ditto (29.0250°S 32.1967°E),

-310–320 m, glutinous sandy mud, dredged NMDP, RV *Meiring Naude*, st'n ZQ9, 13.vi.1988 (E3167); off Glenton Reef (29.2450°S 32.0370°E), -200–210 m, sandy mud, dredged NMDP, RV *Meiring Naude*, st'n ZRR9, 18.vi.1989 (S457); off Matigulu River mouth (29.3567°S 31.9417°E), -145 m, mud, shell rubble, dredged NMDP, RV *Meiring Naude*, st'n ZR7, 16.vi.1989 (E8788); ditto (29.3650°S 31.9367°E), -200–220 m, mud and coarse sand with *Dendrophyllia*, dredged NMDP, RV *Meiring Naude*, st'n ZR9, 16.vi.1989 (E9014); off Umhlanga Rocks (29.7499°S 31.1685°E), 59 fath. [-107 m], dredged A.D. Connell, 7.vii.1983 (B6296); off Durban (29.8333°S 31.2367°E), living, -130 m, sandstone gravel and some rocks, dredged NMDP, RV *Meiring Naude*, st'n XX115, 9.vii.1986 (D4231); ditto (29.8400°S 31.2333°E), living, -150 m, sandstone gravel and some sponge, dredged NMDP, RV *Meiring Naude*, st'n XX114, 9.vii.1986 (D4146); off Umlaas Canal (30.0133°S 31.0600°E), -150 m, muddy sand and fine pebbles, dredged NMDP, RV *Meiring Naude*, st'n XX75, 10.vii.1985 (D1155); ditto (30.0183°S 31.0533°E), living, -150 m, coarse sand and pebbles with numerous spatangoids, dredged NMDP, RV *Meiring Naude*, st'n XX70, 9.vii.1985 (E7597, D796); ditto (30.0317°S 31.0450°E), -150 m, coarse sand, dredged NMDP, RV *Meiring Naude*, st'n XX72, 10.vii.1985 (D859); ditto (30.0367°S 31.0650°E), living, -250 m, coarse sand, dredged NMDP, RV *Meiring Naude*, st'n XX67, 9.vii.1985 (D1449); off Amanzimtoti (30.0783°S 31.0550°E), -300–305 m, medium sand, dredged NMDP, RV *Meiring Naude*, st'n XX66, 9.vii.1985 (D1315); ditto (30.0883°S 31.0417°E), -260–270 m, medium sand, dredged NMDP, RV *Meiring Naude*, st'n XX65, 9.vii.1985 (D1180); ditto (30.0967°S 30.9950°E), living, -115–125 m, medium sand, dredged NMDP, RV *Meiring Naude*, st'n XX61, 9.vii.1985 (D1267); ditto (30.1000°S 31.0267°E), living, -245–250 m, medium sand, dredged NMDP, RV *Meiring Naude*, st'n XX64, 9.vii.1985 (D1663); ditto (30.1067°S 31.0133°E), -160–170 m, medium sand, dredged NMDP, RV *Meiring Naude*, st'n XX62, 9.vii.1985 (D1489); off Park Rynie (30.3838°S 30.8355°E), living, -140 m, some sand, sponge rubble, dredged NMDP, RV *Meiring Naude*, st'n X6, 19.viii.1981 (C1590); ditto (30.3838°S 30.8350°E), living, -140 m, some sand, sponge rubble, dredged NMDP, RV *Meiring Naude*, st'n X7, 19.viii.1981 (C1628); Port Edward, slightly north of (31.0967°S 30.3133°E), living, -140 m, live sponges, dredged NMDP, RV *Meiring Naude*, st'n XX57, 8.vii.1985 (D1402); off Port Edward (31.1067°S 30.3000°E), living, -125 m, living sponges, dredged NMDP, RV *Meiring Naude*, st'n XX58, 8.vii.1985 (D906); ditto (31.1133°S 30.2967°E), living, -120–125 m, living sponges, dredged NMDP, RV *Meiring Naude*, st'n XX59, 8.vii.1985 (D1358, E7372); ditto (31.1400°S 30.2766°E), living, -160 m, sponge, gorgonians and sand, dredged NMDP, RV *Meiring Naude*, st'n A18, 7.vii.1986 (C9650, S3190); ditto (31.1650°S 30.2516°E), living, -140 m, sponge rubble, dredged NMDP, RV *Meiring Naude*, st'n A6, 18.viii.1981 (E225). *Eastern Cape*: off Mtentu River (31.2333°S 30.1833°E), living, -150–160 m, sponges rocks, dredged NMDP, RV *Meiring Naude*, st'n XX12, 15.vi.1983 (C5225); off Msikaba River (31.3867°S 30.0433°E), living, -100 m, sponge rubble, dredged NMDP, RV *Meiring Naude*, st'n C3, 12.viii.1981 (C1125, E192); ditto (31.4166°S 29.9833°E), -150 m, sponge, gorgonians, dredged NMDP, RV *Meiring Naude*, st'n D23, 2.vii.1986 (C9808); off Port Grosvenor (31.4166°S 29.9666°E), living, -95–100 m, coarse sand, very gorgonians, dredged NMDP, RV *Meiring Naude*, st'n D12, 16.viii.1981 (E209); ditto (31.4166°S 29.9333°E), -80–84 m, calcareous nodules, sand, dredged NMDP, RV *Meiring Naude*, st'n D19, 16.viii.1981 (E196); ditto (31.4317°S 29.9650°E), -120–128 m, coarse sand, some mud, solitary coral, shells, dredged NMDP, RV *Meiring Naude*, st'n D2, 13.viii.1981 (C1151); off Waterfall Bluff (31.5017°S 29.9200°E), living, -200 m, some sponges, rocks, dredged NMDP, RV *Meiring Naude*, st'n E10, 4.vii.1986 (C9837); off Mgazi River (31.7283°S 29.5317°E), -140–145 m, glutinous black mud, dredged NMDP, RV *Meiring Naude*, st'n J13, 4.vii.1985 (C9304, S3192); off Rame Head (31.8450°S 29.4750°E), living, -150–160 m, some sponges, dredged NMDP, RV *Meiring Naude*, st'n K10, 20.vii.1982 (C1896); ditto (31.8583°S 29.4683°E), living, -170–200 m, sandstone, yellow hydroids, dredged NMDP, RV *Meiring Naude*, st'n K11, 20.vii.1982 (C1911); off Ubombo Head (31.9050°S 29.2967°E), living, -60–62 m, coarse sand, oyster shell conglomerate, dredged NMDP, RV *Meiring Naude*, st'n L4, 16.vii.1982 (E248); ditto (31.9700°S 29.3900°E), living, -200 m, smooth bedrock, living sponges, dredged NMDP, RV *Meiring Naude*, st'n L11, 8.vii.1985 (C8970); off Whale Rock (31.9800°S 29.2800°E), living, -90 m, sponge rubble, coarse sand, some rocks, dredged NMDP, RV *Meiring Naude*, st'n M12, 3.vii.1985 (C9502); ditto (32.0166°S 29.3166°E), living, -150–200 m, sponge rubble, dredged NMDP, RV *Meiring Naude*, st'n M8, 20.vii.1982 (E289); ditto (32.0283°S 29.3050°E), living, -150–165 m, some coarse sand, discoid corals, dredged NMDP, RV *Meiring Naude*, st'n M9, 20.vii.1982 (C2313); ditto (32.0333°S 29.3166°E), living, -200–210 m, sponge rubble, some sandstone rocks, dredged NMDP, RV *Meiring Naude*, st'n M13, 3.vii.1985 (C9276); off Mncwasa Point (32.1033°S 29.1083°E), -68 m, sand, dredged NMDP, RV *Meiring Naude*, st'n N8, 10.vii.1982 (E337); off Nthlonyane River (32.2183°S 28.9950°E), -80 m, sand, broken shell, dredged NMDP, RV *Meiring Naude*, st'n P6, 17.vii.1982 (C2577); ditto (32.2400°S 29.0233°E), living, -95 m, sponge rubble, dredged NMDP, RV *Meiring Naude*, st'n P4, 17.vii.1982 (E329); ditto (32.2567°S 29.0133°E), living, -90–95 m, lithothamnion pebbles, dredged NMDP, RV *Meiring Naude*, st'n P5, 17.vii.1982 (C2565); ditto (32.2750°S 29.0100°E), living, -240 m, sponge rubble, dredged NMDP, RV *Meiring Naude*, st'n P1, 17.vii.1982 (C3305); ditto (32.2867°S 29.0817°E), living, -220–230 m, branching sponges, gorgonians, dredged NMDP, RV *Meiring Naude*, st'n P2, 17.vii.1982 (C3300, E264); off Mbashe River (32.3033°S 29.0683°E), living, -200–220 m, sponge rubble, dredged NMDP, RV *Meiring Naude*, st'n Q1, 18.vii.1982 (V1944); off Qora River (32.3967°S

28.8117°E), living, -196 m, sponge, dredged NMDP, RV *Meiring Naude*, st'n U9, 14.vi.1983 (C5154); off Nqabara Point off (32.4533°S 28.9317°E), living, -250 m, live sponges with some corals, dredged NMDP, RV *Meiring Naude*, st'n S10, 12.vii.1984 (V4056); ditto (32.4550°S 28.9267°E), living, -210 m, live sponges, dredged NMDP, RV *Meiring Naude*, st'n S9, 11.vii.1984 (W7627); off Shixini Point (32.4900°S 28.8967°E), living, -240 m, sponge rubble, some sandstone, dredged NMDP, RV *Meiring Naude*, st'n T11, 11.vii.1984 (C6301); ditto (32.5233°S 28.8650°E), -240 m, sand and old rubble, dredged NMDP, RV *Meiring Naude*, st'n T13, 11.vii.1984 (C6342); off Qora River (32.5633°S 28.8067°E), living, -150–168 m, stones and sponges, dredged NMDP, RV *Meiring Naude*, st'n U7, 14.vi.1983 (C5095); ditto (32.5700°S 28.6567°E), -400 m, sand, dredged NMDP, RV *Meiring Naude*, st'n U8, 14.vi.1983 (C4877); off Sandy Point (32.6233°S 28.6150°E), -90 m, coarse sand, dredged NMDP, RV *Meiring Naude*, st'n W1, 11.vi.1983 (V2882); off Stony Point (32.6250°S 28.7333°E), living, -150–152 m, calcareolite and coral, dredged NMDP, RV *Meiring Naude*, st'n V9, 14.vi.1983 (C4371); off Qolora River (32.7733°S 28.5900°E), living, -174 m, sponge rubble, dredged NMDP, RV *Meiring Naude*, st'n Y2, 12.vi.1983 (C4637); ditto (32.7633°S 28.6067°E), living, -240–250 m, live sponges, dredged NMDP, RV *Meiring Naude*, st'n Y9, 14.vii.1984 (C7131).

Type locality: Barnard's type material originated from two *Pieter Faure* stations, but he did not select one in particular as the type locality. The given data for one of these stations (off Hood Point (East London), 49 fath. [-90 m]) has since been shown to be erroneous (Herbert 1987: 344). In this instance, the Hood Point locality is not far out of the known range of the species, but for other taxa it is widely so. The dredge haul was more probably taken off Durban. In view of this inaccuracy I here select the provenance of Barnard's other type lot, off Cape Morgan [close to mouth of Great Kei River] 77 fath. [-141 m], as type locality.

Distribution and habitat (Fig. 8): South-eastern Africa; from southern Mozambique (Inhambane) to the Great Kei River, Eastern Cape, South Africa; -60–400 m, living specimens -60–277 m, on hard substrata with abundant marine growths, particularly sponges.

Remarks: When compared to other species here transferred to *Clypeostoma*, *C. salpinx* differs from *C. meteorae*, *C. nortoni* and *C. townsendianum* in having slightly flatter whorls, commonly four rather than five or six spiral cords above the suture, fewer tubercles on the callus shield near the basal columella tooth, less elongate, more widely spaced denticles inside the outer lip and a more extensive inductural callus. *C. elongata* Vilvens, 2001 from Indonesia and *C. reticulatum* are both considerably larger, have coarser sculpture and more robust columella teeth. Within southern Africa, juvenile *C. salpinx* may be confused with those of *Danilia textilis*, but the latter have finer, more regularly cancellate sculpture, a sunken rather than an exsert protoconch and more rounded whorls with a more narrowly channelled suture.

Specimens from the northern limit of the distribution (off Inhambane) are surprisingly small, almost half the size South African specimens (Fig. 10G). However, this is the only significant conchological difference between this material and typical *C. salpinx*, and I consider it to be insufficient evidence upon which to base the description of a new species. Other species of *Clypeostoma* also exhibit considerable variation in size at maturity.

### *Clypeostoma meteorae* (Neubert, 1998) **comb. n.**

Figs 8, 12A–E

*Agathodonta meteorae*: Neubert 1998: 465, figs 4–7. Type loc.: 'Bab al-Mandab' [Bab-el-Mandeb] (12°21.4'N 43°26.9'E), -45 m, Djibouti, Red Sea–Gulf of Aden.

Material examined: MADAGASCAR: South-west of Cap d'Ambre, Antsiranana (12.133°S 48.933°E), -238–249 m, Campagne *Miriky*, st'n DW3196, dredged, 28.vi.2009 (MNHN); off Mahajamba Bay (14.883°S

46.933°E), -90–257 m, Campagne *Miriky*, st'n DW3245, dredged, 7.vii.2009 (MNHN); East of Faux-Cap (25.633°S 46.217°E), -128–133 m, Exped'n Atimo Vatae, st'n CP3561, dredged *Nosy Be 11*, 6.v.2010 (MNHN); between Lokaro and Ste Luce (24.865°S 47.467°E), -80–83 m, Exped'n Atimo Vatae, st'n DW3519, dredged *Nosy Be 11*, 30.iv.2010 (MNHN).

Remarks: Five shells matching the description of this little-known Red Sea–Gulf of Aden species were obtained during dredging surveys undertaken by the MNHN off Madagascar (Campagne *Miriky* and Exped'n Atimo Vatae). In this material the aperture is clearly distinct from that of *C. salpinx* in having stronger columella teeth and a much less extensive inductural callus shield. There are also in-running ridges extending from the labral denticles into the aperture and the callus shield, though less extensive, bears superficial ridges in the parietal region and additional granules, particularly around the columella base. Like the original material of *C. meteorae*, these specimens have four spiral cords on the spire whorls, but 1–2 intermediary cords appear during the penultimate whorl such that the last adult whorl has 5–6 spiral cords above and including the peripheral one.

In terms of its apertural features, this Malagasy material is also close to *C.* cf. *nortoni* (see below) and *C. townsendianum*, but it is considerably smaller than both. The specimens all have mature apertural dentition and range in length from 5.3–6.9 mm. In addition, the protoconch is also smaller, diameter 220–240 µm (compared to 310–320 µm for *C.* cf. *nortoni*). Specimens at the smaller end of this size range show considerable similarity with *Perrinia docili* Poppe, Tagaro & Dekker, 2006 from the Philippines, which I strongly suspect may also belong to *Clypeostoma*.

### *Clypeostoma* cf. *nortoni* (McLean, 1984) **comb. n.**

Figs 8, 12H–L

*Agathodonta nortoni*: McLean 1984: 122, figs 1–3; Tsuchida & Kurozumi 1996: 37, fig. 3; Vilvens 2001: figs 11–13; Vilvens & Héros 2003: figs 12, 13; Poppe *et al*. 2006: 30, pl. 7, figs 3, 4; Poppe & Tagaro 2008: 166, pl. 28, figs 4, 6. Type loc.: off Baltazar Is. (13°14'N 121°49'E), Marinduque Province, Philippines.

A number of *Clypeostoma* shells resembling *C. nortoni* have been dredged off Madagascar and obtained *ex piscibus* from the Sofala Bank, off central Mozambique. Similar material evidently also occurs off Réunion and was recorded there by Jay (2009 as *Clanculus ceylonicus*). Compared with *C. meteorae*, these specimens are consistently larger (mature length 9.6–14.6 mm) and have a larger protoconch (diameter 310–320 µm). In addition, the basal callus shield is more extensive and smoother, bearing (apart from 3–5 strong, in-running parietal ridges overlying the basal sculpture of the previous whorl) only traces of superficial ridging in the parietal region and a small number of granules associated with the medial columella area. *C. townsendianum* (Fig. 12F, G), from the Persian Gulf, is of a similar size (figured syntype, length 10.4 mm), but has stronger apertural dentition more similar to that of *C. meteorae*. The form of the apertural dentition in the present material is closest to that of the Philippine *C. nortoni*, but the shell attains a relatively larger size (length up to 14.6 mm) than does *C. nortoni*, and the suture is slightly less indented and the whorls thus less convex. With the limited amount of material available and the geographical distances involved, it is difficult to assess the significance of these differences. I cannot thus confidently identify this material as *C. nortoni*, but rather draw attention to its existence and its similarity to that species.

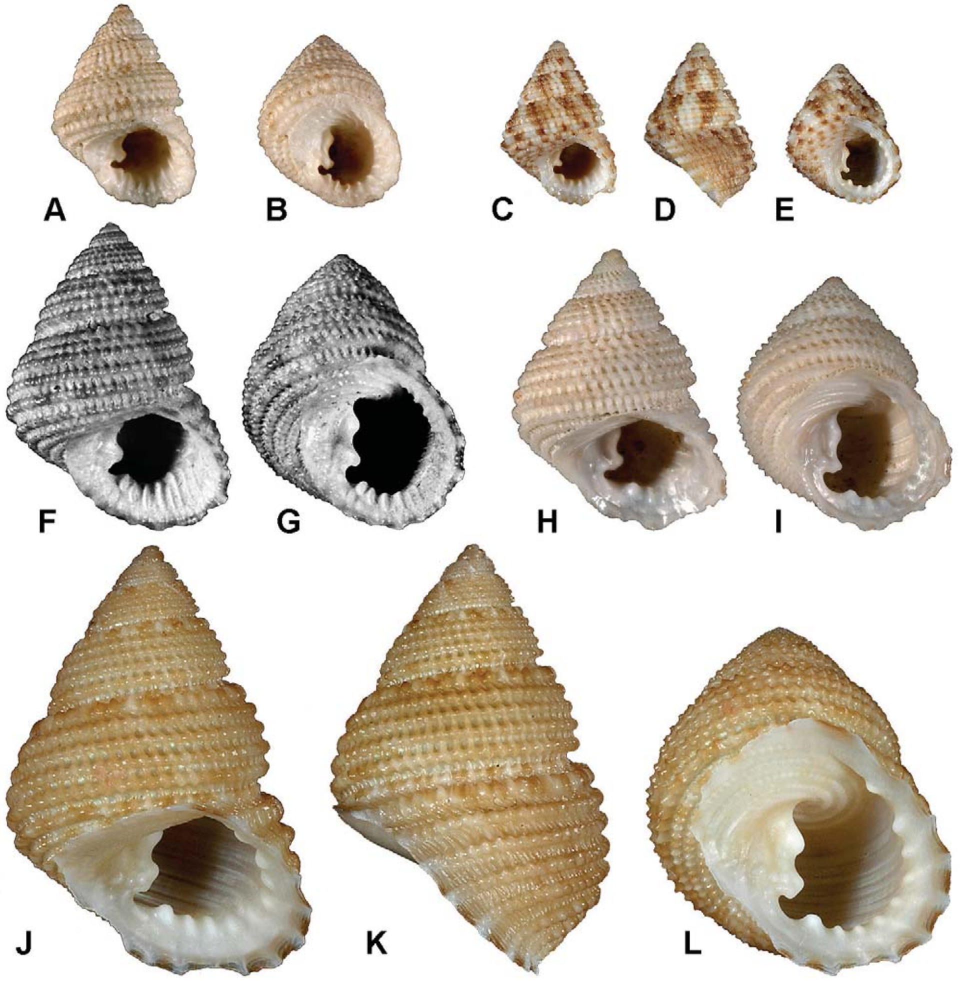

Fig. 12. *Clypeostoma* species: (A, B) *C. meteorae* (Neubert, 1998), SW of Cap d'Ambre, Antsiranana, northern Madagascar, length 6.9 mm (MNHN); (C–E) *C. meteorae*, small specimen, off Mahajamba Bay, northern Madagascar, length 5.6 mm (MNHN); (F, G) *Euchelus townsendianus* Melvill & Standen, 1903, figured syntype, length 10.4 mm (NHMUK 1903.12.15.119); (H, I) *C.* cf. *nortoni* (McLean, 1984), west of Nosy Be, northern Madagascar, length 9.6 mm (MNHN); (J–L) *C.* cf. *nortoni*, large specimen, Sofala Bank, central Mozambique, length 14.6 mm (J. Rosado coll'n).

Material examined: MADAGASCAR: West of Nosy Be (13.400°S 47.967°E), -210–310 m, Campagne *Miriky*, st'n DW3232, dredged, 03.vii.2009 (MNHN); south of Faux-Cap (26.133°S 45.650°E), -280–333 m, Exped'n ATIMO VATAE, st'n DW3553, dredged *Nosy Be 11*, 5.v.2010 (MNHN); ditto (26.117°S 45.650°E), -264–280 m, Exped'n ATIMO VATAE, st'n DW3552, dredged *Nosy Be 11*, 5.v.2010 (MNHN). MOZAMBIQUE: Between Beira and Bazaruto, Sofala Bank (20.123°S 35.543°E), -90–145 m, *ex pisce*, J. Rosado 2005–2008 (J. Rosado coll'n).

## Genus *Danilia* Brusina, 1865

*Olivia*: Cantraine 1835: 387 [*non Olivia* Bertolini, 1810 (?Porifera)]. Type species: *Olivia otaviana* Cantraine, 1835, by monotypy.

*Craspedotus*: Philippi 1847: 23 [*non Craspedotus* Schoenherr, 1844 (Coleoptera)]. Type species: *Monodonta limbata* Philippi, 1844 [= *Monodonta tinei* Calcara, 1839], by monotypy.

*Otavia*: Gray 1847: 145 (*non* Risso, 1826), *laps. cal.* for *Olivia* Cantraine, 1835.

*?Heliciella*: O.G. Costa 1861: 64. Type species: *Heliciella costellata* O.G. Costa, 1861, by subsequent designation (Dall 1927: 134).

*Danilia*: Brusina 1865: 25. Type species: *Monodonta limbata* Philippi, 1844 [= *Monodonta tinei* Calcara, 1839], by monotypy.

Nomenclatural remarks: Beu and Climo (1974) stated that Brusina (1865) proposed the name *Danilia* as a replacement name for the homonymous *Olivia* Cantraine, 1835. However, I can find no evidence in either Brusina (1865) or Brusina (1866) that this was his intention. In fact, he made no mention of *Olivia* Cantraine, 1835. Had he proposed *Danilia* expressly as a replacement for *Olivia*, the type species of *Danilia* would have been that of *Olivia* (ICZN 1999: Art. 67.8), namely *Olivia otaviana* Cantraine, 1835 (by monotypy). Instead, the type species of *Danilia* (by monotypy) is *Monodonta limbata* Philippi, 1844 [= *Monodonta tinei* Calcara, 1839]. The type species of *Olivia*, *O. otaviana*, has traditionally also been considered to be synonymous with Calcara's *Monodonta tinei* and is the earlier name, but Palazzi and Villari (2001) consider *O. otaviana* to represent a distinct fossil species – an opinion shared by Landau *et al*. (2003). In such case, the type species of *Danilia* and Cantraine's *Olivia* are not the same and they are thus subjective rather than objective synonyms.

Keen (1960) listed *Heliciella* O.G. Costa, 1861, in the synonymy of *Olivia*, but Beu and Climo (1974) considered the affinity of this taxon with *Olivia* and thus with *Danilia* to be debateable, since its type species, *H. costellata* O.G. Costa, 1861[2], was based on a very juvenile shell. (The specimen of *H. costellata* figured by O.G. Costa (1861) has a diameter of 1.0 mm and comprises only approx. 1.5 teleoconch whorls.) They chose instead to employ the younger name *Danilia* on account of this uncertainty. However, Monterosato (1884) had earlier stated that *H. costellata* was a juvenile shell of *Danilia tinei* and certainly the figures of juvenile *D. tinei* provided by Scaperrotta *et al*. (2009) clearly support the view that *H. costellata* is a juvenile *Danilia*. However, Palazzi and Villari (2001), recognising *H. costellata* as a species of *Danilia*, believed it to be distinct from *D. tinei* and to represent a second Recent European species of this genus. Thus *Heliciella* and *Danilia* are evidently synonymous and since both are valid names, the earlier one, *Heliciella*, ought to be afforded priority. However, in order to maintain prevailing usage, and in accordance with ICZN, Art. 23.9 (ICZN 1999), the principle of priority can be moderated, provided the conditions of Art. 23.9.1.1 and Art. 23.9.1.2 are met. In this regard, I am not aware that *Heliciella* has been used as a valid name after 1899 (Art. 23.9.1.1) and *Danilia* has been used more than 25 times in the last 50 years by at least 10 different authors (Art. 23.9.1.2) (Beu & Climo 1974; Powell 1979; Piani 1980; Aimassi *et al*. 1983; Guidastri *et al*. 1984; Spadini 1986; Graham 1988; Vaught 1989; Hickman & McLean 1990; Poppe & Goto 1991; Wilson 1993; Giannuzzi-Savelli *et al*. 1994; Jansen 1996; Millard 1997; Higo *et al*. 1999; Sasaki 2000; Palazzi & Villari 2001; Vilvens 2001; Spencer *et al*. 2002; Landau *et al*. 2003; Rolán 2005; Vilvens &

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[2] Beu and Climo (1974) cited the type species of *Heliciella* as *H. costellata* O.G. Costa, 1861, by monotypy. In fact, O.G. Costa (1861) described two species within his new genus *Heliciella*, *H. costellata* and *H. mutabilis*. The type species of *Heliciella* was not fixed until Dall (1927: 134) formally designated it to be *H. costellata* [although Monterosato (1884: 109) might also be deemed to have done the same]. A subsequent designation of *H. mutabilis* as the type species of *Heliciella* by Bouchet and Warén (1988: 86) is invalid.

Héros 2005; Poppe *et al*. 2006; Crocetta & Spanu 2008; Poppe & Tagaro 2008; Kano 2009; Scaperrotta *et al*. 2009; Spencer *et al*. 2009; Bandel 2010; De Simone & Kosuge 2010). Some of these, despite recognising the priority of *Heliciella* over *Danilia,* have continued to use the latter as the valid name. Therefore, in accordance with Art. 23.9, *Danilia* is to be afforded priority over the earlier, but unused *Heliciella*. *Danilia* thus becomes a *nomen protectum* and *Heliciella* a *nomen oblitum*.

Remarks: The genus *Danilia* is known primarily from relatively deep water and has a fossil record extending back to the Lower Cretaceous (Beu & Climo 1974). Nine Recent species are known from the Indo-West Pacific, eight of which were discussed and illustrated (mostly type specimens) in a useful contribution by Vilvens and Héros (2005). The differences between the species are in some cases small, and Beu and Climo (1974) cautioned that without more detailed comparative study, it is impossible to be certain whether each of these nominal taxa represents a genuinely distinct species, or whether there are fewer, more widespread and sculpturally variable ones – an observation with which I concur. The problem is exacerbated by the fact that most descriptions have been based on very few specimens and thus give no indication of intraspecific variability. These difficulties notwithstanding, I describe below two additional species, since neither appears clearly referable to any of the described taxa.

*Danilia* species generally live on hard substrata. Whilst most species seem to be scarce, a Mediterranean species, tentatively identified as *Danilia costellata* (O.G. Costa, 1861), may be locally abundant in colonies of the gorgonian *Corallium rubrum* (Linnaeus, 1758) (Crocetta & Spanu 2008). Schepman (1908), Beu & Climo (1974) and De Simone & Kosuge (2010) also reported species living in deep-water coral communities. *D. textilis* (below) was found living primarily in sponge dominated communities, but such communities frequently included deep-water corals. Guidastri *et al*. (1984) and Smriglio *et al*. (1989) reported a similar association between *Putzeysia wiseri* (Calcara, 1842) and deep-water Scleractinia in the Mediterranean.

The radula of *Danilia tinei* (Calcara, 1839) was illustrated by Guidastri *et al*. (1984 as *D. otaviana*) and that of *D. insperata* was figured and discussed in detail by Beu and Climo (1974). That of *D. textilis* described below is very similar.

### Key to species of *Danilia* in the south-western Indian Ocean

1 Shell relatively small (adult length <6 mm); spiral cords of unequal size, the two largest delimiting a cylindrical peripheral band; axial pliculae fine, close-set and sharp ........................................ **boucheti**

– Shell larger (adult length >10 mm); periphery more or less rounded; spiral cords of approximately equal size (peripheral one may be slightly larger), axial pliculae rounded, relatively widely spaced ........................................ **textilis**

## **Danilia boucheti** sp. n.

Figs 13, 14

Etymology: Named for Prof. Philippe Bouchet (MNHN), well-known malacologist and co-ordinator of numerous important dredging expeditions.

Description:

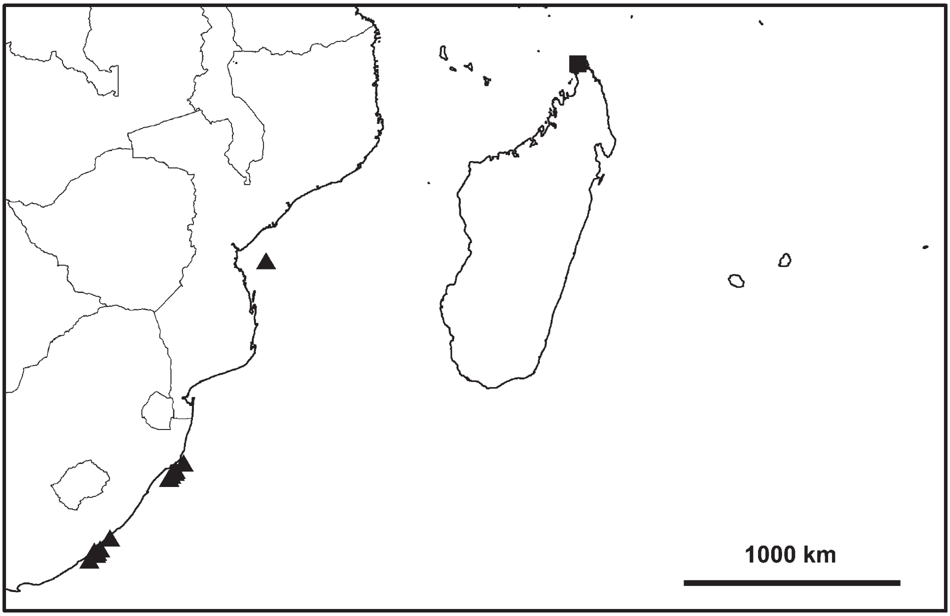

Fig. 13. Distribution of *Danilia* species in the south-western Indian Ocean: *D. boucheti* (square), *D. textilis* (triangles). Each symbol represents one or more records.

*Shell*: Turbiniform with moderately elevated spire (L/D=1.09–1.14); teleoconch of 4.25–4.5 whorls; apical angle approx. 75°; whorls convex and suture indented, level with periphery on spire, but descending below this just prior to outer lip; protoconch sunken and apex thus appearing truncated; outer lip with well-developed subterminal varix. First teleoconch whorl sculptured with approx. 17 orthocline axial pliculae; 4 spiral cords develop during second whorl (P1–P4); additional secondary and tertiary cords arising during subsequent whorls; abapical cord (P4) strongest; axial pliculae narrow, becoming strongly prosocline on later whorls, the crest crisp and leaning forward; spiral cords beaded where crossed by axial pliculae, beads on primary cords scale-like; last adult whorl with P2–P4 (particularly P3 and P4) stronger than other cords; P3 and P4 delimiting an almost cylindrical peripheral band; subsutural cord (P1) also slightly larger and with angular beads that intermesh in a zip-like manner with beads of peripheral cord (P4) of preceding whorl, delimiting a narrow sutural channel; number of intermediary cords variable, generally only 1–2 between P3 and P4; 5–6 between P1 and P3 (including P2); beading of intermediary cords weaker; cords generally somewhat narrower than their intervals and slightly stronger than axial pliculae; interaction of cords and pliculae producing a fine, regular, oblique cancellation with rhomboidal interstices. Base with approx. 10 spiral cords of alternating size; the second one below peripheral cord generally the strongest; axial pliculae continue onto base rendering basal cords finely beaded. Peristome markedly oblique, more or less in one near-tangential plane; aperture roundly D-shaped and flattened in parietal region; columella lip a thickened pillar set with 2 teeth, lower one a well-developed, rounded peg, the upper one smaller; interval between teeth shallowly concave; umbilical region medial to thickened columella pillar sunken, forming an elongate curved pit, broadening basally; umbilical/parietal region

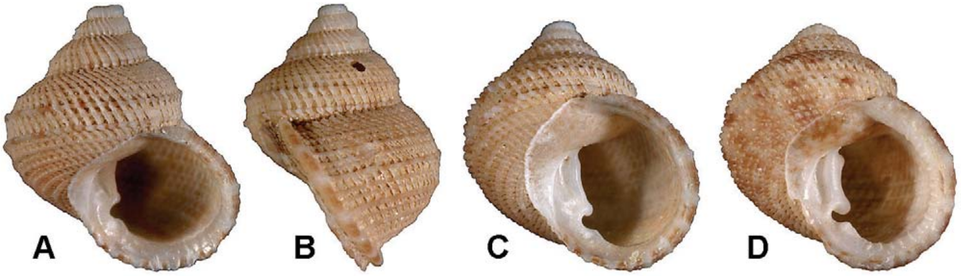

Fig. 14. *Danilia boucheti* sp. n., south-west of Cap d'Ambre, Antsiranana, Madagascar: (A–C) holotype (apertural features subadult), length 5.3 mm (MNHN 24648); (D) paratype (apertural features adult, apex missing), diameter 4.46 mm (MNHN 24649).

covered by a thin, extensive inductural callus; callus translucent, smooth and glossy, raised somewhat basally and confluent with flaring margin of outer lip; interior of outer lip with an in-set varix lying beneath external outer lip varix; internal varix swollen to form prominent bulge near junction of basal and columella lips, creating deep, U-shaped notch below lower columella tooth; apertural varix set with numerous small, ridge-like denticles, these restricted to varix, not running into deeper portions of aperture; interior of aperture with traces of nacre (specimens not fresh), not spirally lirate, though spiral cords of shell exterior visible by translucence; margin of outer lip flaring; external varix *ca* 0.25 mm wide and set back a similar distance behind lip edge.

Microsculpture: Irregular, vermiform spiral threads present on early whorls; later whorls with evidence of scratch-like sculpture, but sculptural details largely obscured by dirty intritacalx deposit, particularly in interstices.

Protoconch: Present only in holotype; translucent white; diameter 320 µm; sunken into first teleoconch whorl and somewhat tilted; terminal lip evidently more or less straight.

Colour: First teleoconch whorl uniform white, later whorls pale buff with faint brown spots on primary spiral cords; flared outer lip and external varix with brown marks in intervals between paler primary spiral cords. One paratype with darker brown subsutural blotches, stronger spots on the primary peripheral cords and irregular brownish mottling on the base.

Dimensions: Holotype (largest specimen), length 5.32 mm, diameter 4.66 mm.

*Operculum, radula and external anatomy*: Unknown.

Holotype (Fig. 14A–C): MADAGASCAR: Antsiranana, south-west of Cap d'Ambre (12.133°S 48.933°E), -238–249 m, Campagne *Miriky*, st'n DW3196, dredged, 28.vi.2009 (MNHN 24648).

Paratypes: Same data as holotype (MNHN 24649, 2 specimens).

Note: The holotype is the most complete specimen, but its apertural dentition is subadult; one of the paratypes has more mature apertural features (Fig. 14D), but is missing the apical whorls.

Distribution (Fig. 13): Known only from off the coast of the far north of Madagascar, -238–249 m.

Remarks: *Danilia boucheti* is smaller than any of the other described species of *Danilia*, most of which attain or exceed 10 mm in length (Vilvens & Héros 2005). Perhaps the most similar species is *D. angulosa* Vilvens & Héros, 2005 from Melanesia and the Philippines, which is also small (length up to 7.9 mm) and has stronger spiral cords associated with the periphery, creating a cylindrical peripheral band. In that species, however, the cords are stronger than in *D. boucheti*, the whorls more distinctly shouldered, and there is only one intermediary cord between the shoulder cord (upper peripheral cord) and the subsutural cord. In *D. boucheti* there are 5 or 6 intermediary cords in this region.

### **Danilia textilis** sp. n.

Figs 4E, 6C, 13, 15–17

Etymology: From Latin *textilis* (woven); in reference to the regular, net-like sculpture.

Description:

*Shell*: Trochoid-turbiniform, moderately elevated (L/D=1.10–1.30); teleoconch of 5–6 whorls; whorls rounded, but peripheral spiral cord frequently slightly stronger than others, giving the appearance of a weak peripheral angulation; apical angle approx. 75°; protoconch sunken and apex thus appearing truncated; suture indented, but somewhat adpressed, narrowly channelled, inserted at level of subperipheral cord, but descending below this just prior to outer lip; outer lip with well-developed subterminal varix. First

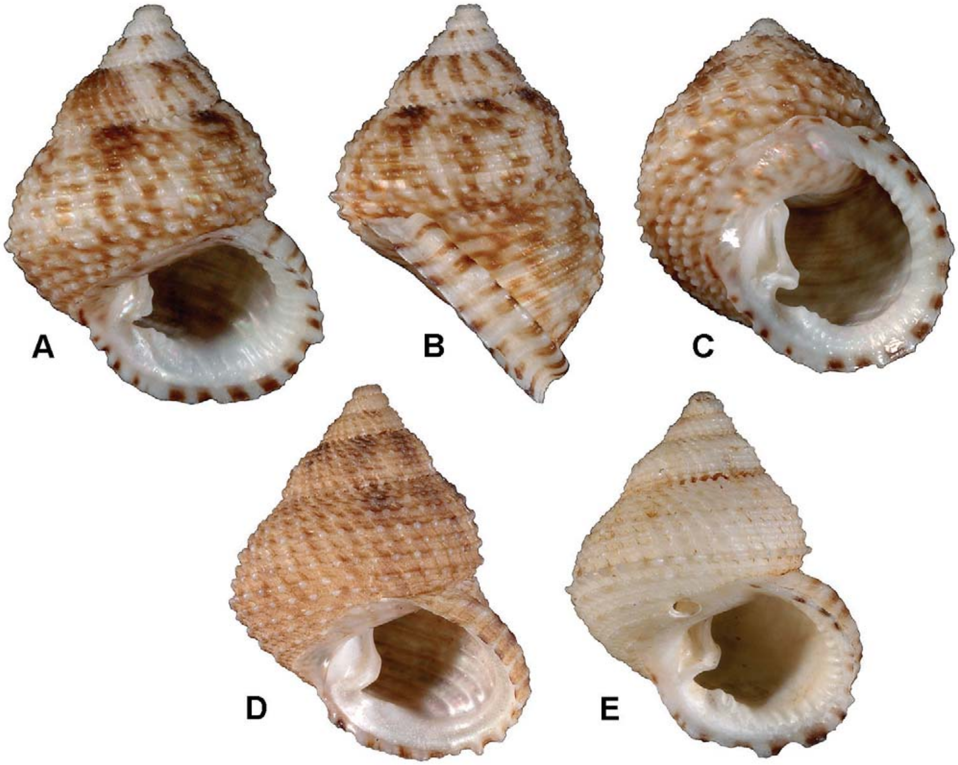

Fig. 15. *Danilia textilis* sp. n.: (A–C) holotype, length 11.4 mm (NMSA E7756/T2595); (D) paratype retaining periostracal deposit, subadult, length 10.9 mm, from type locality (NMSA S9912/T2594); (E) weakly patterned paratype, length 10.6 mm, off Qolora River, Eastern Cape (NMSA C7026/T2598).

teleoconch whorl sculptured with 15–18 axial pliculae; 4 spiral cords develop during second whorl, others arising by intercalation with growth; penultimate and last adult whorls with ±8 primary spiral cords between suture and periphery (inclusive); cords well defined, narrower than their intervals; an intermediary cord often developing between primary cords in latter half of last adult whorl. Axial sculpture of prosocline pliculae persists throughout growth; pliculae generally slightly weaker than cords, these together producing a regular, oblique cancellation with equilaterally rhomboidal interstices; cords roundly beaded where crossed by pliculae; beads stronger and more angular on subsutural cord and still larger and scale-like or spine-like on peripheral cord. Base with ±7 primary spiral cords, their intervals usually with a weaker intermediary in final half whorl; axial pliculae continue onto base but their number appears to double in latter third of last adult whorl, rendering spiral cords more finely and closely beaded; umbilicus lacking in all except small juveniles (<4 whorls), but often obscured by reflected columella even in these. Peristome markedly oblique, more or less in one tangential plane; aperture roundly D-shaped, flattened parietally; columella lip a thickened pillar with 2 well developed teeth separated by a shallow concavity; lower tooth stronger and frequently squarish with a raised ridge along its lower margin, upper tooth weaker and clearly representing the end of a subparietal spiral pleat; pleat separated from paries by a U-shaped notch; umbilical region median to thickened columella pillar sunken, forming an elongate, more or less rectangular pit; pit bordered basally by a medial extension of ridge of lower columella tooth; umbilical/parietal region covered by inductural callus; callus translucent, smooth and glossy, raised somewhat basally and confluent with flaring margin of outer lip; interior of outer lip with a subterminal thickening corresponding in position with the external labral varix; thickening set with numerous elongate denticles and rounded tubercles, these not running into deeper portions of aperture; 2–3 denticles closest to junction of basal and columella lips larger, forming a two- to three-humped bulge, which together with the lower columella tooth delineates a pronounced U-shaped notch; margin of outer lip flaring; interior of aperture nacreous, somewhat angled beneath spiral cords of shell exterior, but not spirally lirate.

Microsculpture (Fig. 16B, C): First teleoconch whorl with vermiform spiral threads, replaced on subsequent whorls by prosocline, scratch-like microsculpture, filled with intritacalx deposit.

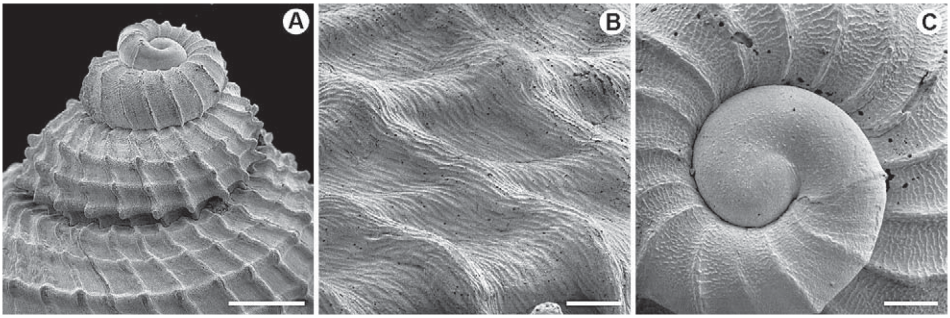

Fig. 16. *Danilia textilis* sp. n.: (A) side view of spire showing truncated apex and tilted protoconch, off Nqabara Point, Eastern Cape, bar = 0.5 mm (paratype, NMSA W7502/TT2671); (B) adult microsculpture, SE of Port Durnford, KZN, bar = 100 µm (paratype, NMSA E3119/T2597); (C) protoconch, SE of Port Durnford, KZN, bar = 100 µm (paratype, NMSA E3119/T2597).

Protoconch (Fig. 16A, C): Translucent white; diameter *ca* 360 µm; level with or slightly sunken below first teleoconch whorl and somewhat down-tilted; degree of tilting variable between individuals; surface mostly worn, but with traces of irregular granulation; terminal lip weakly sinuous.

Colour: Spire apex uniform white, later whorls (3rd onwards) with pale fawn ground patterned with darker, brownish markings; markings initially in the form of axial bands or blotches, but penultimate and last adult whorls rather more randomly mottled; subterminal varix and flaring edge of outer lip with brownish spiral bands in cord intervals; precise shade and density of colour pattern variable between individuals, some specimens very sparsely marked, but outer lip varix evidently patterned in all; cord intervals with pink/green iridescence; living and fresh specimens with a buffish intritacalx deposit. Shell exterior of live-taken specimens often with some encrustation by other marine organisms, but not (in the material available) entirely covered with sponge.

Dimensions: Holotype (largest specimen), length 11.4 mm, diameter 8.8 mm.

*Operculum* (Fig. 4E): Initially tightly multispiral, but whorls broadening with growth and becoming more openly multispiral.

*Radula* (Fig. 17): Formula ∞+4+1+4+∞, with *ca* 60 transverse rows of teeth. Lateral flanges of rachidian well developed creating a distinct hood, base of cusp with well-

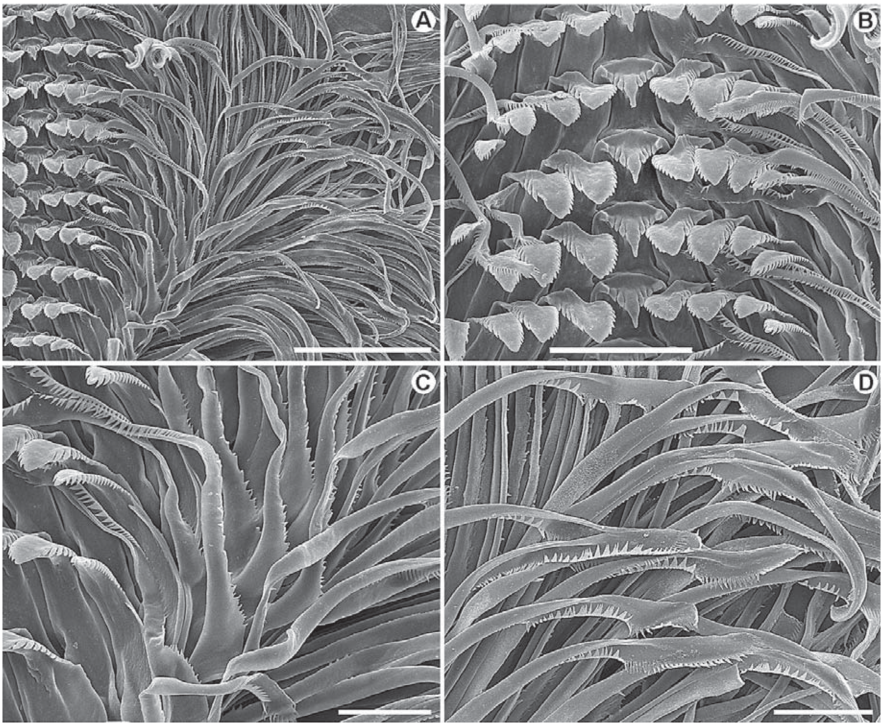

Fig. 17. *Danilia textilis* sp. n., radula: (A) half-row, bar = 100 µm; (B) rachidian and laterals, bar = 50 µm; (C) latero-marginal area, showing buttressed, jaggedly serrate outer shaft bases of inner marginal teeth, bar = 25 µm; (D) tips of marginal teeth, bar = 25 µm. All NMSA S9912/T2594, paratype, dredged off Rame Head, Eastern Cape, South Africa.

developed transverse ridge, cutting edge coarsely dentate with elongate-lanceolate central denticle with narrowly acuminate tip, and up to 5 lateral denticles on each side, last of which forms a rounded boss at shoulder of tooth. Laterals with overlapping shafts and trigonal, distinctly asymmetrical cusps, decreasing in size from first to fourth; inner cutting edge curved and finely serrate almost from tip, outer cutting edge nearly straight and set with coarse, close-set, more elongate denticles, starting some distance back from tip; first lateral strongly hunched at outer base of cusp. Marginals very long and slender, the cusp elongate, sides frequently in-rolled, and with a fringe of fine denticles on outer margin and at tip; outer shaft base of inner 1 or 2 marginals expanded and jaggedly serrate; serrations continue sparsely up shaft.

*External anatomy* (Fig. 6C): Body whitish with some brownish pigmentation on sides of foot, lateral regions of snout and around base of cephalic tentacles. Cephalic lappets distinct, their free margin smooth or at most shallowly lobate (rather than digitate), its edge minutely papillate; lateral expansions of snout broad; right post-ocular peduncle present in both sexes, a longitudinal groove on its upper surface; right subocular tentacle not evident; right neck lobe with approx. 4 moderately large, first-order tentacles anteriorly; left neck lobe with a group of 8–10 slightly smaller first-order tentacles anteriorly, with even smaller intermediaries; left neck lobe with approx. 5 epipodial sense organs on under surface, right lobe with approx. 3; posterior part of both lobes smooth; epipodial fold with 7–9 tentacles of various sizes, but without very small intermediary tentacles; larger tentacles each with a distinct epipodial sense organ at the base.

Holotype (Fig. 15A–C): SOUTH AFRICA: *Eastern Cape*: off Rame Head (31.8450°S 29.4750°E), living, -150–160 m, sponges, dredged NMDP, RV *Meiring Naude*, st'n K10, 20.vii.1982 (NMSA E7756/T2595).

Paratypes: SOUTH AFRICA: *KwaZulu-Natal*: SE of Neill Peak [Cunge Hill] (28.7400°S 32.5367°E), -320–340 m, sandy mud, dredged NMDP, RV *Meiring Naude*, st'n ZP5, 12.vi.1988 (MNHN 24817, 1 specimen); SE of Port Durnford (29.0150°S 32.2017°E), -215 m, glutinous sandy mud, dredged NMDP, RV *Meiring Naude*, st'n ZQ8, 13.vi.1988 (NMSA E3119/T2597, 4 specimens); SE of Port Durnford (29.0967°S 32.1567°E), -165 m, mud with sand, dredged NMDP, RV *Meiring Naude*, st'n ZQ15, 17.vi.1989 (NHMUK 20110382, 1 specimen); off Matigulu River mouth (29.3567°S 31.9417°E), -145 m, mud, shell-rubble, dredged NMDP, RV *Meiring Naude*, st'n ZR7, 16.vi.1989 (NMSA E8790/T2599, 1 specimen). *Eastern Cape*: same data as holotype (NMSA S9912/T2594, 1 specimen); off Qora River (32.3967°S 28.8117°E), living, -196 m, sponge, dredged NMDP, RV *Meiring Naude*, st'n U9, 14.vi.1983 (NMSA C5153/T2593, 1 specimen); off Nqabara Point (32.4533°S 28.9317°E), living, -250 m, live sponges, some corals, dredged NMDP, RV *Meiring Naude*, st'n S10, 12.vii.1984 (NMSA W7501/T2592, 1 specimen); off Nqabara Point (32.4550°S 28.9267°E), living, -210 m, live sponges, dredged NMDP, RV *Meiring Naude*, st'n S9, 11.vii.1984 (NMSA W7502/T2671, 1 specimen); off Qolora River (32.7633°S 28.6067°E), -240–250 m, live sponges, dredged NMDP, RV *Meiring Naude*, st'n Y9, 14.vii.1984 (NMSA C7026/T2598, 1 specimen).

Additional material examined (all NMSA): MOZAMBIQUE: off Beira, -110–145 m, *ex pisce*, v.2005 (J. Rosado coll'n). SOUTH AFRICA: *KwaZulu-Natal*: SE of Neill Peak [Cunge Hill] (28.7400°S 32.5367°E), -320–340 m, sandy mud, dredged NMDP, RV *Meiring Naude*, st'n ZP5, 12.vi.1988 (E3977, E3978, E6958); SE of Port Durnford (29.0250°S 32.1967°E), -310–320 m, glutinous sandy mud, dredged NMDP, RV *Meiring Naude*, st'n ZQ9, 13.vi.1988 (E3168); ditto (29.0967°S 32.1567°E), -165 m, mud with sand, dredged NMDP, RV *Meiring Naude*, st'n ZQ15, 17.vi.1989 (E8697); off Glenton Reef (29.2450°S 32.0367°E), -200–210 m, sandy mud, dredged NMDP, RV *Meiring Naude*, st'n ZRR9, 18.vi.1989 (S481); off Matigulu River mouth (29.3650°S 31.9367°E), -200–220 m, mud and coarse sand with *Dendrophyllia*, dredged NMDP, RV *Meiring Naude*, st'n ZR9, 16.vi.1989 (E8989). *Eastern Cape*: off Rame Head (31.8583°S 29.4683°E), -170–200 m, sandstone, yellow hydroids, dredged NMDP, RV *Meiring Naude*, st'n K11, 20.vii.1982 (S9944); off Mbashe River (32.3033°S 29.0683°E), -200–220 m, sponge rubble, dredged NMDP, RV *Meiring Naude*, st'n Q1, 18.vii.1982 (V495); off Shixini Point (32.5267°S 28.8833°E), -500 m, muddy sand, coral rubble, dredged NMDP, RV *Meiring Naude*, st'n T17, 13.vii.1984 (C7060).

Distribution and habitat (Fig. 13): Known primarily from Zululand to south-western Transkei (Neill Peak [Cunge Hill] to Qolora River), with one additional record from central Mozambique; -110–500 m (living specimens -150–250 m). Evidently a rather rare species, dead shells have been dredged in relatively deep water on rather lifeless muddy substrata (e.g. the Tugela Bank), but the five living specimens available were all collected in sponge communities on hard substrata near the continental shelf break. The absence of records from off central KwaZulu-Natal probably reflects less extensive dredging on the outer continental shelf and upper slope in this area.

Remarks: *Danilia textilis* closely resembles *D. discordata* Vilvens & Héros, 2005 from Vanuatu, particularly in terms of the number and relative strength of the spiral cords. In both species there are eight spiral cords above (and including) the periphery (the ninth cord mentioned by Vilvens and Héros (2005) is subperipheral), of which the peripheral cord is somewhat larger and distinctly more spiniform than those above it. Both species also have a strong, squarish lower columella tooth and a colour pattern of brown, frequently axial, markings on a pale fawn ground. However, in *D. discordata* the six spiral cords between the subsutural and peripheral cords are wider and conspicuously flattened, as are the beads where the cords are crossed by the axial pliculae. In *D. textilis* the spiral cords are rounded and narrower than their intervals and retain raised rounded beads. The sculpture throughout is of a regular, open, oblique, net-like reticulation. In this regard it resembles *D. insperata* Beu & Climo, 1974 from New Zealand, but that species has more evenly rounded whorls with fewer spiral cords (six above and including periphery) and a less robust lower columella tooth. *D. weberi* Schepman, 1908 from Indonesia and the western Pacific has more numerous spiral cords due to intercalation of intermediaries, has beads that are angular rather than rounded and has a broader, more robust basal columella tooth. The recently described *D. stratmanni* Poppe, Tagaro & Dekker, 2006 from shallower water (-50–150 m) in the Philippines has much finer sculpture, more numerous spiral cords and lacks spiniform beads on the peripheral spiral cord. *D. boucheti*, the only other species of *Danilia* recorded from the south-western Indian Ocean, is considerably smaller and has an almost biangular whorl profile.

The precise form of the apertural dentition varies considerably between individuals and is presumably related to maturity. There is evidently further thickening of the columella lip and its teeth, even after the subterminal varix and flared outer lip margin have formed.

## Genus **Ascetostoma** gen. n.

Etymology: From Greek *asketos* (curiously wrought or ornamented) and *stoma* (a mouth); in reference to the complex apertural features. Gender neuter.

Type species: *Euchelus providentiae* Melvill, 1909.

Diagnosis: Whorls rounded, suture indented and somewhat channelled; sculpture of finely beaded spiral cords; umbilicus present, lined and apically plugged with callus; columella pillar with a well developed, squarish, basal tooth and a smaller, more rounded, upper one; parietal region with spreading, glossy, translucent callus deposit bearing short oblique ridges; callus deposit extending around umbilical margin and joining basal lip; umbilical margin with several small denticles and one larger one in parietal region; interior of outer lip subterminally thickened and bearing ridge-like denticles arranged more or less in 2 rows; base of columella with pronounced U-shaped notch between basal columella tooth and first outer lip denticle; exterior of outer lip also with a low, broad, subterminal thickening; suture descending at aperture when mature.

Remarks: Similar to the *Herpetopoma* group of species, but characterised by the callus lined umbilical depression, spirally ridged parietal callus and denticulate umbilical margin. *Danilia* also has a callus lined depression in the umbilical region, but in members of that genus it is shallower and trough-like; they also possess a strong, well-defined, rib-like external varix behind the outer lip. *Clypeostoma* has at most a faint umbilical depression and a much more extensive inductural callus deposit. In *Ascetostoma* the sculpture is also more finely and closely beaded than in *Clypeostoma*.

### *Ascetostoma providentiae* (Melvill, 1909) **comb. n.**

Figs 4F, 5A, 6A, 18–20

*Euchelus providentiae*: Melvill 1909: 78, pl. 5, fig. 1; Viader 1937: 56; Kaicher 1990: Nº 5709. Type loc.: Providence Is. (Seychelles group), north east of Madagascar.
not *Clanculus providentiae*: Kosuge & Chino 1998: 79, pl. 26, fig. 1.

Description:

*Shell*: Trochoid-turbiniform, moderately elevated (L/D=1.04–1.26); teleoconch of 5.0–5.5 rounded whorls; suture indented and somewhat channelled, that between last adult whorl and penultimate whorl inserted at level of second subperipheral cord, but descending below this just prior to aperture; exterior of outer lip with a broad low subterminal thickening. First teleoconch whorl with approx. 20 axial pliculae; 3 spiral cords develop during second whorl (lowest level with abapical suture), and a fourth arising beneath adapical suture near end of whorl; subsequent whorls with further cords arising through intercalation; penultimate whorl with 7–9 cords, sometimes alternating a little in strength, sometimes not; seventh cord usually peripheral; cords well defined, equal to or wider than their intervals. Axial pliculae of first whorl persist on later whorls rendering spiral cords beaded where they cross them; beads of early whorls more or less rounded, but later becoming somewhat axially elongate, those on subsutural cord usually largest; axial pliculae well developed on spire whorls rendering sculpture cancellate, usually less prominent on last adult whorl. Base with 6–7 primary spiral cords and occasional intermediaries, sculptured as above. Peristome markedly oblique, more or less in one tangential plane; aperture subcircular to D-shaped, flattened parietally; columella lip protrudes into aperture as a thickened pillar which bears 2 well-developed teeth separated by a concavity; basal tooth often squarish, upper one somewhat smaller and more rounded; a deep U-shaped notch separates basal tooth from first denticle of basal lip; parietal region with glossy, translucent inductural callus, sculptured with a variable number of ridges extending into aperture; ridges sometimes bifid terminally; a well-developed parietal tooth projects from paries over umbilical depression; umbilicus present, lined and apically plugged with smooth, white callus when mature, conventionally patent in juveniles; umbilical margin thickened, also covered with callus and bearing ridge-like denticles (only in fully mature of specimens); callus slightly raised basally and confluent with flaring margin of outer lip; interior of outer lip with 2 rows of ridge-like denticles (at maximal maturity), the inner row stronger and lying on subterminal thickening of lip interior, the outer row (on non-nacreous flaring lip margin) weaker and less distinct; 2 denticles of inner row, nearest basal columella

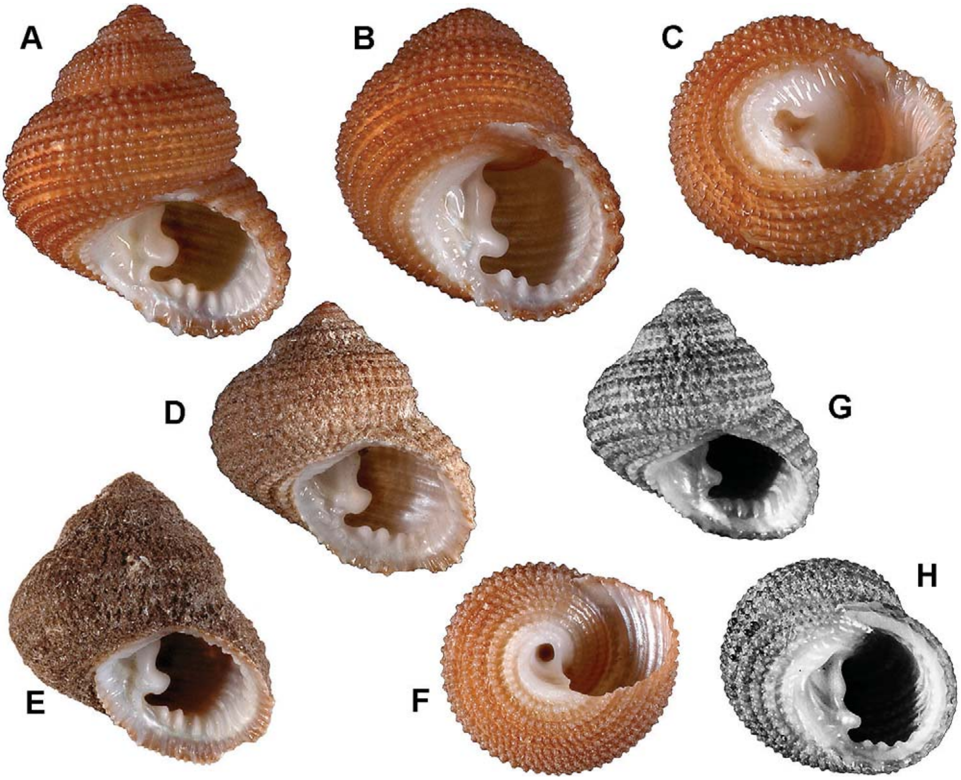

Fig. 18. *Ascetostoma providentiae* (Melvill, 1909): (A–C) adult specimen cleaned of encrustations, SE of Lala Neck, KZN, length 8.8 mm (NMSA S7232); (D) depressed specimen, off Rocktail Bay, KZN, length 7.2 mm (NMSA D9154); (E) sponge-encrusted specimen, off Rocktail Bay, KZN, length 7.7 mm (NMSA D9154); (F) juvenile specimen, off Dog Point, KZN, diameter 6.25 mm (NMSA S8968); (G, H) paratype of *Euchelus providentiae* Melvill, 1909, length 6.6 mm, diameter 5.9 mm (NHMUK 1910.3.17.2–3).

notch, usually larger; a small rounded or elongate granule may be present on columella near bottom of basal columella notch; interior of aperture nacreous, somewhat angled beneath spiral cords of shell exterior, but not spirally lirate.

Microsculpture (Fig. 19B, C): Early teleoconch whorls with fine vermiform spiral threads; microsculpture of subsequent whorls often completely obscured by encrusting organisms; little evidence of any superficial intritacalx deposit and scratch-like sculpture scarcely evident; microsculpture instead comprising irregular, somewhat oblique, vermiform threads, most noticeable on the spiral cords (Fig. 19B).

Protoconch (Fig. 19C): Translucent white, peripherally tinged with orange; diameter *ca* 240 µm; somewhat globose and protruding slightly above first teleoconch whorl; sculptured with 3 fine, widely spaced, spiral threads, between which lie numerous, fine, close-set, oblique, axial threads; terminal lip with a well-developed angular projection just above mid-whorl.

Colour: Most specimens uniformly rich orange-brown with darker spots on spiral cords of second and third whorls; occasional specimens with alternating darker and lighter blotches below suture; cord intervals faintly iridescent; umbilical region white;

pigmentation of old, dead shells frequently rather more pinkish/purplish brown. Shell exterior of live-taken specimens usually more or less entirely covered with a thin, brownish or blackish, spiculiferous, encrusting sponge (Fig. 18E).

Dimensions: Greatest length 9.0 mm, greatest diameter 8.0 mm, but size at maturity evidently variable; some specimens of length *ca* 7.0 mm possess mature apertural dentition.

*Operculum* (Fig. 4F): Initially tightly multispiral, but whorls broadening with growth and becoming more openly multispiral.

*Radula* (Fig. 19D, E): Formula ∞+4+1+4+∞; *ca* 75 transverse rows of teeth. Rachidian with trigonal cusp and well-developed hood; base of cusp with weak transverse ridge; cutting edge coarsely dentate, central denticle largest, lanceolate and with 3 or 4 smaller denticles on each side. Lateral tooth cusps with an elongate, rather spathulate central denticle and relatively coarse secondary denticles on outer margin, inner margin with few if any denticles. Inner marginals more slender with a recurved, dentate cusp, the denticles on outer margin extending some way down shaft; middle marginals very slender, but outermost ones shorter, broader and very delicate.

*External anatomy* (Figs 5A, 6A): Head-foot with extensive dark brown to black pigmentation in living animal; cephalic tentacles more or less uniformly dark; blackish colour of neck lobes and epipodial tentacles contrasting with whitish upper parts of foot. Cephalic lappets finely digitate, not meeting in mid-line; snout laterally expanded,

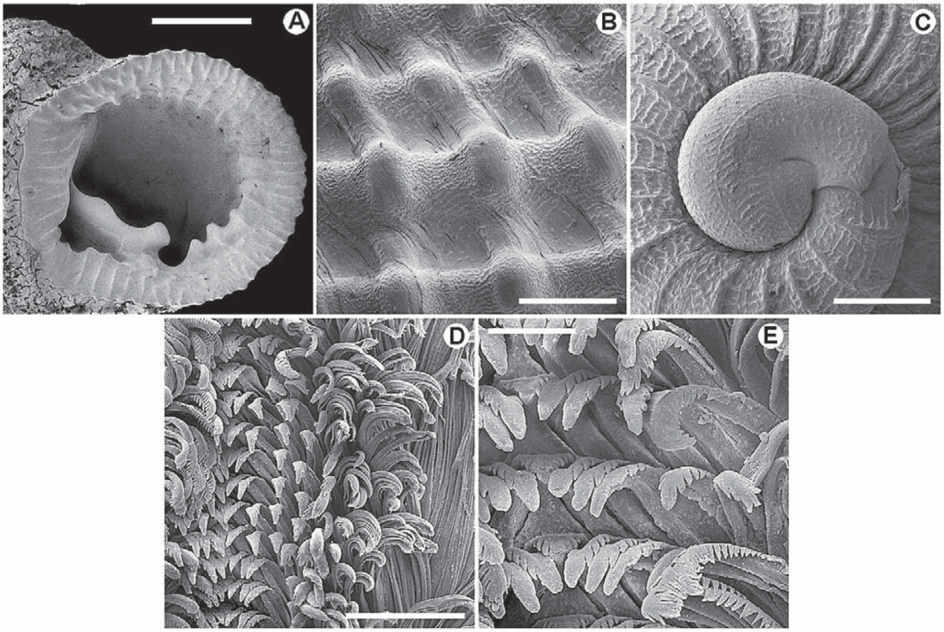

Fig. 19. *Ascetostoma providentiae* (Melvill, 1909): (A) oblique view of aperture showing complex dentition and deep umbilical cavity [shell exterior encrusted with sponge], off Lala Neck, KZN, bar = 2.5 mm (NMSA S7335); (B) microsculpture on penultimate whorl, off Boteler Point, KZN, bar = 200 µm (NMSA E2943); (C) protoconch with angular projection on terminal lip, off Dog Point, KZN, bar = 100 µm (NMSA E1743); (D, E) radula, off Lala Neck, KZN, bars = 100 µm and 25 µm respectively (NMSA S7335).

transversely striped with black, lips split mid-ventrally; right post-ocular peduncle relatively small, arising from base of eyestalk; subocular tentacle not evident; right neck lobe with approx. 5 closely spaced tentacles anteriorly (increasing in size from first to last) followed by 2 or 3 more widely spaced ones; left neck lobe with numerous, close-set tentacles along most of its length, more or less similar in size; epipodial fold with approx. 10 tentacles of various sizes, the larger ones each with a basal epipodial sense organ; epipodial sense organs not evident beneath neck lobes, but some larger neck lobe tentacles with a pale basal spot that may represent such a structure.

Type material: Melvill (1909) stated that he had examined two specimens and selected the larger as the 'type' [holotype]. The second specimen would therefore be a paratype. Two specimens were originally registered under NHMUK 1910.3.17.2–3, but only one is now present. This is smaller than the dimensions given by Melvill and is presumably the paratype; length 6.6 mm, diameter 5.9 mm. It is a subadult specimen in which the apertural dentition is not fully developed (Fig. 18G, H).

Additional material examined (all NMSA unless indicated otherwise): MADAGASCAR: W Banc du Leven (12.5333°S 47.6675°E), -35–150 m, Benthedi Exped'n, st'n 5, dredged (MNHN); west of Nosy Be (13.417°S 47.950°E), -71–158 m, Campagne *Miriky*, st'n DW3230, dredged, 03.vii.2009 (MNHN). RÉUNION: off Étang-Salé-les-Bains, *Marion-Dufresne* 32, st'n DC176 (21.3333°S 55.1833°E), -165–195 m, dredged, 1982 (MNHN). MOZAMBIQUE: Sofala Bank (approx. 20.123°S 35.543°E), -110–145 m, *ex pisce*, v.2007 (J. Rosado coll'n); between Beira and Bazaruto (approx. 20.58°S 35.73°E), -95–125 m, *ex pisce* (J. Rosado coll'n); off Lacerda Lighthouse (25.56167°S 32.84472°E), -72–75 m, dredged, vii.2008 (J. Rosado coll'n); off Ponta Techobanine (26.68132°S 32.95093°E), -60–100 m, dredged J. Rosado, xii.2005 (D. Slater coll'n). SOUTH AFRICA: *KwaZulu-Natal*: off Kosi River mouth (26.9100°S 32.9433°E), living, -75 m, sandstone, marine growths, dredged NMDP, RV *Meiring Naude*, st'n ZA13, 7.vi.1987 (D9009, E1413); SE of Kosi estuary mouth (26.9167°S 32.9300°E), -65 m, sponge, gorgonians, medium sand, dredged NMDP, RV *Meiring Naude*, st'n ZA12, 7.vi.1987 (D8018); off Boteler Point (27.0083°S 32.9117°E), living, -50 m, coral rubble, lithothamnion, dredged NMDP, RV *Meiring Naude*, st'n ZB7, 6.vi.1987 (E2943); ditto (27.013°S 32.905°E), -50 m, dead coral rubble, lithothamnion, dredged NMDP, RV *Meiring Naude*, st'n ZB2, 6.vi.1987 (D9199); ditto (27.0117°S 32.9200°E), living, -70 m, rocks and sand, dredged NMDP, RV *Sardinops*, st'n ZB19, 6.vi.1990 (S4904, S8715, S8961); ditto (27.0133°S 32.9183°E), -70 m, some coarse sand, some shell rubble, dredged NMDP, RV *Meiring Naude*, st'n ZB4, 6.vi.1987 (D7415); ditto (27.0183°S 32.9200°E), -78 m, coarse sand, dredged NMDP, RV *Meiring Naude*, st'n ZB6, 6.vi.1987 (D7475); ditto (27.0183°S 32.9183°E), living, -69–73 m, sponges, rocks and sand, dredged NMDP, RV *Sardinops*, st'n ZB20, 6.vi.1990 (S5026); ditto (27.0400°S 32.9150°E), living, -75 m, rocks, sand, gorgonians, dredged NMDP, RV *Sardinops*, st'n ZB22, 6.vi.1990 (S5381); ditto (27.0500°S 32.9117°E), -78 m, marine growths, dredged NMDP, RV *Sardinops*, st'n ZB23, 6.vi.1990 (S6651); off Dog Point (27.1000°S 32.8883°E), living, -74 m, sandstone rubble and gorgonians, dredged NMDP, RV *Sardinops*, st'n ZC10, 7.vi.1990 (S6485); ditto (27.1083°S 32.8817°E), living, -70 m, sandstone conglomerate, dredged NMDP, RV *Meiring Naude*, st'n ZC3, 4.vi.1987 (D6477, E1743); ditto (27.1267°S 32.8733°E), living, -76 m, sandstone rubble and gorgonians, dredged NMDP, RV *Sardinops*, st'n ZC12, 7.vi.1990 (S8968); off Rocktail Bay (27.1850°S 32.8483°E), -100 m, sand, dredged NMDP, RV *Sardinops*, st'n ZD4, 7.vi.1990 (S5182); ditto (27.1900°S 32.8500°E), -100 m, sandstone rubble, dredged NMDP, RV *Meiring Naude*, st'n ZD1, 4.vi.1987 (D7597); ditto (27.1900°S 32.8433°E), living, -75 m, sandstone rubble, dredged NMDP, RV *Meiring Naude*, st'n ZD2, 4.vi.1987 (D6361, D9154); SE of Rocktail Bay (27.1917°S 32.8400°E), living, -78 m, sandstone rocks, dredged NMDP, RV *Sardinops*, st'n ZD10, 8.vi.1990 (S4639); ditto (27.2017°S 32.8300°E), living, -60 m, coarse sand, dredged NMDP, RV *Sardinops*, st'n ZD9, 8.vi.1990 (V894); NE of Lala Neck (27.2150°S 32.8283°E), living, -66–71 m, coarse sand, sandstone rocks, dredged NMDP, RV *Sardinops*, st'n ZD7, 8.vi.1990 (S6137); off Lala Neck (27.2292°S 32.8217°E), living, -72 m, slightly muddy sand with pennatulids, dredged NMDP, RV *Sardinops*, st'n ZDD1, 7.vi.1990 (S7335); SE of Lala Neck (27.2433°S 32.8133°E), living, -74 m, sandstone rocks, dredged NMDP, RV *Sardinops*, st'n ZDD2, 7.vi.1990 (S7232); off Hully Point (27.343°S 32.778°E), living, -60 m, shell rubble, dredged NMDP, RV *Meiring Naude*, st'n ZF4, 5.vi.1987 (D7332); off Sodwana Bay (27.530°S 32.717°E), living, -70 m, coral rubble, dredged NMDP, RV *Sardinops*, st'n ZH22, 2.vi.1990 (W7477); off Jesser Point (27.5467°S 32.7100°E), living, -68 m, sponge, coral rubble, dredged NMDP, RV *Meiring Naude*, st'n ZH3, 3.vi.1987 (D6512); ditto (27.5533°S 32.7133°E), living, -85 m, sponge, coral rubble, dredged NMDP, RV *Meiring Naude*, st'n ZH4, 3.vi.1987 (D6789); off Sodwana Bay (27.5567°S 32.7133°E), -77 m, dead coral rubble, dredged NMDP, RV *Sardinops*, st'n ZH19, 2.vi.1990 (S4781); ditto (27.5833°S 32.6967°E), -70 m, medium sand, dredged NMDP, RV *Meiring Naude*, st'n ZH16, 9.vi.1987 (D8441); Leadsman Shoal (27.8000°S 32.6167°E), -100 m, dredged A.D. Connell, iv.1980 (B4054); off Gipsy Hill (27.8117°S 32.6567°E), -100–125 m, broken shell, dredged NMDP, RV *Meiring Naude*, st'n ZK9, 11.vi.1988 (E3248); SE of Mission Rocks (28.2917°S 32.5433°E), -50 m, old coral rubble, lithothamnion, dredged NMDP, RV *Meiring Naude*, st'n ZN1, 10.vi.1988 (E4640).

Distribution and habitat (Fig. 20): Islands of the western Indian Ocean (southern Seychelles group and Mascarenes) and the Mozambique Channel south to north-eastern South Africa (28.3°S, off Mission Rocks); -35–195 m (living specimens -50–85 m). In Zululand this species appears to inhabit hard substrata beyond the line of the near-shore reef system, where the sea floor is composed of fragmented sandstone or coral rubble, and is generally rich in marine life. Evidently a mid to outer continental shelf species throughout its range and not part of the shallow-water coral reef biota.

Remarks: This species is very similar to *Euchelus ringens* Schepman, 1908 from the Sulu Archipelago, Indonesia, and the two may eventually prove to be synonyms. The columella lip of the holotype of *E. ringens* (Fig. 68A, B) is somewhat damaged (perhaps due to occupation by a hermit crab) and looks rather deformed. Compared with south-western Indian Ocean material it differs in being slightly less elevated and in having a narrower umbilicus; there are also minor differences in terms of coloration and aperture characters. In the absence of data on variation in Indonesian material, I have chosen, to err on the side of caution and maintain *Ascetostoma providentiae* as a distinct species. There can be no doubt, however, that *E. ringens* is also a species of *Ascetostoma*.

*A. providentiae* is easily distinguished from the other southern African chilodontid taxa by its rounded whorl profile, very strong, complex apertural dentition and patent, callus lined umbilicus. '*Clanculus*' *crassilabrum* Sowerby, 1905 (Fig. 68C, D) from Sri Lanka has a similar overall facies, but lacks the unusual umbilical features of *Ascetostoma* and is probably closer to *Herpetopoma*. Also similar is *Herpetopoma rubrum* (A. Adams, 1853), from Japan to SE Asia, which is likewise often vividly coloured, but

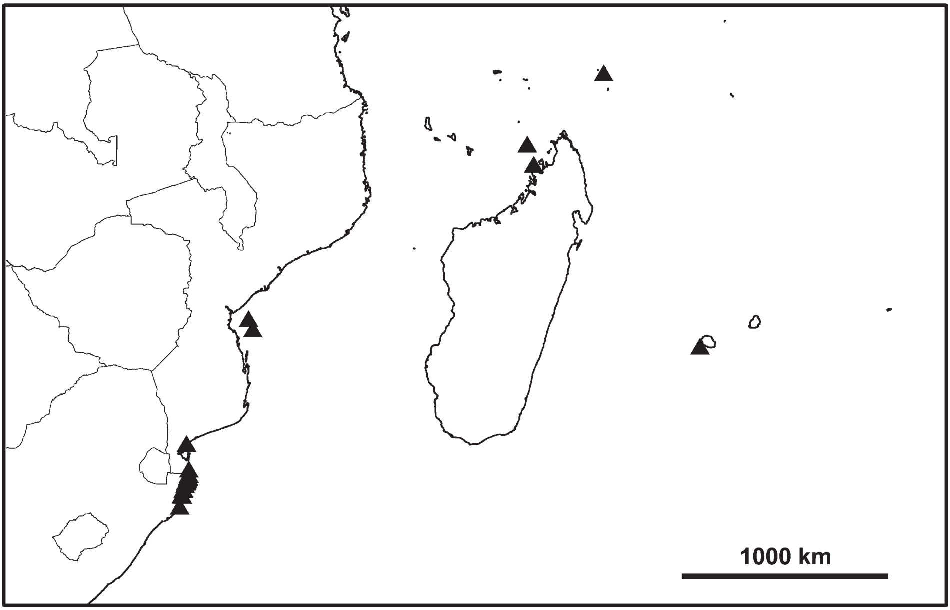

Fig. 20. Distribution of *Ascetostoma providentiae*. Each triangle represents one or more records.

in that species the inductural callus does not extend over the umbilical region and the umbilicus remains conventionally patent even at full apertural maturity. The Japanese *Euchelus lischkei* Pilsbry, 1904 also resembles *A. providentiae* in size, shape and sculpture, but has a much weaker basal columella tooth and has a simple, patent umbilicus. The Philippine material identified under this name (as *Clanculus*) by Kosuge and Chino (1998) is not in fact referable to this species.

The Cretaceous *Chilodonta* (*Agathodonta*) *africana* Rennie, 1930 from the Pondoland coast, Eastern Cape (holotype, SAMC 8630) is superficially similar to *A. providentiae*, but it has finer granules above the periphery, distinct prosocline pliculae below the suture and a smoother base. It has a well-developed tubercle on the basal lip separated from the columella by a U-shaped notch, but no details of its umbilicus are apparent.

## Genus *Euchelus* Philippi, 1847

*Euchelus*: Philippi 1847: 20. Type species: *Trochus quadricarinatus* [Chem.] Holten, 1802 [=*Trochus asper* Gmelin, 1791], by subsequent designation (Herrmannsen 1847: 430).

Species of *Euchelus* s.s. are generally larger shelled than those of *Herpetopoma,* have a single weak columella tooth and lack a deep U-shaped notch at the base of the columella. Evidently *Euchelus* s.s. is scarce in the south-western Indian Ocean. Only two species have been recorded from the region and I have seen no further material referable to this genus.

### *Euchelus alabastrum* (Reeve, 1858)

Fig. 21

*Trochus* (*Euchele*) *alabastrum*: Reeve 1858 in 1857–58: 209, pl. 38, figs 1a, b; Pilsbry 1890 in 1889–90: 448. Type loc.: Island of Diego Garcia.

*Euchelus alabastrum*: Pilsbry 1890: 344.

not *Trochus alabastrum*: Beck ms Philippi 1847 in 1846–55: pl. 15, fig. 14; *idem* 1849 in 1846–55: 9 [= *Margarita alabastrum*: Beck ms Lovén, 1846 = *Calliostoma occidentale* (Mighels & C.B. Adams, 1842)].

There is no type material for this species in the NHMUK and although Reeve mentioned additional material in the Cuming collection, no specimens identified under this name could be found in the NHMUK general collection. Nonetheless, two specimens labelled '*triangulata* var.' (without locality), from the Cuming collection, bear considerable resemblance to Reeve's original figure of *Trochus alabastrum* (Fig. 21A). The larger of the two is here figured for comparison (Fig. 21B). Like *alabastrum* it is chalky-white with small spots (now much faded and pale purple-brown rather than black) on the spiral keels.

This material represents pale, particularly strongly keeled individuals of the *quadricarinatus* form of the highly variable *Euchelus asper* (Gmelin, 1791). Although it can not be considered type material for *T. alabastrum*, its resemblance to the description and original figure of the latter strongly suggests that it may have been the Cumingian material referred to by Reeve. There can be little doubt that it is conspecific therewith. I therefore propose that *Trochus alabastrum* Reeve, 1958 be considered a synonym of *Euchelus asper* (Gmelin, 1791) and that it represents the form *quadricarinatus* (Holten, 1802) (cited figure reproduced in Fig. 21C) of that species. *Monodonta tricarinata* Lamarck, 1822 is already established as another synonym (Fischer 1878 in 1875–80). This

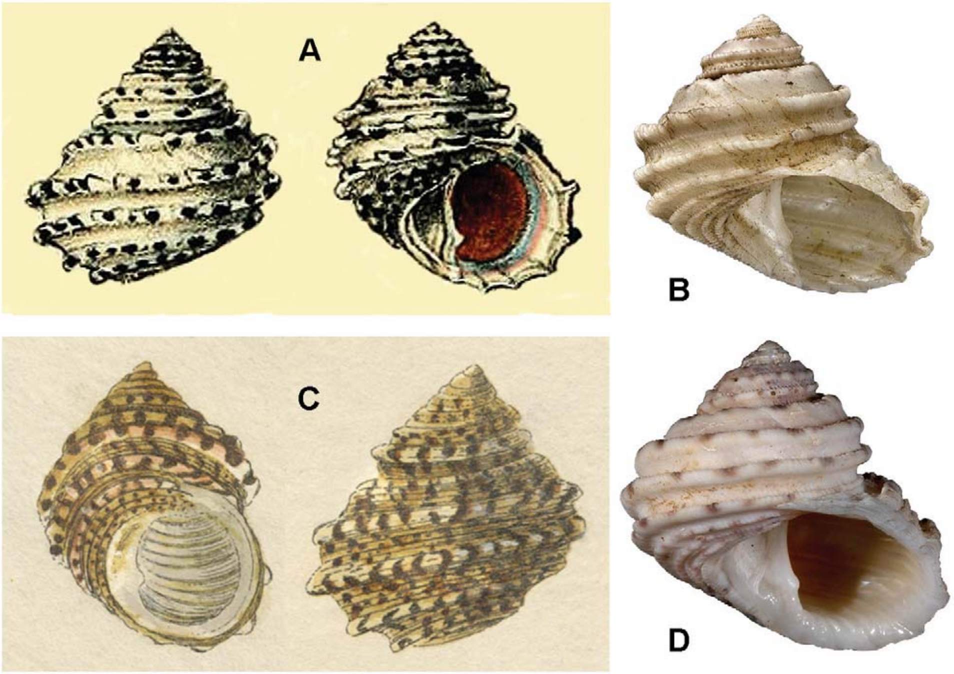

Fig. 21. *Euchelus alabastrum* (Reeve, 1858): (A) original figure of *Trochus* (*Euchele*) *alabastrum* given by Reeve (1858), diameter 5/8 poll. [=15.9 mm]; (B) *Euchelus* '*triangulata* var.' subadult, diameter 15.5 mm, Cuming coll'n (NHMUK); (C) original Chemnitz figure *Trochus quadricarinatus* cited by Holten (1802), dimensions not given; (D) *Euchelus asper* form *quadricarinatus* (Holten, 1802), Pattani, Gulf of Thailand, diameter 17.0 mm (NMSA L5162).

form of the species is evidently widespread in the Indo-West Pacific, occurring as far east as Japan (Sasaki 2000). It was also recorded from Durban by Sowerby (1897), but it seems more probable that this was a misidentified or mislocalised specimen. Fresher material from Thailand is illustrated for comparison (Fig. 21D) and an additional figure was provided by Poppe and Tagaro (2008: pl. 43:8). The extent of variation within *E. asper* is considerable and requires further study in order to evaluate its significance and to determine if it is genetically, environmentally or sexually determined.

The original *Trochus alabastrum* material described by Reeve (1858) came from the collection of Sir David Barclay, which was sold at auction in 1891 (Dance 1986). Some types from this collection were subsequently purchased by the NHMUK from G.B. Sowerby (3rd), but the whereabouts of others is not known (J. Pickering pers. comm., Feb. 2011).

### *Euchelus atratus* (Gmelin, 1791)

*Turbo atratus*: Gmelin 1791: 3601, Nº 53. Type loc.: Nicobar Islands.
*Euchelus atratus*: Pilsbry 1890 in 1889–90: 439 (further references and synonymy), pl. 38, fig. 22; Thiele 1917: 563; Drivas & Jay 1988: 36, pl. 3, fig. 6.

Thiele (1917) and Drivas & Jay (1988) recorded this species from the Comoros and Réunion respectively. A single specimen is present in the Jay coll'n (MNHN), but it is in very poor condition, most of the surface sculpture having flaked off. However, what remains is of a pale colour, which combined with the fact that the specimen has a closed umbilicus, suggests that it may not in fact be referable to *E. atratus*. In the absence of additional material in better condition I cannot confirm the occurrence of this species in the south-western Indian Ocean.

### Genus *Herpetopoma* Pilsbry, 1890

*Huttonia*: Kirk 1882: 282 [*non* Pickard-Cambridge, 1880 (Araneae) *nec* Marshall, 1896 (Diptera)]. Type species: *Euchelus bellus* Hutton, 1873, by subsequent designation (Pilsbry 1890 in 1889–90: 429).

*Herpetopoma*: Pilsbry 1890 in 1889–90: 430, 445. Type species: *Euchelus scabriusculus* Adams & Angas in Angas, 1867, by original designation.

The type species of *Herpetopoma*, *Euchelus scabriusculus* Adams & Angas in Angas, 1867, from southern and south-eastern Australia, is a small gemmate species with a simple, open umbilicus bordered by a strongly beaded spiral cord. The columella is likewise relatively simple with a single well-developed tooth at its base. Another well-developed tooth is situated on the basal lip, close to its junction with the columella, the space between these teeth forming a deep U-shaped notch. The inner margin of the outer lip is set with numerous small, ridge-like denticles and the operculum is openly multispiral, with a broad growing margin (Fig. 4H).

*Herpetopoma* has frequently been treated as a subgenus of *Euchelus*, but like most more recent authors, I consider it to represent a distinct radiation and to be worthy of recognition at generic level. Species of *Euchelus* s.s. are generally larger and have an operculum with fewer, more rapidly expanding whorls (see above). Although they may have a single simple tooth/denticle at the base of the columella, they mostly lack the characteristic pattern of two teeth at the junction of the columella and basal lips, separated by a U-shaped notch, which is typical of *Herpetopoma*. Other taxa (e.g. *Ascetostoma*, *Clypeostoma* and *Danilia*) that exhibit this last feature have additional characters, which set them apart from *Herpetopoma*.

However, even when recognised as a genus itself, *Herpetopoma*, may prove to be a composite taxon, given the diversity of shell form evident in the species assigned to it. I have reasonable confidence that *H. instrictum*, *H. seychellarum*, *H. serratocinctum* and *H. stictum* are correctly placed in this genus and refer them to *Herpetopoma sensu stricto*. However, I am less certain about *H. helix*, *H. ?naokoae* and *H. xeniolum* and thus consider them *Herpetopoma sensu lato*. The protoconch is more exsert and evidently less strongly sculptured, the juvenile microsculpture sometimes granular rather than vermiform and, at least in *H. helix*, the operculum is tightly multispiral throughout.

No well preserved alcohol material is available for any of the local species of *Herpetopoma* and thus details of the external anatomy are not available. However, I have been able to extract a radula from *H. helix* as well as from dried specimens of the type species loaned from the Australian Museum, Sydney. Details of the latter are given below.

*Radula* (Fig. 22): Formula $\infty+(3\text{–}4)+1+(3\text{–}4)+\infty$; *ca* 55 transverse rows of teeth; transition from lateral to marginal series relatively clear. Rachidian with broad, trigonal cusp and well-developed hood; cusp with strong transverse ridge at its base, this generally concave due to medial indentation near cusp base; cutting edge coarsely

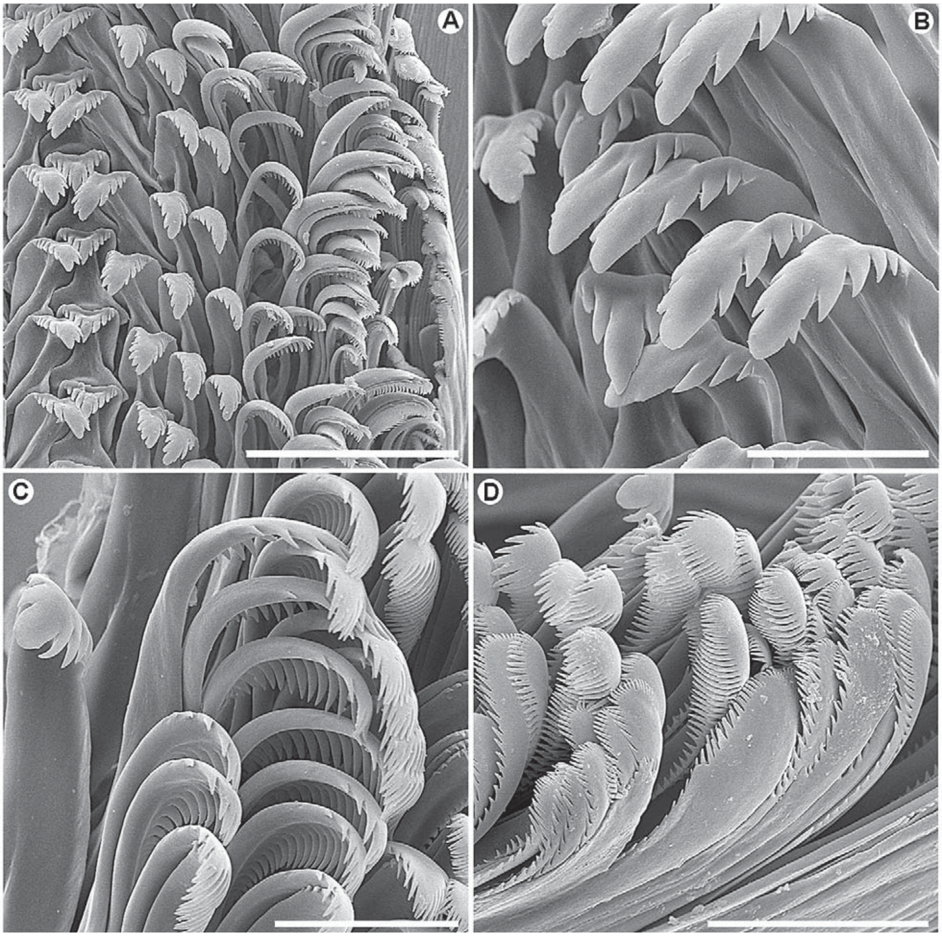

Fig. 22. *Herpetopoma scabriusculum* (Adams & Angas in Angas, 1867), radula: (A) half-row, specimen with only 3 pairs of lateral teeth, bar = 50 µm; (B) rachidian and lateral teeth, specimen with 4 pairs of laterals, bar = 15 µm; (C) inner marginal teeth with sparsely barbed inner margin and coarsely pectinate outer margin, bar = 15 µm; (D) radula margin showing finely pectinate cusps of outer marginals and broad cusp of the outermost one, bar = 20 µm. All AMS C304695, Bradleys Head, Sydney Harbour, NSW, Australia.

dentate, central denticle largest, lanceolate, with 2–4 smaller denticles on each side. Lateral teeth progressively decreasing in size from first to last, but not markedly so; one specimen with 3 pairs of laterals per row, another with four; cusp elongate-trigonal to spathulate, bearing coarse lateral denticles on both margins (3–6). Marginals longer and more slender than laterals, but relatively shorter than in other genera; inner marginals distinctive in having a slender, recurved cusp with a few short, barb-like denticles near the tip on inner margin and a series of much longer, close-set, curved denticles on outer margin, the central part of the cusp appearing as a rib-like structure from which the two series of denticles project (Fig. 22C); remaining marginals with smaller, ladle-shaped cusps with a finely pectinate margin, the outermost one with a somewhat enlarged cusp (Fig. 22D).

### Key to species of *Herpetopoma* in the south-western Indian Ocean

1 Basal columella tooth a well-developed peg with a deep U-shaped notch separating it from the first (usually the largest) tooth inside the basal lip (Fig. 23)................2
– Basal columella tooth smaller and roundly trigonal; U-shaped notch at base of columella relatively shallow (Fig. 32) ....................................................................5

2 Umbilicus remaining patent in adult ..................................................................3
– Umbilicus closed in adult.......................................................................................4

3 Adult shell length exceeding 5.0 mm; spire trochiform, usually with reddish brown markings........................................................................................**instrictum**
– Adult shell length less than 4.0 mm; spire low, evidently without colour pattern... ..........................................................................................**seychellarum**

4 Shell small, adult length rarely >3.0 mm; profile globose with a well-developed serrate spiral cord at periphery; coast of tropical East Africa ........**serratocinctum**
– Shell larger, adult length >3.0 mm; spire profile more trochiform; peripheral cord not enlarged or conspicuously serrate; Mascarene Islands ........................**stictum**

5 Sculpture relatively coarse with 3 strong spiral cords above and including periphery; beads on spiral cords axially elongate.......................................................... **helix**
– Sculpture fine with 4 or more spiral cords above and including periphery; beads more or less rounded ........................................................................................6

6 Shell relatively low-spired, L/D<1.23; labral denticles largely restricted to thickened inner lip; whorls rounded, sculpture relatively coarse ............................?**naokoae**
– Shell higher-spired, L/D>1.23, some labral denticles extending into aperture as in-running ridges; whorls rather flat-sided, sculpture fine .......................**xeniolum**

### *Herpetopoma* (s.s.) *instrictum* (Gould, 1849)

Figs 4G, 23–25

*Trochus* (*Monodonta*) *instrictus*: Gould 1849 in 1846–50: 107; 1852: 190, pl. 13, fig. 225a–c; 1862: 59; Johnson 1964: 92. Type loc.: Pacific Islands.

*Monodonta alveolata*: A. Adams 1853: 176. Type loc.: 'Guidulman, island of Bohol, rocky ground, 60 fathoms [-110 m]; Baclayon, island of Bohol, under stones, low water; island of Capul, on the reefs at low water'.

*Monodonta bourcierei*: Crosse 1863: 178, pl. 4, fig. 6; Pilsbry 1890 in 1889–90 [= *Trochus instrictus* Gould, 1849]. Type loc.: New Caledonia.

*Turcica instricta*: A. Adams 1864*b*: 143.

*Trochus* (*Euchelus*) *alveolatus*: Smith 1876: 559.

*Trochus bourcierei*: Fischer 1878 in 1875–80: 249, pl. 84, fig. 3.

*Euchelus alveolatus*: Melvill & Sykes 1897: 172; Kaicher 1990: Nº 5706, syntype.

*Euchelus instrictus*: Pilsbry 1890 in 1889–90: 440, pl. 67, figs 62, 63; Hedley 1899: 405; Hidalgo 1904–5: 256; Shirley 1911: 96; Cernohorsky 1978b: 33, pl. 8, fig. 6 [= *Monodonta alveolata* Adams, 1853]; Kaicher 1990: Nº 5705, holotype; Wells & Slack-Smith 1986: 44; Jansen 1996: 7, Nº 21 [doubtful]; Kosuge & Chino 1998: 78, pl. 25, fig. 3 [doubtful]; Chang 2003: 4, figs C–F.

*Monodonta bourcieri* [*sic*]: Smith 1897: 232.

*Euchelus intricatus* [*sic*]: Schepman 1908: 71.

*Euchelus* (*Euchelus*) *alveolatus*: Solem 1953: 218.

*Euchelus* (*Euchelus*) *instrictus*: Hirase & Taki 1954: pl. 70, fig. 6; Solem 1958: 217.

*Euchelus instricta*: Habe 1964: 10, pl. 4, fig. 14.

*Euchelus* (*Herpetopoma*) *instrictus*: Ladd 1966: 33, pl. 3. figs 11–13; Springsteen & Leobrera 1986: 36, pl. 5, fig. 10.

*Euchelus bourcieri* [*sic*]: Kaicher 1990: Nº 5707, type.

*Euchelus* (*Vaceuchelus*) *instrictus*: Fukuda 1993: 24, pl. 6, fig. 70.

*Herpetopoma instricta*: Wilson 1993: 68; Higo *et al*. 1999: 52, Nº G280; Sasaki 2000: 57, Nº 18; Vilvens & Héros 2003: fig. 5; Taylor & Glover 2004: 264; Héros *et al*. 2007: 209.
*Herpetopoma instrictum*: Poppe *et al*. 2006: 37, pl. 10, fig. 4; Poppe & Tagaro 2008: 174, pl. 32, figs 2, 6.
not *Euchelus* cf. *instrictus*: Orr Maes 1967: 103, pl. 3, fig. E.

Description:

*Shell*: Trochoid-turbiniform, moderately elevated (L/D=1.10–1.25); teleoconch of up to 6.5 whorls; spire whorls somewhat flat-sided; suture strongly indented, inserted at level of subperipheral cord and thus appearing somewhat channelled, descending slightly just prior to outer lip. First teleoconch whorls sculptured with curved axial pliculae; 2–3 spiral cords arise during second whorl, and additional ones with subsequent growth; penultimate whorl with approx. 5 well developed cords, a sixth level with suture; subsutural cord strongest, but becoming distinctly weaker just behind outer lip; cords

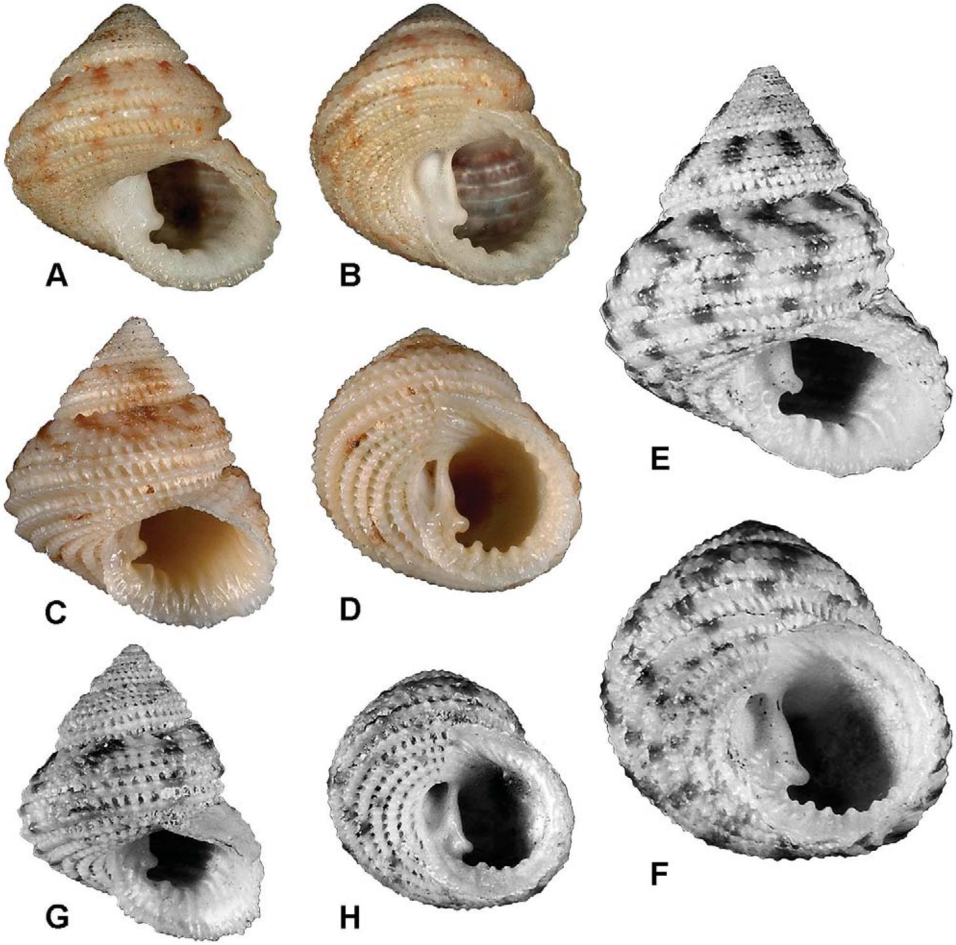

Fig. 23. *Herpetopoma instrictum* (Gould, 1849): (A, B) holotype of *Trochus instrictus* Gould, 1849, length 8.3 mm, diameter 7.5 mm (USNM 5625); (C, D) Conducia Bay, northern Mozambique, length 9.0 mm, diameter 7.7 mm (NMSA J4175); (E, F) lectotype of *Monodonta alveolata* A. Adams, 1853, length 11.9 mm, diameter 10.0 mm (NHMUK 196872); (G, H) holotype of *Monodonta bourcierei* Crosse, 1863, length 8.6 mm, diameter 7.0 mm (NHMUK 96.12.1.13).

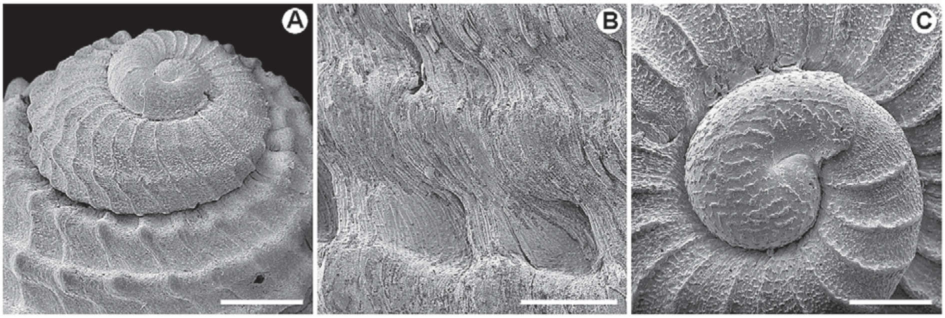

Fig. 24. *Herpetopoma instrictum* (Gould, 1849), Low Isles, Great Barrier Reef, Queensland (AMS C.304699): (A) shell apex, bar = 250 µm; (B) adult microsculpture, bar = 200 µm; (C) protoconch, bar = 100 µm.

equal to or narrower than their intervals. Axial pliculae of first whorl persist on later whorls producing a distinct cancellation and rendering spiral cords granular where they cross them; granules of subsutural cord usually largest, becoming smaller and more numerous toward periphery; interstices more or less square on spire whorls, becoming axially elongate on last adult whorl, particularly so just behind outer lip. Base similarly sculptured with approx. 6 spiral cords, the last of which forms umbilical margin; umbilicus remaining open at maturity (very occasionally almost occluded by reflected columella). Peristome oblique; aperture D-shaped, flattened parietally; columella thickened, bearing a low bulge in the mid region and a well-developed, peg-like tooth basally; a deep U-shaped notch separates basal columella tooth from first denticle of basal lip; parietal callus not extending far beyond aperture, bearing spiral ridges; margin of outer lip somewhat flaring, the edge finely and rather irregularly crenulate; interior of outer lip with a subterminal thickening which is set with relatively strong, in-running, ridge-like denticles, these become weaker toward lip margin and develop finer intermediaries (at maximal maturity); denticles not extending far into aperture, one nearest basal columella notch usually larger; 1 or 2 small rounded granules may be present on columella near bottom of basal columella notch; interior of aperture nacreous; exterior of outer lip sometimes with a broad low subterminal thickening, but lacking a rib-like varix.

Microsculpture (Fig. 24A–C): Juvenile shell with vermiform spiral threads; later whorls with close-set, scratch-like marks beneath intritacalx.

Protoconch (Fig. 24A, C): White, more or less level with first teleoconch whorl or at most weakly exsert, with a weak apical beak; diameter 220–240 µm; terminal lip distinctly convex; superficial sculpture well developed, arranged in irregular axial lines, with a weak spiral element.

Colour: White to yellowish white, later whorls with reddish to brown spots, blotches or axial flames; markings generally browner in fresh specimens; a white to dirty brown intritacalx is present in fresh specimens but this is worn off in most museum material. Shell surface often encrusted by other marine organisms.

Dimensions: Largest specimen seen, length 11.9 mm, diameter 10.0 mm (lectotype of *Monodonta alveolata* A. Adams, 1853).

*Operculum* (Fig. 4G): Initially tightly multispiral, but whorls broadening with growth and becoming more openly multispiral.

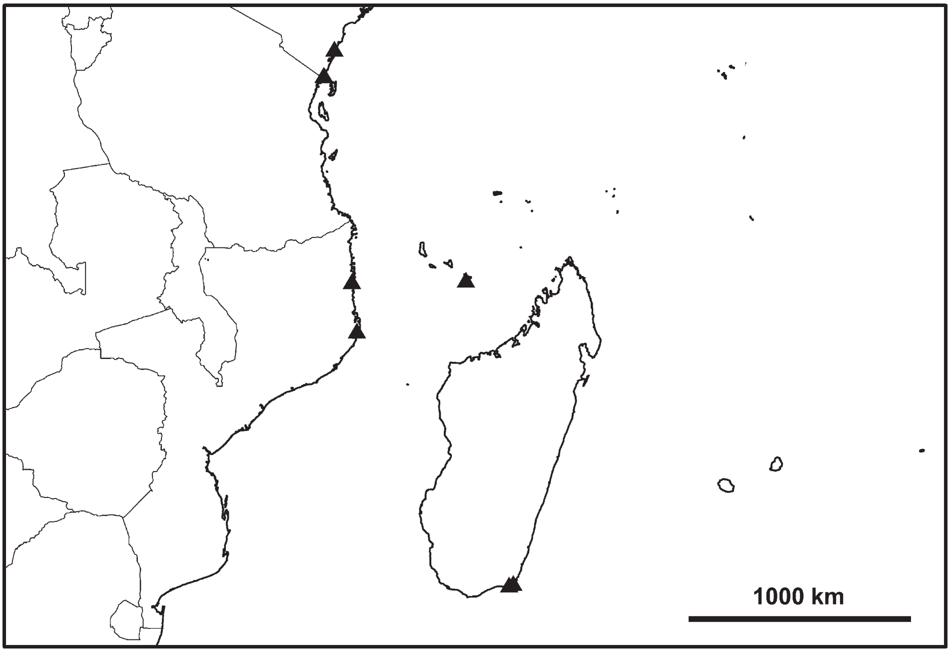

Fig. 25. Distribution of *Herpetopoma instrictum* in the south-western Indian Ocean. Each triangle represents one or more records.

*Radula and external anatomy*: Unknown except for some brief comments on the external anatomy made by A. Adams (1864*b*). A figure of a living specimen was also provided by Sasaki (2000: 56).

Type material: Holotype of *Trochus instrictus* Gould, 1849, in USNM (5625) (Fig. 23A, B see also Kaicher 1990), length 8.3 mm, diameter 7.5 mm (measured from photograph scale, dimensions given by Gould equate to 9.5×7.6 mm); four syntypes of *Monodonta alveolata* A. Adams, 1853 in NHMUK (196872), the best of which is here figured and designated lectotype, length 11.9 mm, diameter 10.0 mm (Fig. 23E, F); holotype of *Monodonta bourcierei* Crosse, 1863 in NHMUK (96.12.1.13), length 8.6 mm, diameter 7.0 mm (Fig. 23G, H).

Regional material examined: KENYA: Kilifi (3.60236°S 39.81190°E), *ca* -4 m, lagoon inshore of coral reef, sand from base of coral outcrops, D. Herbert, 20.xii.1991 (K8265); Shimoni, SE of Wasini Is. (4.65°S 39.39°E), J.D. Taylor (NHMUK); Shimoni area, Shungalunzi (1.2 km east of Shimoni) (4.67°S 39.41°E), J.D. Taylor (NHMUK). COMOROS: Mayotte (12.87°S 45.09°E), V.W. MacAndrew coll'n (NHMUK). MADAGASCAR: Ouest Cap Antsirabe (25.04167°S 46.99500°E), -4–5 m, fond rocheux en limite de platier, Exped'n Atimo Vatae, st'n TS12, 9.v.2010 (MNHN); Pointe d'Ambero (25.11167°S 46.83167°E), intertidal substrat dur, mode battu, Exped'n Atimo Vatae, st'n TM16, 08.v.2010 (MNHN); Baie des Galions (25.1483°S: 46.7567°E), intertidal, platier rocheux et sable, Exped'n Atimo Vatae, st'n TM21, 12.v.2010 (MNHN). MOZAMBIQUE: Pemba (12.937°S 40.521°E), J. Rosado, x.1993 (NMSA L2055); ditto, living amongst dead coral in shallow subtidal, J. Rosado, xi.2010 (NMSA L8398); ditto, Praia do Uimbe, amongst dead coral in shallow subtidal, J. Rosado, xi.2010 (J. Rosado coll'n); Conducia Bay (14.9128°S 40.7178°E), K.J. Grosch, purch. ix.1975 (NMSA J4175).

Other material examined: ANDAMAN ISLANDS: Port Blair area, E.M. Man (NMSA F7170); same, Winckworth coll'n (NHMUK). PHILIPPINES: Matabugkay, 115 km SSW of Manila, short algae on reef flat, W. Ponder (AMS); Punta Engaño, Mactan Is., Cebu, deep-water shell grit, F.J. Springsteen (NMSA K2549); Palawan Is., Tadio Is., coral rubble washings, low tide patch-reef, W. Ponder (AMS); beach at Santa Cruz Is., off Zamboanga, Mindanao, A.J. Meagher (AMS C.71800); west of Zac Is., Pearl Bank, Sulu Archipelago, coarse sand (WAM). PAPUA-NEW GUINEA: Bougainville Straits, W. Burrows (AMS); East Cape, Papua, H.T. Williams (AMS); Kuia Is., Lusancay Islands, Trobriand group [Kiriwina], Ponder & Colman (AMS);

ditto, near Okaiboloma village, rubble and algae washings, living Ponder & Colman (AMS). AUSTRALIA: *Western Australia*: Kendrew Is., Dampier Archipelago, -27–28 m (WAM); ditto, in *Caulerpa* washings from reef flat (WAM); ditto, transect 1, C.o.T. survey, -67–68 m (WAM); ditto, transect 2, C.o.T. survey, -146–147 m (WAM); ditto, under rocks (WAM); Lighthouse Beach, NW Cape, shell sand, L. Figgis (AMS C.304705); north of Tantabiddi, NW Cape, at base of outer reef slope (WAM); Turtle Bay, NW Cape, J. Hewitt (WAM); Quobba, Hewitt, Plant, Buick (WAM). *Queensland*: Bramble Cay, Torres Strait, C. Hedley (AMS C.051290); Darnley Is., Torres Strait, under stones on shore, *Chevert* Exped'n (AMS C.061508); Murray Is., Torres Strait, C. Hedley (AMS C.29253); Rocky Isle, off Cape Flattery, C. Hedley (AMS C.041235). *Great Barrier Reef*: south end of Lizard Is., -15 m, on outer side of reef, W. Ponder (AMS); Three Isles, north of Cooktown, Iredale (AMS); Arlington Reef, intertidal, living, I. Loch (AMS); Low Isles, living, British GBR Exped'n 1928 (AMS C.304699); Low Isles, J. Hewitt (WAM); Michaelmas Cay, GBR Boring Exped'n 1926 (AMS C.304704); North West Is., Capricorn Group, J. Kerslake coll'n (AMS C.304701). CORAL SEA: NE Herald Cays (16.95°S 149.17°E), D.F. McMichael & J.C. Yaldwyn, xi.1964 (AMS C.304700). NEW CALEDONIA: Nouméa, R.C. Rossiter (AMS C.003734). TUVALU: Funafuti Atoll, R. Soc. Coral Boring Exped'n 1896 (AMS C.005838). FIJI: Nadi Bay, Viti Levu, -9–35 m, J. Laseron (AMS).

Distribution and habitat (Fig. 25): Indo-West Pacific; from southern Japan, SE Asia and the south-western Pacific to western Australia, the Andaman Islands and East Africa; in the western Indian Ocean extending south to southern Madagascar, but not yet recorded from central or southern Mozambique, or South Africa. Recorded from Quaternary deposits in the Marshall Islands (Ladd 1966). Little information regarding the habitat of living animals is available. Adams (1864*b*) reported a living specimen dredged at 55 fath. [-100 m] off southern Japan, but most of the specimens available (live and dead collected) have come from near-shore reef systems with a coralline facies (AMS and WAM material). Wilson (1993) gave the bathymetric distribution as intertidal to -140 m, but did not specify whether this concerned living or dead material. Sasaki (2000) cited the habitat as intertidal and upper subtidal, on coral rubble, and in northern Mozambique, J. Rosado has collected it alive amongst dead coral in the shallow subtidal.

Remarks: The synonymy of *Trochus instrictus* Gould, 1849, *Monodonta alveolata* Adams, 1853 and *M. bourcierei* Crosse, 1863 has been noted previously on several occasions (e.g. Pilsbry 1890 in 1889–90; Cernohorsky 1978*b*; Kaicher 1990). Other species with similar apertural dentition and umbilical form include *H. crassilabrum* (Sowerby, 1905) from Sri Lanka, *H. exasperatum* (A. Adams, 1853) from the Philippines, *H. gemmatum* (Gould, 1845) from Hawaii, and *H. seychellarum* (G. & H. Nevill, 1869). *H. exasperatum* (Fig. 68E, F) and *H. seychellarum* (Fig. 29), however, are much less elevated, whilst *H. gemmatum* and *H. crassilabrum* (Fig. 68C, D) have more rounded whorls with relatively close-set and more obviously beaded spiral sculpture, the latter also has a more strongly developed upper columella denticle and a partially occluded umbilicus; all are smaller than *H. instrictum*. Amongst south-western Indian Ocean chilodontid taxa, only *H. seychellarum* retains a simple and deep umbilicus when mature, but that species is considerably smaller and more depressed.

### **Herpetopoma (*s.s.*) serratocinctum** sp. n.

Figs 26–28

Etymology: From Latin *serratus* (toothed like a saw) and *cinctum* (a belt or girdle); in reference to the strong, toothed peripheral cord.

Description:

*Shell*: Small, turbiniform, relatively solid; length more or less equal to diameter (L/D= 0.97–1.1); teleoconch of approx. 3.5 whorls; whorls rounded at periphery, but with a strong peripheral spiral cord; suture indented, level with subperipheral cord, but descending below this immediately prior to aperture in mature individuals; first teleoconch whorl initially sculptured with strong, widely spaced, curved, axial pliculae; pliculae becoming thinner and more close-set after one quarter whorl; 2 spiral cords arising in latter half of whorl; both axial and spiral sculpture strengthening during second whorl and a third spiral cord arising beneath adapical suture; axial pliculae prosocline, more close-set than spiral cords creating obliquely rectangular interstices; cords with rounded nodules where crossed by axial pliculae; 2 further spiral cords arise by intercalation during third whorl, end of penultimate whorl thus with 5 spiral cords of alternating strength above suture; interstices more nearly square; beads on peripheral cord, well developed, stronger, more angular and fewer in number than on other cords (approx. 25 on last adult whorl), but those in final quarter whorl smaller, less angular and more close-set. Base with 4 primary spiral cords, a weaker fifth beneath peripheral cord and a sixth mostly hidden by reflected columella; beads of basal spiral cords progressively lower and more rounded toward umbilicus. Umbilicus closed in adults, but remaining open and steep-sided in juveniles, its edge marked by the sixth basal spiral cord. Peristome markedly oblique, almost tangential; aperture subcircular to D-shaped, flattened parietally; columella pillar well developed, protruding slightly into aperture, a strong, peg-like tooth at its base and a low bulge above its mid region; interior of outer lip subterminally thickened and set with 8–10 elongate denticles which extend into aperture as in-running ridges; that nearest columella larger, a deep U-shaped notch separating it

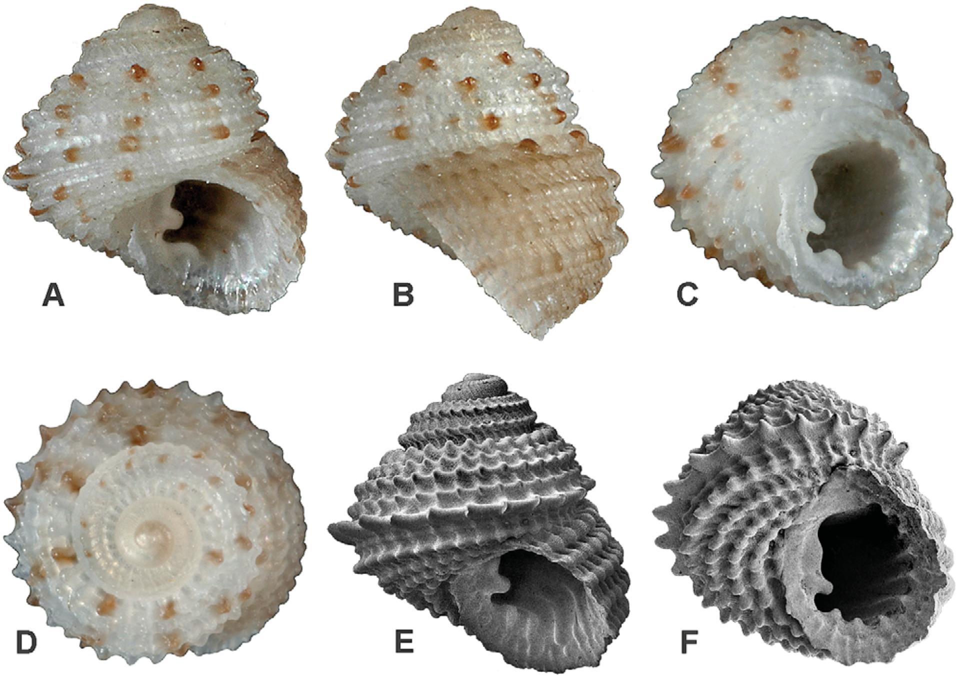

Fig. 26. *Herpetopoma serratocinctum* sp. n.: (A–D) holotype, length 3.07 mm (NMSA K7929/T2640); (E, F) SEM of paratype with strongly serrate peripheral cord, Kilifi, Kenya, length 3.00 mm (NMSA L8270/T2641).

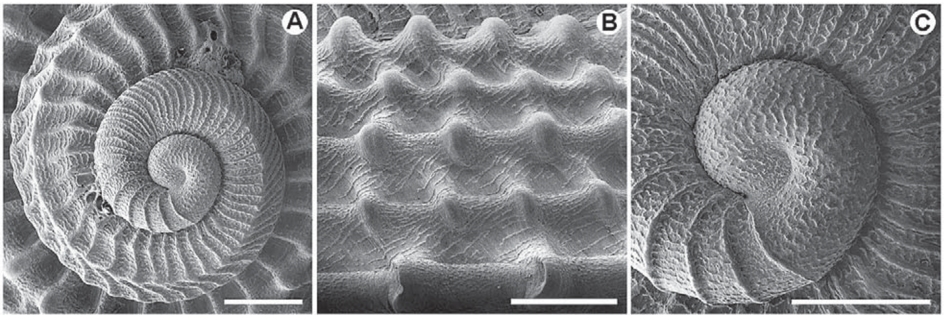

Fig. 27. *Herpetopoma serratocinctum* sp. n., Kilifi, Kenya (paratype, NMSA L8270/T2641): (A) apex, bar = 250 µm; (B) microsculpture at start of last adult whorl, bar = 250 µm; (C) protoconch, bar = 200 µm.

from basal columella tooth; outer portion of lip flaring and bearing additional secondary granules and wrinkles distal to primary denticles; these continue around reflected portion of columella lip; parietal region covered with glossy callus bearing superficial wrinkle-like ridges; callus not extending beyond limit of peristome; interior of aperture nacreous.

Microsculpture (Fig. 27B, C): Juvenile shell with vermiform spiral threads, these continue throughout shell, becoming oblique on last adult whorl (cf. *Ascetostoma providentiae*); the scratch-like adult microsculpture of other species is not evident.

Protoconch (Fig. 27A, C): Greyish white, more or less level with first teleoconch whorl or at most weakly exsert; diameter *ca* 270 µm; terminal lip distinct, shallowly convex; superficial sculpture well developed, irregular and wavy, with a predominant axial alignment; no spiral component evident.

Colour: Fresh specimens translucent white with regular reddish spotting, mostly on the spiral cords and usually in more or less axially aligned rows; final portion of last adult whorl washed with pale orange-brown; some evidence of a dirty white intritacalx deposit remaining in sculptural interstices of fresh specimens.

Dimensions: Holotype (largest specimen), length 3.07 mm, diameter 2.93 mm.

*Operculum, radula and external anatomy*: Unknown.

Holotype (Fig. 26A–D): KENYA: Kilifi (3.60236°S 39.81190°E), lagoon inshore of coral reef, *ca* -4 m, in sand from base of coral outcrops, 20.xii.1991, D. Herbert (NMSA K7929/T2640).

Paratypes: Same data as holotype (NMSA L8270/T2641, 15 specimens; MNHN 24650, 1 specimen; NHMUK 20110383, 1 specimen). MOZAMBIQUE: Pemba (12.937°S 40.521°E), Praia do Uimbe, living amongst dead coral in shallow subtidal, J. Rosado, xi.2010 (J. Rosado coll'n).

Distribution and habitat (Fig. 28): Known only from the coast of central Kenya and northern Mozambique, evidently in shallow subtidal habitats associated with fringing reef systems.

Remarks: Amongst the regional fauna, *H. serratocinctum* most closely resembles the Mascarene *H. stictum* (see below), particularly in terms of size, coloration and apertural dentition. The less elevated spire, more angular sculpture and strong, saw-toothed peripheral cord of *H. serratocinctum*, however, are distinctive. There is also some similarity with *H. fimbriatum* (Pease, 1861) (Fig. 69C, D), reportedly from Hawaii (but see Kay 1979), and *H. corallinum* Jansen, 1994 from the Great Barrier Reef, but in both these species the columella has a weaker basal tooth and lacks a low bulge above this.

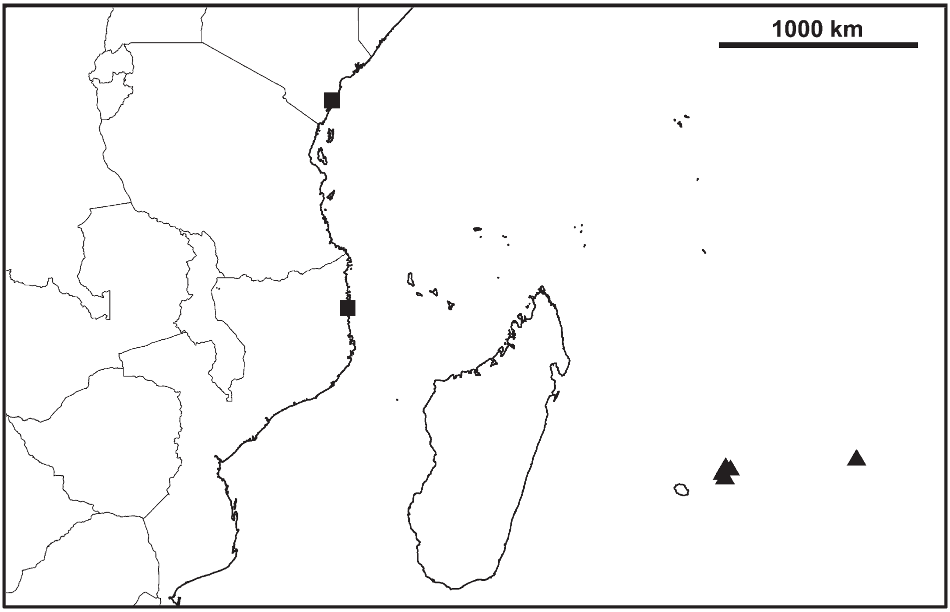

Fig. 28. Distribution of *Herpetopoma serratocinctum* (squares) and *H. stictum* (triangles). Each symbol represents one or more records.

They also have fewer spiral cords on the penultimate whorl (four) and a flatter base giving a more trochiform profile.

### *Herpetopoma* (s.s.) *seychellarum* (G. & H. Nevill, 1869) **comb. n.**

Fig. 29

*Euchelus seychellarum*: G. & H. Nevill 1869: 157, pl. xvii, fig. 107; Pilsbry 1890 in 1889–90: 438, pl. 57, fig. 13. Type loc.: Island of Mahé, Seychelles.

Type material: Five syntypes of *Euchelus seychellarum* G. & H. Nevill, 1869, in the Indian Museum, Kolkata (M13143/2), one is here figured and designated lectotype.

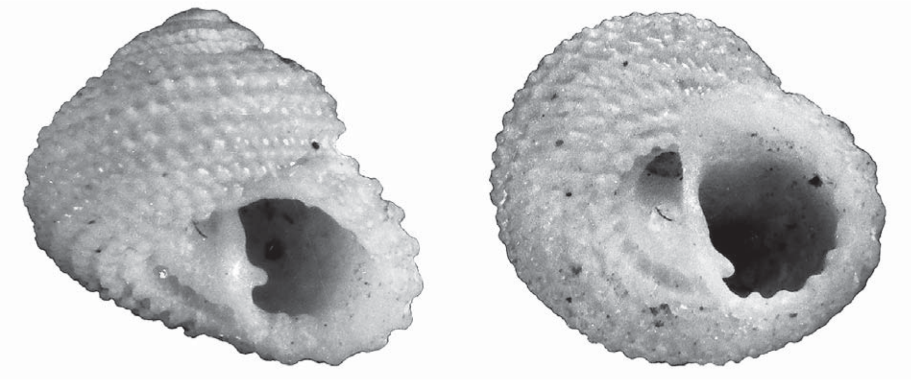

Fig. 29. *Herpetopoma seychellarum* (G. & H. Nevill, 1869): lectotype (here designated) of *Euchelus seychellarum* G. & H. Nevill, 1869, diameter 2.8 mm (Indian Museum, Kolkata, M13143/2; photographs courtesy of R. Kilburn).

Remarks: This species does not appear to have been recorded subsequent to the original description. Its small size (diameter 2.8 mm), depressed profile and wide umbilicus, together with the distinct, peg-like basal columella tooth and dentate interior of the outer lip render it easily separable from other south-western Indian Ocean chilodontids. Obviously such small species are easily overlooked, but the evident absence of additional material from the Seychelles raises the possibility that the original material was mislocalised. Comparison with taxa from other areas may shed further light on this subject. The Philippine *H. exasperatum* (A. Adams, 1853) has a similarly depressed shape, but is larger (diameter attaining 6.5 mm) and has spiral cords of alternating size and crisper sculpture (Fig. 68E, F).

### **Herpetopoma (*s.s.*) stictum** sp. n.

Figs 28, 30, 31

*Euchelus gemmatus* [*non* Gould, 1845]: Jay 2009.

Etymology: From Greek *stiktos* (spotted); in reference to the colour pattern.

Description:

*Shell*: Small, trochoid-turbiniform, relatively solid; length slightly exceeding diameter (L/D=1.07–1.19); teleoconch of approx. 4.5 whorls; spire whorls rather flat-sided, last adult whorl rounded, but slightly flatter below periphery; suture indented, level with subperipheral spiral cord, but descending below this immediately prior to aperture in fully mature individuals; first teleoconch whorl initially sculptured only with axial pliculae (*ca* 20); 2 spiral cords arising in latter half of whorl, a third arising beneath adapical suture during second whorl, a fourth arising below subsutural cord during third whorl; end of penultimate whorl with 4 spiral cords of more or less equal strength above abapical suture; cords equal to or slightly narrower than their intervals and crossed by prosocline axial pliculae; pliculae slightly narrower than spiral cords, the latter with roundly angular beads where crossed by pliculae, those on subsutural and peripheral cords slightly stronger (*ca* 30 on peripheral cord of last adult whorl); interstices roundly quadrate. Base with 5 spiral cords, the outer (subperipheral) one strongest and with

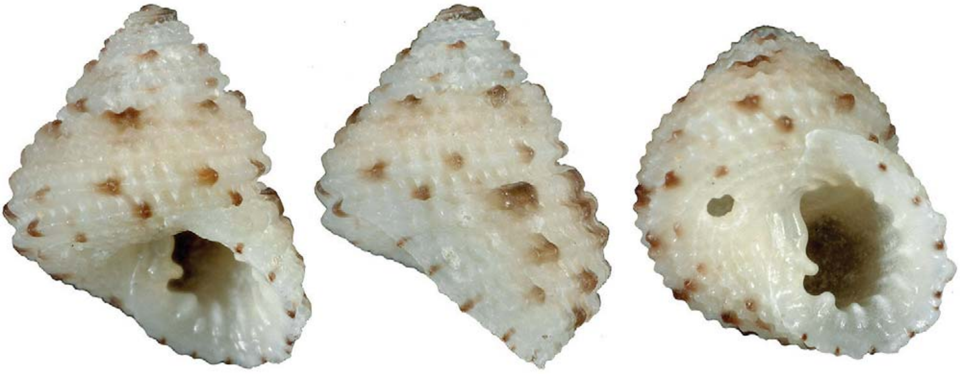

Fig. 30. *Herpetopoma stictum* sp. n.: holotype, length 4.9 mm, diameter 4.25 mm, Réunion (M. Jay coll'n, MNHN).

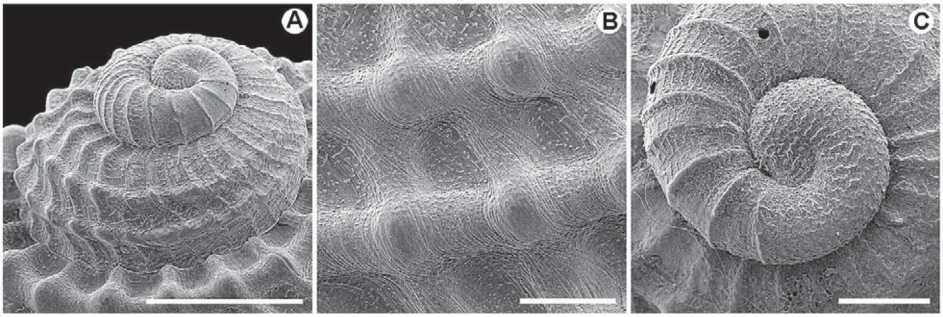

Fig. 31. *Herpetopoma stictum* sp. n., paratypes, off Troux aux Biches, Mauritius (NMSA K8593/T2739): (A) apex, bar = 0.5 mm; (B) adult microsculpture, bar = 200 µm; (C) protoconch, bar = 100 µm.

roundly angular beads, the others progressively with lower, more rounded beads; a weak sixth cord bordering umbilicus; cords slightly wider than their intervals. Umbilicus open in juveniles and subadults, steep-sided, occasionally remaining narrowly patent even at maturity, but generally occluded by reflected columella lip and if evident at all then only as a shallow depression. Peristome markedly oblique, almost tangential; aperture D-shaped, somewhat flattened parietally; columella pillar well developed, a little oblique and protruding slightly into aperture; a distinct, peg-like tooth at its base with a second low bulge sometimes evident above this; interior of outer lip thickened and set with 7 or 8 primary denticles which extend into aperture as in-running ridges; that nearest columella larger, a deep U-shaped notch separating it from basal columella tooth; outer portion of lip flaring and bearing additional secondary granules and wrinkles external to primary denticles; these continue around reflected portion of columella lip, one particularly strong secondary granule near base of basal columella notch; parietal callus not extending beyond limit of peristome, sometimes with traces of superficial wrinkle-like ridges; interior of aperture nacreous.

Microsculpture (Fig. 31B, C): Apical whorls with vermiform spiral threads; weak scratch-like sculpture developing subsequently, but retaining traces of vermiform threads on spiral cords; interstices with sparse microscopic granules.

Protoconch (Fig. 31A, C): Translucent whitish in fresh specimens, last quarter whorl and initial half of first teleoconch whorl mauve-brown; more or less level with early part of first teleoconch whorl, its apex slightly down-tilted; diameter 250–280 µm; terminal lip weakly convex; superficial sculpture well developed, irregular and wavy, with a predominant axial alignment; no spiral component evident.

Colour: Whitish with sparse, mauve-brown spots on spiral cords; spots sometimes aligned into diffuse axial bands on last adult whorl; base with fewer spots, generally more uniform white; spots fading to pinkish brown in old or worn specimens; fresh examples with a thin, dirty-buff, chalky intritacalx deposit.

Dimensions: Holotype, length 4.9 mm, diameter 4.25 mm; length variation of mature specimens 3.3–5.3 mm.

*Operculum, radula and external anatomy*: Unknown.

Holotype (Fig. 30): RÉUNION: not further localised (M. Jay coll'n, MNHN 24651).

Paratypes: RÉUNION: same as holotype (M. Jay coll'n, MNHN 24652, 12 specimens). MAURITIUS: off Troux aux Biches (20.0325°S 57.5411°E), reef front, *ca* -5 m, fine sand, D. Herbert, ix.1991 (NMSA

K8309/T2757, 1 specimen); ditto (20.0325°S 57.5408°E), reef front, *ca* -10 m, fine sand, D. Herbert, ix.1991 (NMSA K8593/T2739, 11 specimens); Riambel lagoon (20.5206°S 57.4883°E), beach-drift, R. Kilburn & D. Herbert, ix.1991 (NMSA K7767/T2755, 45 specimens, K7771/T2756, 5 specimens); Gris Gris (20.5243°S 57.5239°E), debris on surf beach opposite reef-break, R. Kilburn & D. Herbert, ix.1991 (NMSA K8294/TT2753, 1 specimen, K9324/T2754, 10 specimens).

Additional material examined (all NMSA): MAURITIUS: Pointe Radeau, south of Roches Noires (20.1287°S 57.7573 E), shell debris near reef gap, R. Kilburn & D. Herbert, ix.1991 (K9587); Tamarin Bay (20.3264°S 57.3775°E), beach-drift, R. Kilburn & D. Herbert, ix.1991 (K8497); Souillac, lagoon below cliffs west of Gris Gris (20.525854°S 57.527375°E), living, in washings from algae and dead coral blocks, D. Herbert, 14.ii.2011 (L8356, L8402 living juvenile). RODRIGUES: Between Anse aux Anglais and Pointe Venus (19.6752°S 63.4313°E), beach-drift, D. Herbert, ix.1991 (K7795); Anse aux Anglais (19.6716°S 63.4334°E), reef crest and platier nécrose, exposed at LT, D. Herbert, ix.1991 (K8672); Grand Baie (19.67175°S 63.45089°E), beach-drift near stream, D. Herbert, ix.1991 (K9162).

Distribution and habitat (Fig. 28): Known only from the Mascarene Islands. Dead shells are moderately common in beach-drift samples, but living material has rarely been found. Jay (2009) reported it (as *Euchelus gemmatus*) as 'living under stones at 10–15 m. Rare' in Réunion, and I obtained a single live-taken juvenile from algal and coral washings collected at LST on the reef crest at Souillac, Mauritius.

Remarks: With its spotted colour pattern, *Herpetopoma stictum* resembles *H. serratocinctum*, however, the present species attains a larger size (max. length 5.3 *vs* 3.1 mm), and has a less globose, more trochiform profile. In addition, *H. serratocinctum* has sharper sculpture, with spiral cords of alternating size and a saw-toothed peripheral cord. *H. howensis* Jansen, 1994 from Lord Howe Is. is also spotted, but has a less elevated spire, a weaker basal columella tooth and has intermediary spiral threads between the primary spiral cords.

The Hawaiian *H. corrugatum* (Pease, 1861) has a more roundly beaded sculpture, a weaker basal columella tooth, a less obviously spotted colour pattern and commonly retains an open umbilicus (Fig. 69A, B). *H. fimbriatum* (Pease, 1861), also reportedly from Hawaii, has a more angular periphery and only three spiral cords on the penultimate whorl, and lacks a spotted colour pattern (Fig. 69C, D). Jay (2009) confused the present species with another Pacific species, *H. gemmatum* (Gould, 1845), but that species has more rounded whorls, a more finely beaded sculpture and a clearly patent umbilicus. (NB: The shell figured by Johnson (1964: pl. 15, fig. 10) as the lectotype of *Trochus* (*Monodonta*) *gemmatus* Gould, 1845, with a diameter of 20 mm cannot in fact be the genuine lectotype.) *Diloma verruca* Gould, 1861, a very poorly documented species from Chinese waters, also belongs within this group of *Herpetopoma* species, but has two widely spaced primary spiral cords at and just above the periphery of the last adult whorl (Fig. 69E, F).

### *Herpetopoma* (s.l.) *helix* (Barnard, 1964) **comb. n.**

Figs 4I, 32–34

*Turcica helix*: Barnard 1964: 21, fig. 3e; Kensley 1973: 44, fig. 110. Type loc.: off Cape Vidal, KZN, South Africa, 80–100 fath. [-146–183 m].

Description:

*Shell*: Turbiniform (L/D=1.10–1.25), teleoconch of 4–5 whorls; whorls rounded, sutures indented and inserted at level of subperipheral cord; first teleoconch whorl with 14–16 axial pliculae; second and subsequent whorls with axial pliculae and relatively strong

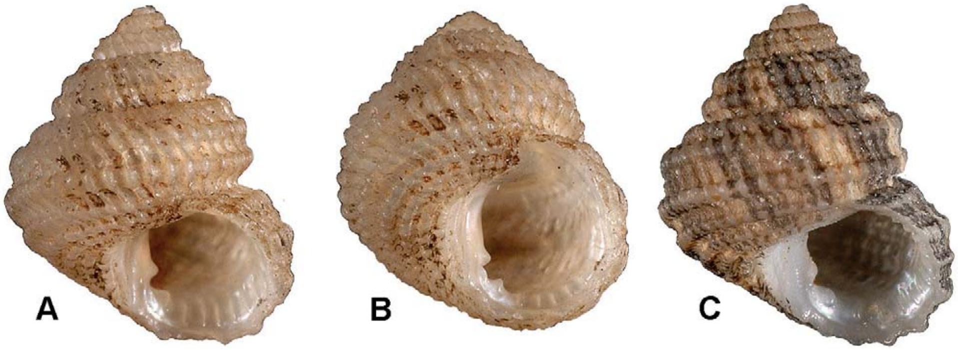

Fig. 32. *Herpetopoma helix* (Barnard, 1964): (A, B) typically coloured specimen, intritacalx deposit largely missing, off Umzinto, KZN, length 4.0 mm (NMSA D5427); specimen retaining intritacalx deposit, SE of Cape Vidal, KZN, length 4.0 mm (NMSA E7514).

spiral cords, 2 on second whorl, 3 on subsequent ones; cords bearing axially elongate beads where crossed by pliculae; last adult whorl with 40–50 axial pliculae and 3 spiral cords above and including periphery, occasional specimens with weaker intermediaries; intervals between cords equal to or wider than cords themselves and rendered obliquely cancellate by axial pliculae; interval between second and third cords frequently wider than others. Base with 4–5 somewhat less well developed spiral cords, sometimes with a sixth close to columella; axial pliculae of base progressively less elevated toward shell axis and cords thus less obviously granular. Umbilicus lacking in adult specimens, but sometimes evident as a narrow chink in juveniles; umbilical region usually at least partially covered by parietal/columella callus. Peristome oblique; aperture subcircular, flattened at paries; columella with a single simple tooth at its base; interior of outer lip thickened, bearing approx. 12 ridge-like denticles, one where basal portion of lip joins columella frequently larger, with a shallow notch separating it from columella tooth; an additional small granule is usually present just external to this notch; exterior of outer lip thickened subterminally but not distinctly varixed; interior nacreous, deeper region lacking in-running ridges, but cords of outer surface showing through.

Microsculpture (Fig. 33A–C): Vermiform spiral threads not evident on apical whorls; microsculpture between axial pliculae instead comprising numerous crisp granules, frequently connected by thread-like axial elements; adult microsculpture similar but rather more irregular and often completely obscured by thick intritacalx deposit.

Protoconch (Fig. 33C): Translucent white; diameter 260–280 µm; moderately exsert and relatively globose; worn in all available material; terminal lip shallowly convex; superficial sculpture mostly eroded, but with traces of granulation remaining near suture.

Colour: Shell evidently more or less uniformly greyish white to yellowish white and somewhat translucent; intritacalx deposit usually yellowish white to buff-brown, but some specimens patterned with broad bands in shades of brownish grey.

Dimensions: Largest NMSA specimen length 4.0 mm, diameter 3.4 mm.

*Operculum* (Fig. 4I): Relatively tightly multispiral throughout.

*Radula* (Fig. 33D, E): Formula ∞+4+1+4+∞; *ca* 40 transverse rows of teeth; transition from lateral to marginal series not well defined, the fourth lateral could also be interpreted

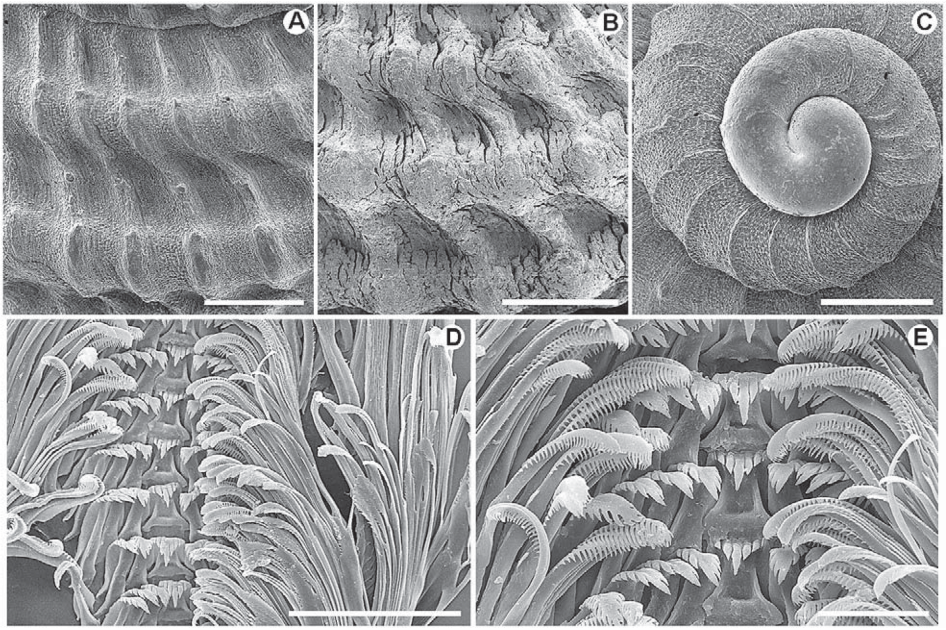

Fig. 33. *Herpetopoma helix* (Barnard, 1964): (A) adult microsculpture of cleaned shell, SE of Cape Vidal, KZN, bar = 250 µm (NMSA E7514); (B) uncleaned shell with thick intritacalx deposit, off Mtamvuna River, Eastern Cape, bar = 250 µm (NMSA E224); (C) protoconch and juvenile microsculpture, SE of Cape Vidal, KZN, bar = 200 µm (NMSA E7154); (D, E) radula, SE of Green Point, KZN (NMSA D5990): (D) central field and right marginals, bar = 50 µm; (E) central field and pectinate cusps of inner marginals, bar = 25 µm.

as a marginal. Rachidian with broad, trigonal cusp and well-developed hood, but lacking a distinct transverse basal ridge and near-basal medial indentation; cutting edge with a very long, acuminate, central denticle and 2 or 3 smaller, likewise elongate denticles on each side. Lateral teeth progressively decreasing in size from first to last, but not markedly so, their cusps obliquely trigonal with coarse lateral denticles on both margins (3–5). Marginals closely resembling those of *H. scabriusculum*, but a little more elongate; cusps of inner marginals with well-developed pectinate outer margin; outermost marginals shorter and with a somewhat dilated, fringed cusp.

*External anatomy*: Evidently chilodontid, but material insufficiently well preserved to provide meaningful detail.

Type material: SOUTH AFRICA: *KwaZulu-Natal*: Holotype of *Turcica helix* Barnard, 1964 (SAMC) off Cape Vidal (Zululand), 80–100 fath. [-146–183 m] (A9295), and one paratype, off Umkomaas, 40 fath. [-73 m] (A9256, broken).

Material examined (all NMSA unless indicated otherwise): MADAGASCAR: Secteur de Manantenina (24.3833°S 47.5330°E), -158–168 m, dredged *Nosy Be 11*, Exped'n Atimo Vatae, st'n DW3522, 1.v.2010 (MNHN); ditto, (24.3833°S 47.5170°E), -200–220 m, dredged *Nosy Be 11*, Exped'n Atimo Vatae, st'n DW3523, 1.v.2010 (MNHN). MOZAMBIQUE: Inhambane transect, Campagne Mainbaza, RV *Vizconde de Eza*, dredged, st'n CP3144 (23.550°S 35.683°E), living, -171–180 m, 11.iv.2009 (MNHN); Maputo transect, Campagne Mainbaza, RV *Vizconde de Eza*, dredged, st'n CP3130 (25.883°S 33.117°E), living, -112–127 m, 9.iv.2009 (MNHN); ditto, st'n CP3131 (25.933°S 33.117°E), -193–194 m, 9.iv.2009 (MNHN); off Ponta Techobanine (26.68132°S 32.95093°E), -100–135 m, dredged J. Rosado, xii.2005 and i.2010 (D. Slater coll'n). SOUTH AFRICA: *KwaZulu-Natal*: off Boteler Point (27.0133°S 32.9183°E), -70 m, some coarse sand, some shell rubble, dredged NMDP, RV *Meiring Naude*, st'n ZB4, 6.vi.1987 (D7412); off

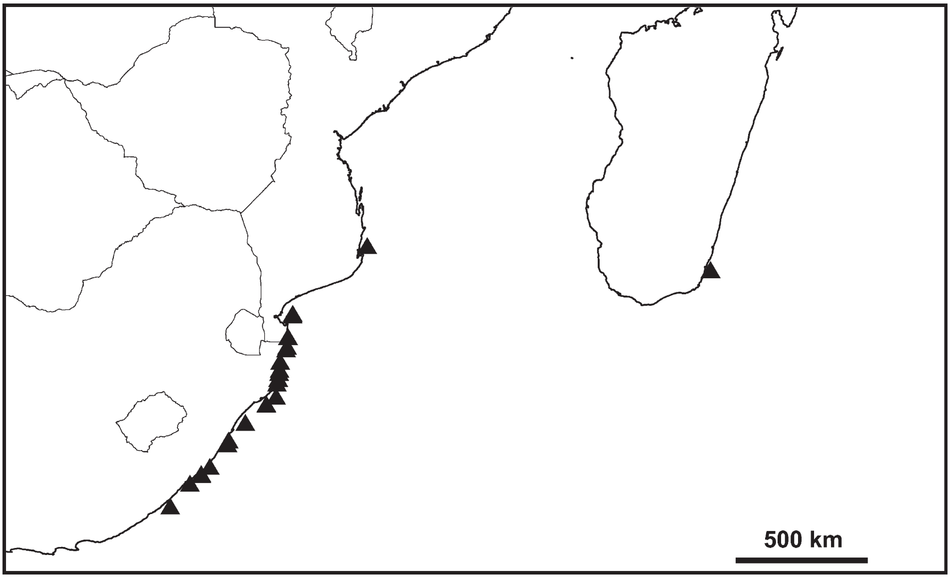

Fig. 34. Distribution of *Herpetopoma helix*. Each triangle represents one or more records.

Dog Point (27.1083°S 32.8817°E ), living, -70 m, sandstone conglomerate, dredged NMDP, R. V. *Meiring Naude*, St'n ZC3, 4.vi.1987 (E1740); Sodwana Bay (27.533°S 32.683°E), -100 m, dredged, CSIR Water Research (A5793); off Gipsy Hill (27.8117°S 32.6570°E), -100–125 m, broken shell, dredged NMDP, RV *Meiring Naude*, st'n ZK9, 11.vi.1988 (E3247); NE of Leven Point (27.9167°S 32.6467°E), -250 m, coarse sand, dredged NMDP, RV *Meiring Naude*, st'n ZL5, 9.vi.1988 (S1143); SE of Cape Vidal (28.1183°S 32.6100°E), living, -145 m, medium sand, dredged NMDP, RV *Meiring Naude*, st'n ZM7, 10.vi.1988 (E7514); ditto (28.1400°S 32.6067°E), -165 m, moderately fine sand, dredged NMDP, RV *Meiring Naude*, st'n ZM8, 11.vi.1988 (E7599); off Mission Rocks (28.2917°S 32.5700°E), -100 m, medium sand, dredged NMDP, RV *Meiring Naude*, st'n ZN7, 11.vi.1988 (E3828); SE of Neill Peak [Cunge Hill] (28.7400°S 32.5367°E), -320–340 m, sandy mud, dredged NMDP, RV *Meiring Naude*, st'n ZP5, 12.vi.1988 (E3976); Port Durnford–Richard's Bay (29.0067°S 32.2000°E), -152 m, mud and stones, dredged NMDP, RV *Meiring Naude*, st'n ZQ7, 13.vi.1988 (V3920); SE of Port Durnford (29.0150°S 32.2017°E), -215 m, glutinous sandy mud, dredged NMDP, RV *Meiring Naude*, st'n ZQ8, 13.vi.1988 (E3118); off Sheffield Beach (29.6442°S 31.4783°E), -110 m, muddy sand, dredged NMDP, RV *Meiring Naude*, st'n ZU14, 19.vi.1989 (E9446); SE of Green Point (30.250°S 30.905°E), living, -100 m, fine sand, rubble, dredged NMDP, RV *Meiring Naude*, st'n XX92, 8.vii.1986 (D5990); off Umzinto (30.3600°S 30.8500°E), living, -84 m, dredged NMDP, RV *Meiring Naude*, st'n X2, 15 vii.1982 (D5427); off Park Rynie (30.375°S 30.855°E), -100 m, sand & sponge rubble, dredged NMDP, RV *Meiring Naude*, 04.iii.1981 (B3717); off Mtamvuna River (31.1650°S 30.2516°E), living, -140 m, sponge rubble, dredged NMDP, RV *Meiring Naude*, st'n A6, 18.viii.1981 (E224). *Eastern Cape*: off Port Grosvenor (31.41°S 29.95°E), -80 m, worn coral nodules, dredged NMDP, RV *Meiring Naude*, st'n D17, 16.viii.1981 (E176); ditto (31.4360°S 29.9516°E), -100–115 m, sand, some mud, solitary coral, shells, dredged NMDP, RV *Meiring Naude*, st'n D3, viii.1981 (C1338); off Mgazi River (31.7450°S 29.5617°E), -180 m, soft mud, dredged NMDP, RV *Meiring Naude*, st'n J1, 15.vii.1982 (E281, E7540); off Shixini Point (32.5267°S 28.8833°E), -500 m, muddy sand, coral rubble, dredged NMDP, RV *Meiring Naude*, st'n T17, 13.vii.1984 (V2789, shells very old).

Distribution and habitat (Fig. 34): Southern Madagascar and south-eastern Africa, from southern Mozambique (Inhambane area) to the central Transkei region, Eastern Cape, South Africa (Shixini Point); -70–500 m, living specimens -70–180 m, on varied hard substrata.

Remarks: Relatively little fresh material of this species is available considering the amount of dredging that has been done between -50–200 m off KwaZulu-Natal and the Transkei region of Eastern Cape. Its small size, rounded whorls and strong spiral sculpture render it easily separable from other local chilodontid taxa. There is some resemblance to *H.* ?*naokoae* (below), but *H. helix* has fewer spiral cords above the suture (three compared with four in *H.* ?*naokoae*) and the cords are stronger. The relatively smooth, globose protoconch, granular microsculpture and weak basal columella tooth place this species apart from *Herpetopoma* (s.s.).

### *Herpetopoma* (s.l.) ?*naokoae* Poppe, Tagaro & Dekker, 2006

Figs 35, 36

*Herpetopoma naokoae*: Poppe *et al*. 2006: 37, pl. 10, figs 1, 3. Type loc.: Punta Engaño, Mactan Is., Philippines.

Material examined: RÉUNION: off Ste-Marie (20.85°S 55.60°E), -280–340 m, *Marion-Dufresne* 32, st'n DC128, dredged, 1982; ditto (20.85°S 55.62°E), -345–375 m, *Marion-Dufresne* 32, st'n DS131, dredged, 1982 (MNHN). SOUTH AFRICA: *KwaZulu-Natal*: off Neill Peak [Cunge Hill, 28.7400°S 32.5367°E], -320–340 m, sandy mud, dredged NMDP, RV *Meiring Naude*, st'n ZP5, 12.vi.1988 (NMSA E6967).

Remarks: A small number of specimens closely resembling the Philippine *H. naokoae* have been dredged in the south-western Indian Ocean, off Réunion (MNHN) and Zululand (NMDP). Although extremely similar to *H. naokoae*, they have a less rounded apex and I am uncertain whether they are genuinely conspecific with that species. In the absence of more material, I can only identify them as *H.* ?*naokoae*. No specimens have been taken alive in the south-western Indian Ocean, but one is fresh and shows the

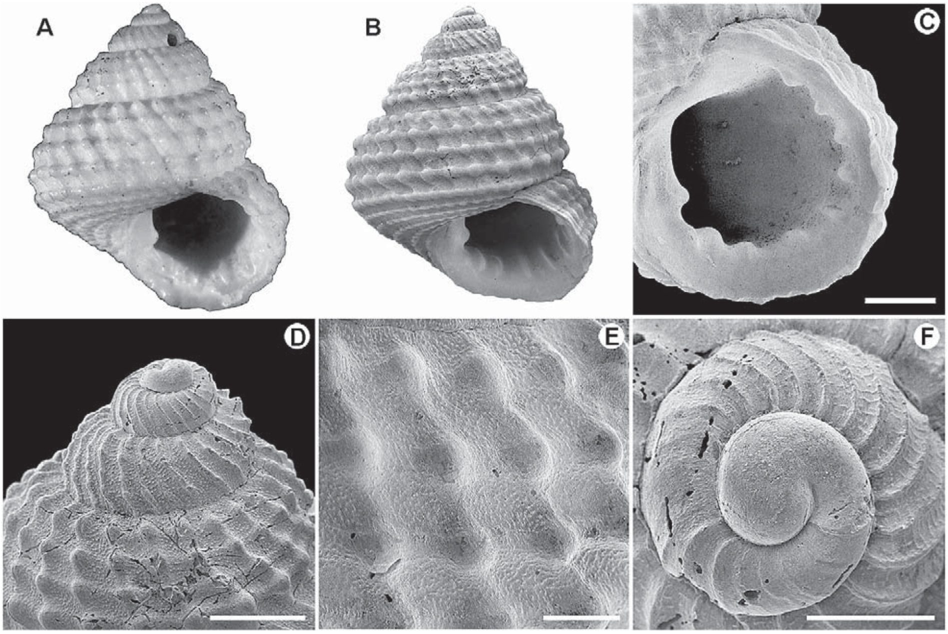

Fig. 35. *Herpetopoma* ?*naokoae* (Poppe, Tagaro & Dekker, 2006): (A) off Neill Peak [Cunge Hill], KZN, length 4.2 mm (NMSA E6967); (B–F) off Ste-Marie, Réunion, -280–340 m, *Marion-Dufresne* 32, st'n DC128 (MNHN): (B) whole shell, length 4.05 mm; (C) aperture, bar = 0.5 mm (MNHN); (D) oblique view of shell apex, bar = 0.5 mm; (E) adult microsculpture, bar = 250 µm; (F) protoconch, bar = 200 µm.

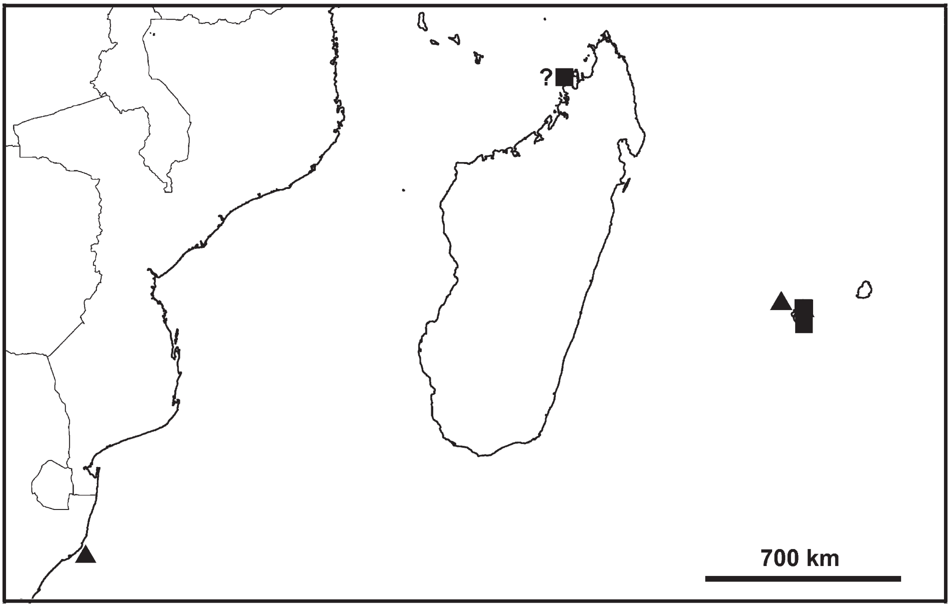

Fig. 36. Distribution of *Herpetopoma ?naokoae* (triangles) and *H. xeniolum* (squares). Each symbol represents one or more records.

characteristic dirty buff and grey intritacalx deposit typical of many chilodontids. All others are uniform off-white. The protoconch is translucent white, globose and exsert, with a diameter of *ca* 285 µm; in the material available the surface is worn and sculptural detail not evident. The apical whorls of the teleoconch have a microsculpture of vermiform spiral threads that become more oblique and fragmented with growth, the adult microsculpture comprising a fine, irregular granulation.

*Herpetopoma pruinosum* (Marshall, 1979), from the Kermadec Ridge, is also similar but has a lower spire and a finer, more obviously cancellate sculpture. Additional similar, but more elongate specimens have been sorted from some of the same dredge samples collected off Réunion and are discussed below (see *H. xeniolum*).

### *Herpetopoma* (s.l.) *xeniolum* (Melvill, 1918) **comb. n.**

Figs 36–38

*Euchelus xeniolum*: Melvill 1918: 154, pl. 5, fig. 27. Type loc.: Chabar, Gulf of Oman [= Chah Bahar, Iran], 5 fath. [-9 m] (Townsend).

*Turcica* (*Perrinia*) *waiwailevensis*: Ladd 1982: 23, pl. 24, figs 10–13. Type loc.: Station C2026, Viti Levu, Fiji; Pliocene. **Syn. n.**

*Herpetopoma eboreum*: Vilvens & Héros 2003: 61, figs 1–4; Poppe *et al*. 2006: 36, pl. 10, fig. 2; Poppe & Tagaro 2008: 174, pl. 32, fig. 1. Type loc.: Touho Pass, Touho area, New Caledonia, -50–62 m. **Syn. n.**

*Euchelus townsendianus* [*non* Melvill & Standen, 1903]: Jay 2009.

Type material: Holotype of *Euchelus xeniolum* Melvill, 1918 in NHMUK (1921.1.28.30); Trew (1987) was in error in stating that there were three specimens registered. Holotype of *Turcica* (*Perrinia*) *waiwailevensis* Ladd, 1982 in USNM (2501420). Holotype of *Herpetopoma eboreum* Vilvens & Héros, 2003 in MNHN.

Other material examined (all MNHN): RÉUNION: off Ste-Marie (20.867°S 55.633°E), -110 m, *Marion-Dufresne* 32, st'n DC126, dredged, 1982; off St-Joseph (21.383°S 55.617°E), -205–215 m, *Marion-Dufresne*

32, st'n DR47, dredged, 1982; Réunion, not further localised (M. Jay coll'n). MADAGASCAR: West of Nosy Be (13.450°S 47.917°E), -187–247 m, Campagne *Miriky*, st'n DW3234, dredged, 3.vii.2009.

Remarks: A number of samples collected off Réunion are evidently referable this species, which I consider is closer to *Herpetopoma* than to *Euchelus* on account of its small size and the U-shaped notch at the columella base (albeit relatively weak). The species is poorly known and has not to my knowledge been recorded subsequent to the original description. The holotype (Fig. 37A, B) has four granular spiral cords on the penultimate whorl as do some Réunion specimens (Fig. 37C, D). However, other specimens in the Réunion samples have five such cords (Fig. 37E, F) and closely resemble the holotype of *Turcica* (*Perrinia*) *waiwailevensis* Ladd, 1982 from the Pliocene of Fiji (Fig. 37G, H). I have no doubt that the Réunion samples belong to a single species and consider the number of spiral cords on the penultimate whorl (four or five) to be a variable character. There is evidently similar variation in the number of spiral cords on the base (6–8). As a consequence, I can find no substantive differences by which to separate *Herpetopoma waiwailevensis* from *H. xeniolum*. In addition, *H. eboreum* Vilvens & Héros, 2003, described from shallow water off New Caledonia and recorded also from deeper water off the Philippines (Poppe *et al*. 2006), appears indistinguishable from *H. waiwailevensis*. I believe that all three names refer to a single widespread species, for which *H. xeniolum* is the earliest name. *Euchelus hummelincki* Moolenbeek & Faber, 1989 from the Caribbean is another similar species, but is evidently smaller (length up to 3.2 mm) and has somewhat coarser sculpture.

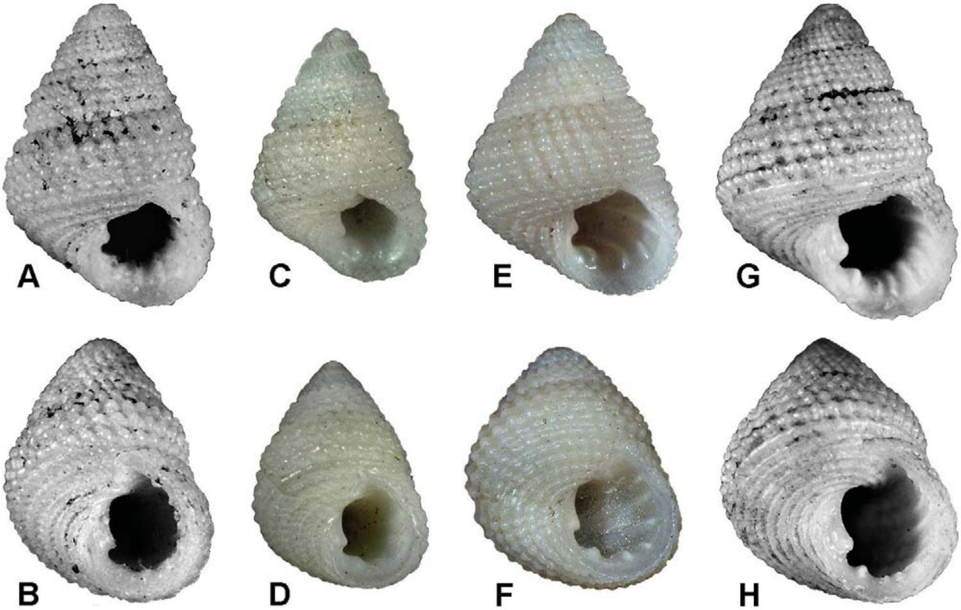

Fig. 37. *Herpetopoma xeniolum* (Melvill, 1918): (A, B) holotype of *Euchelus xeniolum* Melvill, 1918, length 4.2 mm, diameter 3.0 mm (NHMUK 1921.1.28.30); (C, D) Réunion, length 3.5 mm, diameter 2.4 mm (M. Jay coll'n, MNHN); (E, F) Réunion, *Marion-Dufresne* 32, st'n DC126, length 3.9 mm, diameter 2.9 mm (MNHN); (G, H) holotype of *Turcica* (*Perrinia*) *waiwailevensis* Ladd, 1982, length 4.4 mm, diameter 3.3 mm (USNM 2501420).

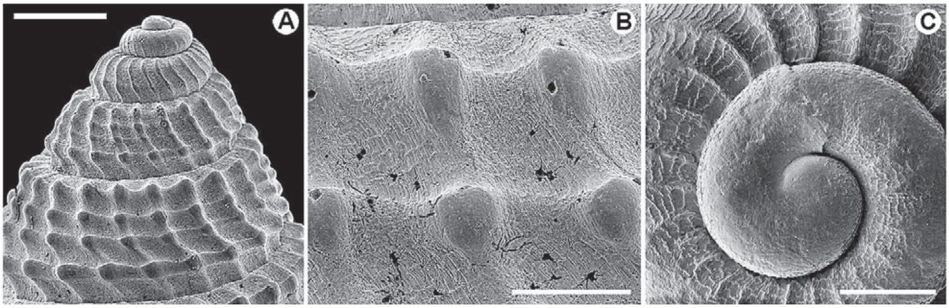

Fig. 38. *Herpetopoma xeniolum* (Melvill, 1918): (A) shell apex, Réunion, bar = 0.5 mm (M. Jay coll'n, MNHN); (B) adult microsculpture, Réunion, bar = 200 µm (M. Jay coll'n, MNHN); (C) protoconch, off Ste-Marie, Réunion, bar = 100 µm (MNHN).

The holotype of *H. xeniolum* was collected in shallow water (-9 m) and similarly the overall facies of the fauna at the type locality of *H. waiwailevensis* is that of a shallow-water, lagoonal system (Ladd 1966, 1982). The depth at which the dredged material from Réunion was obtained (-110–340 m) would thus seem to be anomalous. However, Réunion has a steeply shelving sublittoral zone and dead specimens of typically shallow-water species are frequently found at greater depths. That the species is also present in the M. Jay collection (MNHN) suggests that it does indeed occur in relatively shallow water around Réunion. The same may also apply to some rather worn specimens from off the steeply shelving coast of Nosy Be, which I also tentatively identify as *H. xeniolum*.

This material resembles *H. ?naokoae* (above), but the whorls are less convex and the shell is consistently more elevated, L/D usually >1.23, spire height/aperture height usually >1.60 in *H. xeniolum* (usually <1.23 and <1.60 respectively in *H. ?naokoae*). Additionally, in *H. ?naokoae* the sculpture is coarser and the denticles inside the outer lip, although ridge-like, are restricted to the thickened region just inside the lip edge. In *H. xeniolum* some of these ridges extend deeply into the aperture. Furthermore, in the local *H. ?naokoae* specimens there is an additional small denticle adjacent to the notch between the two larger denticles at the junction of the base and columella, this is not present in the *H. xeniolum* material examined.

The protoconch is translucent white with a diameter of *ca* 220 µm; its surface is eroded in the material available. A microsculpture of irregular vermiform spiral threads is present on the early teleoconch whorls; subsequent whorls with weak oblique vermiform threads and traces of very fine scratch-like marks.

## Genus *Vaceuchelus* Iredale, 1929

*Vaceuchelus*: Iredale 1929: 272. Type species: *Euchelus angulatus* Pease, 1868 [= *Monodonta foveolata* A. Adams, 1853], by monotypy.

The shell of *Vaceuchelus* species is small (length <10 mm), predominantly white and has a cancellate or foveolate sculpture. The aperture lacks a well-developed, peg-like tooth and U-shaped notch at the base of the columella, and may or may not possess denticles inside the outer lip.

Iredale (1929) proposed the genus for *Euchelus angulatus* Pease, 1868 from the Tuamotu Archipelago, noting that it typified a large series of taxa which differed from more typical *Euchelus*-like species primarily in lacking a tooth at the base of the columella. It is certainly true that *Vaceuchelus* species lack the distinctive basal columella dentition of some chilodontid genera, but a number of species still retain some form of apertural dentition. Two subgroupings are evident, namely those which possess denticles inside the outer lip and those that do not. The type species, together with *V. foveolatus* (A. Adams, 1853), *V. scrobiculatus* (Souverbie in Souverbie & Montrouzier, 1866) and *V. semilugubris* (Deshayes, 1863) possess labral denticles, whilst others, e.g. *V. cavernosus* (Sowerby, 1905), *V. clathratus* (A. Adams, 1853), *V. favosus* (Melvill & Standen, 1896), *V. gemmula* (Turton, 1932), *V. jayorum* sp. n. and *V. natalensis* (Smith, 1906), seem to lack all traces of apertural dentition.

To provide a new genus-rank name for such denticle-less taxa would be premature at this stage, since the distinction is based on one character only and, furthermore, there are additional taxa, e.g. *V. cretaceus* (see below), which present a third, somewhat intermediate facies. Until such time as the data set available allows a more meaningful assessment, I employ *Vaceuchelus* in its widest sense. Differences in operculum form and protoconch morphology, such as the presence or absence of a sinusigera lip, are also evident, but information is available for too few taxa.

*V. angulatus* is almost certainly a junior synonym of *V. foveolatus* (A. Adams, 1853), also from the Tuamotu Archipelago (Pilsbry 1890 in 1889–90). The holotype of the former is somewhat worn, but appears to be nothing more than an elevated and perhaps abnormal example of *V. foveolatus* in which the upper spiral cord is weakly developed (compare figs 72–73 and 74–75 in Herbert 1996).

Key to species of *Vaceuchelus* in the south-western Indian Ocean

1 Shell whitish, usually boldly marked with dark brown to black blotches .............. **semilugubris**
– Shell more uniform in colour, whitish to dirty buff, occasionally with ashy-grey axial bands .............. 2

2 Adult length up to 8.5 mm; columella with a broad, low, rounded swelling at its base .............. **cretaceus**
– Small (adult length <5.0 mm); columella lacking a basal swelling .............. 3

3 Base with 3 major spiral cords (sometimes a weaker 4th adjacent to columella); umbilicus closed in adult; protoconch diameter *ca* 340 µm .............. **gemmula**
– Base with 4 major spiral cords (sometimes with a weaker 5th spiralling into umbilicus); umbilicus open in adult, albeit narrow; protoconch 260–300 µm .............. 4

4 Final quarter of last adult whorl with intermediary spiral cords present above periphery .............. **jayorum**
– No intermediary spiral cords present on last adult whorl .............. **natalensis**

## **Vaceuchelus cretaceus** sp. n.

Figs 4J, 6F, 39–41

*Euchelus scrobiculatus* [*non* Souverbie, 1866]: Jay 2009.

Etymology: From Greek *creta* (white earth or chalk); in reference to the superficial chalk-like intritacalx deposit on the shell.

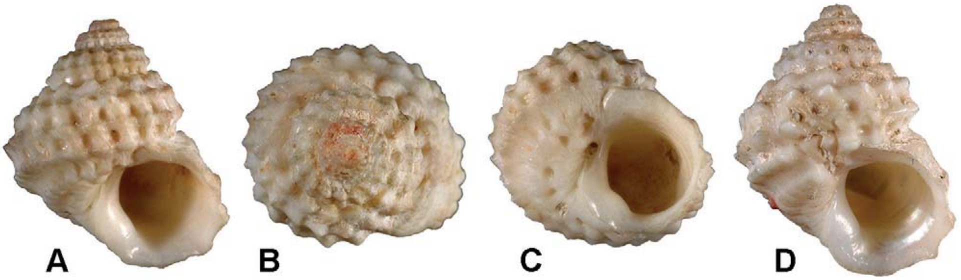

Fig. 39. *Vaceuchelus cretaceus* sp. n.: (A–C) holotype (NMSA E1761/T2600), length 7.6 mm; (D) live-collected specimen with nacreous interior (a severe growth flaw at the beginning of the last whorl has resulted in closure of the umbilicus), SE of Kosi Bay, KZN, length 8.3 mm, paratype (NMSA S4006/T2638).

Description:

*Shell*: Small, but relatively large for genus; elevated-turbiniform (L/D=1.0–1.25); teleoconch of 4.5–5.0 whorls; sculpture initially strongly cancellate, becoming foveolate with growth; spire truncate and protoconch sunken; first teleoconch whorl initially sculptured only by rib-like axial pliculae, but 3 spiral cords develop soon thereafter, one forming shoulder, another level with the abapical suture and the third between these at whorl periphery; cords and pliculae thickening considerably during third whorl and becoming less well defined; intermediary cords absent, with the exception of a fourth cord which usually develops on shoulder during third teleoconch whorl; intervals between cords wider than cords themselves; cords and pliculae interact to produce low conical granules where they cross; last adult whorl with 15–20 pliculae, those behind outer lip usually poorly defined or obsolete; pliculae narrower than cords on early whorls, more or less equal to them on last adult whorl; interstices distinctly quadrate apically, but becoming more rounded and pit-like (foveolate) on last adult whorl; strong growth flaws frequently present on last adult whorl. Base with 3 spiral cords, one level with suture, one marking edge of umbilicus and another between these; interval between outer and middle cords usually broader and with only weakly developed pits, that between middle and inner cords narrower and more strongly pitted; an additional cord is evident within umbilicus of young juveniles, but this becomes obscured with growth; umbilicus usually narrowly patent even in adults, occasionally closed; relatively wider in juveniles. Peristome oblique; aperture subcircular; columella concave with a broad rounded swelling at its base; swelling non-nacreous and rather variable in size; interior of aperture nacreous when fresh, lacking ridges or denticles inside outer lip.

Microsculpture (Fig. 40B, C): Rather poorly defined and mostly covered by intritacalx deposit in fresh specimens; surface of apical whorls appearing etched, but with some traces of vermiform spiral threads; later whorls with close-set, shallow, prosocline, scratch-like marks.

Protoconch (Fig. 40C): White; diameter *ca* 200 μm; sunken; apex very slightly pinched in; terminal lip with a well-developed trigonal projection; superficial sculpture well developed, arranged in irregular axial lines, spiral element scarcely evident.

Colour: Fresh specimens milky-white with a relatively thick, chalky, white to pale buff or ashy-grey intritacalx deposit; deposit usually somewhat eroded.

Dimensions: Holotype, length 7.6 mm, diameter 6.6 mm; largest specimen (NMSA S4006), length 8.65, diameter 6.9 mm.

*Operculum* (Fig. 4J): Initially tightly multispiral, but whorls broadening with growth and becoming more openly multispiral.

*Radula* (Fig. 40 D, E): Formula ∞+3+1+3+∞; *ca* 45 transverse rows of teeth; transition from lateral to marginal series not well delineated. Rachidian with well-developed hood and narrowly trigonal cusp; cusp with small medial indentation near its base; cutting edge with a dominant, lanceolate central denticle, with 2 or 3 smaller denticles on each side. Only 3 lateral teeth evident, the fourth tooth is longer and lacks the robust, alate shaft of the laterals, and I consider it to be a marginal; lateral tooth cusps decreasing slightly in size from first to third, with a large, spathulate central element and smaller lateral denticles on both margins, those on the outer edge coarser. Marginals generally long and very slender, tending to collapse when air dried; inner ones somewhat shorter with a rather weakly and irregularly dentate, recurved cusp, and lacking well-developed pectinate denticles on its outer margin.

*External anatomy* (Fig. 6F): Head-foot largely white, cephalic and most epipodial tentacles blackish; some additional dark pigmentation on snout and lips, and on free margin of cephalic lappets (colour lost in alcohol). Cephalic lappets relatively broad, but not meeting in mid-line, free margin with fine projections; snout with well-developed lateral flanges; right post-ocular peduncle present; right subocular tentacle not evident; free

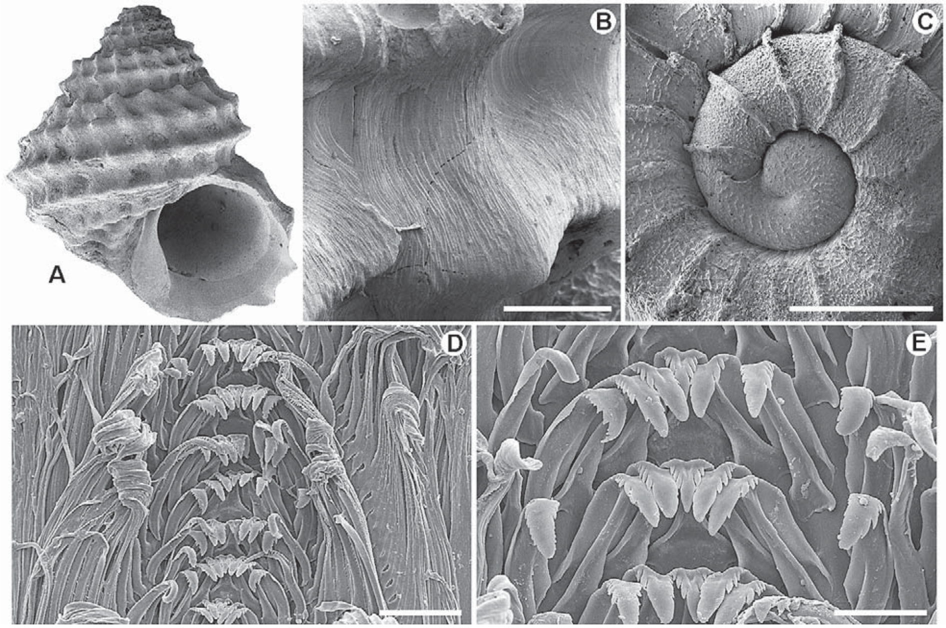

Fig. 40. *Vaceuchelus cretaceus* sp. n.: (A) SEM of paratype, NE of Dog Point, KZN, length 6.6 mm (NMSA S7593/T2637); (B) adult microsculpture, SE of Mission Rocks, KZN, bar = 250 µm (paratype, NMSA E7491/T2608); (C) protoconch, off Rocktail Bay, KZN, bar = 250 µm (paratype, NMSA S5138/T2602); (D, E) radula, SE of Kosi Bay, KZN (paratype, NMSA S4006/T2638): (D) central field and most of the marginals, bar = 50 µm; (E) rachidian and lateral teeth, bar = 25 µm.

margin of left neck lobe more extensively tentaculate than that of right one; approx. 10 epipodial tentacles of varying size on each side; an indistinct epipodial sense organ seemingly present at base of most epipodial tentacles. (Only one preserved specimen available; paratype, NMSA S4006/T2638.)

Holotype (Fig. 39A–C): SOUTH AFRICA: *KwaZulu-Natal*: off Boteler Point (27.00°S 32.92°E), -70 m, coral rubble, dredged NMDP, RV *Meiring Naude*, st'n ZB5, 6.vi.1987 (NMSA E1761/T2600).

Paratypes: RÉUNION: off St-Paul Bay, *Marion-Dufresne* 32, st'n DC85 (21°00'S 55°15'E), living, -58–70 m, dredged, 1982 (MNHN 24655, 54 specimens); Cap la Houssaye, hand-dredged sand, J. Drivas (NMSA K2756/T2603). SOUTH AFRICA: *KwaZulu-Natal*: SE of Kosi Bay (26.9000°S 32.9250°E), living, -50 m, coral slabs, dredged NMDP, RV *Sardinops*, st'n ZA37, 3.vi.1990 (NMSA S4006/T2638, 1 specimen); SE of Kosi River Mouth (26.9167°S 32.9300°E), -65 m, sponge, gorgonians, medium sand, dredged NMDP, RV *Meiring Naude*, st'n ZA12, 7.vi.1987 (NMSA D8017/T2602, 1 specimen); same data as holotype (NMSA V2961/T2639, 3 specimens; NHMUK 20110384, 1 specimen); off Boteler Point (27.0600°S 32.9083°E), -70 m, sand, some stones, dredged NMDP, RV *Sardinops*, st'n ZB24, 6.vi.1990 (NMSA S4157/T2601, 1 specimen); off Boteler Point (27.0133°S 32.9183°E), -70 m, some coarse sand, some shell rubble, dredged NMDP, RV *Meiring Naude*, st'n ZB4, 6.vi.1987 (NMSA D7420/T2636, 1 specimen); NE of Dog Point (27.0800°S 32.89167°E), -65 m, sand, lithothamnion pebbles, dredged NMDP, RV *Sardinops*, st'n ZC9, 7.vi.1990 (NMSA S7593/T2637, 4 specimens); off Rocktail Bay (27.1850°S 32.8483°E), -100 m, sand, dredged NMDP, RV *Sardinops*, st'n ZD4, 7.vi.1990 (NMSA S5138/T2602, 3 specimens); off Rocktail Bay (27.1900°S 32.8500°E), -100 m, sandstone rubble, dredged NMDP, RV *Meiring Naude*, st'n ZD1, 4.vi.1987 (NMSA D7598/T2604, 1 specimen); Sodwana Bay (27.5330°S 32.6830°E), -100 m, dredged CSIR Water Research (NMSA S9831/T2607, 1 specimen); SE of Mission Rocks (28.2917°S 32.5433°E), -50 m, old coral rubble, lithothamnion, dredged NMDP, RV *Meiring Naude*, st'n ZN1, 10.vi.1988 (NMSA E4641/T2605, 1 specimen; E7491/T2608, 3 specimens).

Additional material examined (all NMSA unless indicated otherwise): RÉUNION: off south-east coast of island, *Marion-Dufresne* 32, st'n DC1 (21°13'S 55°49'E), -150–160 m, dredged, 1982 (MNHN); Réunion, not further localised (M. Jay coll'n, MNHN). MOZAMBIQUE: off Lacerda Lighthouse (25.56167°S 32.84472°E), -52–55 m, dredged, vi.2010, (J. Rosado coll'n); off Inhaca Is. (26.020°S 33.066°E), -125 m, dredged J. Rosado, ii.2006 (D. Slater coll'n); off Ponta Techobanine (26.68132°S 32.95093°E), -60–135 m, dredged J. Rosado, xii.2005 and i.2010 (D. Slater coll'n). SOUTH AFRICA: *KwaZulu-Natal*: off Kosi Bay (26.8916°S 32.9266°E), -51 m, sand, stones large algae, dredged NMDP, RV *Sardinops*, st'n ZA48, 4.vi.1990 (S4061); off Boteler Point (27.0067°S 32.9083°E), -51 m, sand, some lithothamnion pebbles, dredged NMDP, RV *Sardinops*, st'n ZB9, 5.vi.1990 (S9668); ditto (27.0083°S 32.9117°E), -50 m, dead coral rubble and lithothamnion, dredged NMDP, RV *Meiring Naude*, st'n ZB7, 6.vi.1987 (E5263); ditto (27.0117°S 32.9200°E), -70 m, rocks, sand, dredged NMDP, RV *Sardinops*, st'n ZB19, 6.vi.1990 (S8701); ditto (27.0200°S 32.9183°E), -76 m, lithothamnion pebbles, sand, dredged NMDP, RV *Sardinops*, st'n ZB15, 5.vi.1990 (S7550); NE of Dog Point (27.0800°S 32.8867°E), -56–57 m, sand, lithothamnion pebbles, dredged NMDP, RV *Sardinops*, st'n ZC8, 6.vi.1990 (S5052); SE of Rocktail Bay (27.2017°S 32.8300°E), -60 m, coarse sand, dredged NMDP, RV *Sardinops*, st'n ZD9, 8.vi.1990 (V875); off Sodwana Bay (27.5300°S 32.7133°E), -70 m, dead coral rubble, dredged NMDP, RV *Sardinops*, st'n ZH18, 2.vi.1990 (S4564); ditto (27.4781°S 32.7232°E), -46 m, sediment at base of drop-off in canyon, dredged UND, Marine Geoscience Unit, 7.xi.1992 (V2609); NE of Liefeldt's Rocks (27.7200°S 32.6617°E), -50 m, lithothamnion, stones, some coarse sand, dredged NMDP, RV *Meiring Naude*, st'n ZJ1, 8.vi.1988 (E4343); Leadsman Shoal (27.8000°S 32.6160°E), -100 m, dredged A.D. Connell, iv.1980 (B4066); off Leven Point (27.9167°S:32.6467°E), -250 m, coarse sand, dredged NMDP, RV *Meiring Naude*, st'n ZL5D, 9.vi.1988 (S9427).

Distribution and habitat (Fig. 41): South-western Indian Ocean, known only from Réunion, southern Mozambique and northern Zululand (south to Mission Rocks); shallow subtidal to -250 m, but mostly shallower than -160 m (living specimens -50–70 m); dead shells not uncommon amongst lithothamnion encrusted pebbles and coral rubble in -50–70 m, beyond the near-shore reef system in northern Zululand.

Remarks: There is no similar species yet reported from the south-western Indian Ocean. *V. gemmula*, *V. jayorum* and *V. natalensis* are much smaller and thinner shelled, lack a basal columella swelling and retain sharply defined spirals and axials throughout. Although they may resemble juvenile *V. cretaceus*, they have a narrower umbilicus, more evenly spaced cords on the base and a less strongly truncated apex. Furthermore,

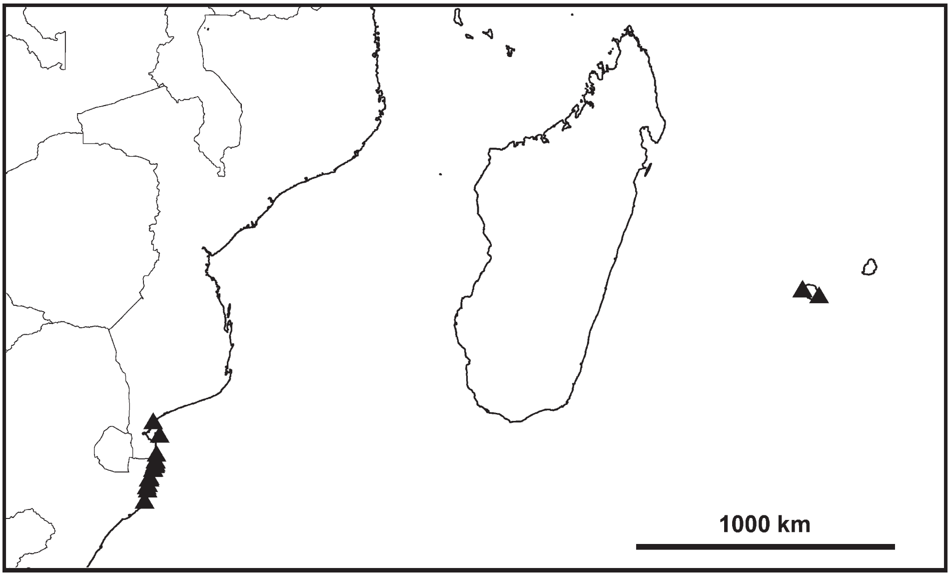

Fig. 41. Distribution of *Vaceuchelus cretaceus*. Each triangle represents one or more records.

in these small species the spiral cords are stronger in relation to the axial pliculae and more elevated than they are in *V. cretaceus*. *V. semilugubris* is also smaller than *V. cretaceus*, has denticles inside the outer lip when fully mature and is typically patterned with bold black markings.

This species differs from *V. angulatus* (Pease, 1868) (type species of *Vaceuchelus*) and similar species from the south-western Pacific, such as *V. foveolatus* (A. Adams, 1853) and *V. scrobiculatus* (Souverbie in Souverbie & Montrouzier, 1866), in being larger and in lacking denticles or ridges inside the outer lip (cf. figures provided by Herbert 1996). More similar to *V. cretaceus* are *V. cavernosus* (Sowerby, 1905) from Sri Lanka (Fig. 70A, B) and *V. clathratus* (A. Adams, 1853) from the Philippines (Fig. 70C, D), both of which are of similar size and also lack sculpture inside the outer lip. Nonetheless, they retain a well defined, relatively fine, cancellate sculpture on the last adult whorl and have four and five spiral cords respectively on the base (including that level with suture) as opposed to three in *V. cretaceus*. Neither possesses the basal columella swelling of *V. cretaceus*. The most similar species is the recently described *Vaceuchelus pagoboorum* Poppe, Tagaro & Dekker, 2006 from the Philippines. This is clearly closely related to *V. cretaceus* and likewise possesses a broad swelling at the base of the columella, but differs in having an additional low rounded tubercle inside the outer lip near its junction with the parietal portion of the aperture, has more evenly spaced basal cords (four in juveniles compared with three in *V. cretaceus*, but the inner one becomes obsolete in adults), retains distinct pits in the interval between the outer and middle basal cords, and frequently has brownish markings on the spiral cords. With no material from intermediate localities, it is difficult to assess the significance of these differences, but they seem to constitute characters by which the populations can be distinguished and I thus describe the south-western Indian Ocean material as a new species.

I refer this species to *Vaceuchelus* with some hesitation. The overall facies of its shell also shows some resemblance to that of *Trochus clathratus* Aradas, 1847, type species of *Putzeysia* Sulliotti, 1889. In that genus, however, the apex is not flattened, and the protoconch is globose and less strongly sculptured (Engl & Rolán 2009). The protoconch of *V. cretaceus* is closer to that of *V. natalensis* and *V. gemmula*, but differs in having a distinct projection on the terminal lip. Furthermore, whereas the radula of *V. natalensis* appears to be simply a reduced version of the *Herpetopoma* radula, that of *V. cretaceus* differs in having a narrower, acutely trigonal rachidian cusp and inner marginals that lack a strongly pectinate outer margin. With no comparable information available concerning the type species of *Vaceuchelus*, these differences are difficult to evaluate, but they suggest a degree of intrageneric variability within *Vaceuchelus* that merits further study.

### *Vaceuchelus gemmula* (Turton, 1932) **comb. n.**

Figs 42–44

*Euchelus gemmula*: Turton 1932: 194, Nº 1347, pl. 49. Type loc.: Port Alfred, South Africa.
*Euchelus natalensis*: Bartsch 1915: 163; Turton 1932: 193, Nº 1346; Barnard 1951: 117, pl. xvi, fig. 16; 1963: 266 (in part).

Etymology: The species name *gemmula*, diminutive of Latin *gemma* (a bud or jewel) was formed as a feminine noun in apposition.

Description:

*Shell*: Small, turbiniform (L/D=0.90–1.15); teleoconch of up to 3.5 whorls; sculpture strongly cancellate; first whorl initially sculptured only with widely spaced, rib-like, axial pliculae (*ca* 15), but 3 spiral cords develop soon thereafter, one forming shoulder, another level with the abapical suture and the third between these at whorl periphery; cords persist and become progressively stronger with growth; an additional (fourth) subsutural cord may or may not develop on the shoulder during the last or penultimate whorl; no intermediary spiral cords; intervals between cords wider than cords themselves; last adult whorl with 20–30 axial pliculae; pliculae narrower than cords and somewhat lamellate, sometimes raised into squamose nodules where they cross cords; interstices obliquely quadrate. Base with 3 spiral cords, including that level with suture, usually with a weaker, rather ill-defined, fourth one present adjacent to columella; umbilicus closed or at most chink-like in adult, more obviously patent in some juveniles. Peristome

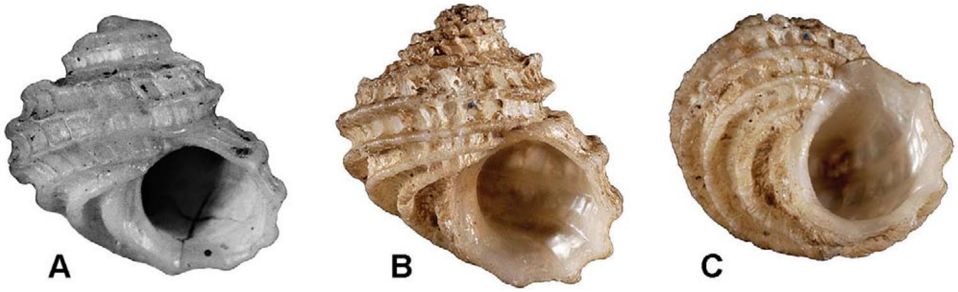

Fig. 42. *Vaceuchelus gemmula* (Turton, 1932): (A) lectotype of *Euchelus gemmula* Turton, 1932, diameter 3.7 mm (OXUM); (B, C) live collected specimen, off Kwelera River, East London, South Africa, diameter 3.8 mm (NMSA S6100).

oblique, aperture subcircular; columella concave, lacking dentition; outer lip notched at ends of spiral cords in juveniles and subadults, but less so in the largest specimens, when growth has ceased; even in the most mature specimens the outer lip is not conspicuously thickened and there is no trace of apertural teeth; interior nacreous and smooth, save for weak angles beneath external cords.

Microsculpture (Fig. 43B, C): Vermiform spiral threads not evident on early whorls; later whorls with a granular microsculpture on the spiral ribs and sparse scratch-like marks in the sculptural interstices.

Protoconch (Fig. 43A, C): White, a little exsert and slightly down-tilted; diameter *ca* 340 µm; terminal lip very weakly convex; superficial sculpture well developed, arranged in irregular axial lines, spiral element weakly evident in some specimens.

Colour: White to pale greyish white, living specimens with dirty buff intritacalx deposit, particularly in sculptural interstices. Most material worn.

Dimensions: Largest specimen, length 4.2 mm, diameter 3.9 mm.

*Operculum*: Relatively tightly multispiral throughout.

*Radula*: Unknown.

*External anatomy*: Uniformly white and evidently chilodontid, but preservation of material inadequate to establish anatomical details.

Type material: The type lot at OXUM contains three specimens, one, the largest, is marked with an X in the aperture. It is here figured and designated lectotype (Fig. 42A). This is probably the originally figured specimen, but it is difficult to be certain since the original illustration was heavily retouched.

Additional material examined (all NMSA unless indicated otherwise): SOUTH AFRICA: *Eastern Cape*: off Mtamvuna River (31.1466°S 30.2666°E), living, -115 m, sponge and rocks, dredged NMDP, RV *Meiring Naude*, st'n A13, viii.1981 (E858); ditto (31.1483°S 30.2617°E), -111 m, sponge, dredged NMDP, RV *Meiring Naude*, st'n A14, 18.viii.1981 (E276); ditto (31.1500°S 30.2583°E), -110 m, some pebbles, dredged NMDP, RV *Meiring Naude*, st'n A9, 18.viii.1981 (E6993); off Port Grosvenor (31.4166°S 29.9667°E), -100–110 m, pebbles, some sand, dredged NMDP, RV *Meiring Naude*, st'n D6, 13.viii.1981 (E285); ditto (31.4166°S 29.9667°E), -95–100 m, coarse sand, few gorgonians, dredged NMDP, RV *Meiring Naude*, st'n D12, 16.viii.1981 (E6981); ditto (31.40°S 29.95°E), -80 m, calcareous coral nodules, lithothamnion sheets, dredged NMDP, RV *Meiring Naude*, st'n D20, 16.viii.1981 (S3174); ditto (31.3833°S 29.9333°E), -60 m, sand and broken shell, dredged NMDP, RV *Meiring Naude*, st'n D22, 16.viii.1981 (E6979); ditto (31.4166°S 29.9333°E), -82 m, worn coral nodules, dredged NMDP, RV *Meiring Naude*, st'n D18, 16.viii.1981 (E6980); ditto (31.4466°S 29.9333°E), -97–100 m, sandstone, pink gorgonians, dredged NMDP, RV *Meiring Naude*, st'n D14, viii.1981 (C974); off N'tafufu River (31.5783°S 29.6617°E), -50 m, mud and sand, dredged NMDP, RV *Meiring Naude*, st'n H6, 14.viii.1981 (E240); Mgazi River mouth (31.7283°S 29.5317°E), don. Mrs P.

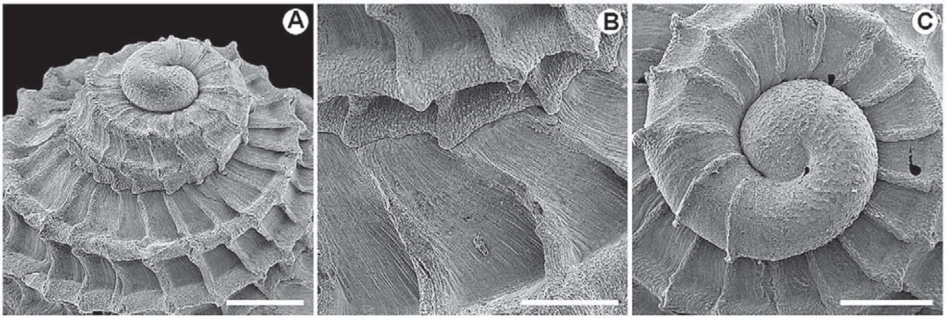

Fig. 43. *Vaceuchelus gemmula* (Turton, 1932), off N'tafufu River, Eastern Cape (NMSA E240): (A) apical whorls showing widely spaced axial pliculae on first whorl, bar = 250 µm; (B) adult microsculpture, bar = 200 µm; (C) protoconch, bar = 200 µm.

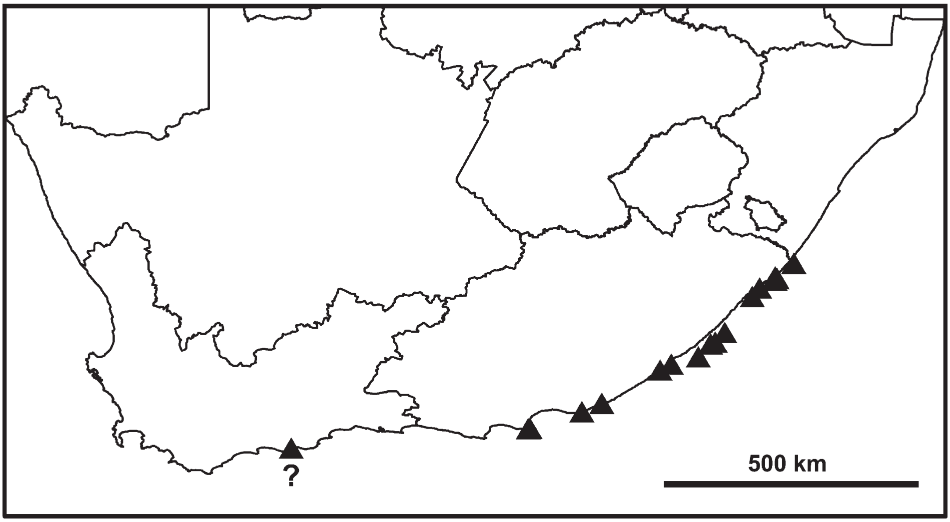

Fig. 44. Distribution of *Vaceuchelus gemmula*. Each triangle represents one or more records.

Palmer, viii.1980 (B3173); off Mbashe River (32.3567°S 29.0500°E), -465–500 m, coarse sand, dredged NMDP, RV *Meiring Naude*, st'n Q13, 6.vii.1985 (C9372); off Shixini Point (32.5267°S 28.8833°E), -500 m, muddy sand, coral rubble, dredged NMDP, RV *Meiring Naude*, st'n T17, 13.vii.1984 (V2786); off Qora River (32.5567°S 28.8000°E), -100 m, coarse sand, some sponge rubble, dredged NMDP, RV *Meiring Naude*, st'n U6,14.vi.1983 (E8266, S2657); off Qolora River (32.7848°S 28.5862°E), -340–350 m, coarse sand, broken shell, dredged NMDP, RV *Meiring Naude*, st'n Y11, 14.vii.1984 (E6997); East London, reef off Kwelera River (32.910°S 28.111°E), living, -20 m, dived B. Hayes, v.1992 (S6100); East London (33.0166°S 27.9166°E), *ex* Albany Mus. 1980 (B6626); Port Alfred (33.6°S 26.9°E), don. W.H. Turton, *ex* Albany Mus. 1980 (B7351); ditto, E.K. Jordan, *ex* Transvaal Mus. 1978 (B3416); Cannon Rocks (eastern end of Algoa Bay) (33.75°S 26.55°E), xii.1987 (E1539 and J. Marais coll'n 278); Port Elizabeth, Noordhoek (34.0405°S 25.6421°E), F. Graeve, ix.1985 (J. Marais coll'n 279); Port Elizabeth, Willows (34.0452°S 25.6070°E), living, under rocks *ca* low neap tide level, G. Carstens, 7.vi.1986 (D3493). *Western Cape*: Still Bay (34.3833°S 21.4500°E), purch. *ex* Mrs. C.M. Connolly, i.1974 (A3199) [record requires confirmation].

Distribution and habitat (Fig. 44): Eastern Cape, South Africa; from the border with KwaZulu-Natal, south and west to the Port Elizabeth area; empty shells from beach drift to -500 m; living intertidally (under rocks), or subtidally on firm substrata to -115 m. A single isolated record from 400 km further to the west at Still Bay (Western Cape) requires confirmation.

Remarks: This species closely resembles *Vaceuchelus natalensis* and was in fact treated as a synonym thereof by Barnard (1963). There are, nonetheless, clear and consistent differences evident in adult individuals which indicate that two distinct taxa are involved. The most obvious of these are the larger protoconch, closed umbilicus and presence of only three major cords on the base in *V. gemmula*. In addition, the spiral cords of *V. natalensis* remain strong at the aperture margin, producing strong notches in the outer lip even in the largest individuals. Juvenile stages can be difficult to separate since the umbilicus of *V. gemmula* sometimes only closes in the later stages of growth. Turton (1932) observed that the axial pliculae were more numerous in *V. gemmula* (about 30 on last adult whorl) than in *V. natalensis* (*ca* 20). I cannot confirm this observation and find considerable overlap between the taxa in terms of the number of axial pliculae, as well as considerable intraspecific variation. The three specimens in the OXUM type lot have 20, 22 and 24 pliculae on the last adult whorl, the latter figure being that of the lectotype. *V. gemmula* evidently attains a somewhat larger size than *V. natalensis*.

Little material of this species is available and most is in poor condition; only one live-collected adult specimen was to hand. The largest examples were obtained from beach-drift, but these are generally badly worn. Specimens from deeper water, off-shore habitats tend to be somewhat smaller, evincing an adult labrum at diameter *ca* 3.0 mm, and as in *V. natalensis* (below) they exhibit stronger nodules where the axial pliculae cross the spiral cords. The larger, less nodular form, which lives on near-shore reefs and washes ashore, is the typical form.

### **Vaceuchelus jayorum** sp. n.

Figs 45, 46, 49

Etymology: Named for Maurice and Danielle Jay of Réunion, in recognition of their contribution to our knowledge of the Mascarene malacofauna, and in gratitude for the hospitality they afforded the author.

Description:

*Shell*: Small, turbiniform (L/D=1.00–1.16); teleoconch of up to 3.5 whorls; sculpture strongly cancellate; first whorl initially sculptured only by axial pliculae, relatively widely spaced at first, but becoming more close-set toward end of first half whorl; 3 spiral cords develop during first whorl, one at mid-whorl, one between this and adapical suture and the third level with abapical suture; that at mid-whorl strongest and becoming peripheral cord of later whorls; cords become progressively stronger with growth, a fourth appearing below adapical suture during third whorl; axial pliculae more widely and regularly spaced from second whorl onward; pliculae cross cords producing angular nodules at intersections; in final quarter of last adult whorl an additional intermediary spiral cord arises between each of the primary cords (Fig. 45F); for the most part, intervals between cords noticeably wider than cords themselves; last adult whorl with 25–30 pliculae; pliculae narrower than cords; interstices obliquely quadrate. Base with 4 somewhat more close-set spiral cords, including that level with suture, a weaker fifth one sometimes evident, closely juxtaposed to the fourth and spiralling into umbilicus; umbilicus remaining patent at maturity, its width variable between individuals, often somewhat obscured by reflected upper part of columella lip. Peristome markedly oblique, almost tangential; aperture subcircular; columella concave, lacking dentition; outer lip notched at ends of spiral cords, somewhat thickened internally, but lacking both internal teeth and in-running ridges; interior of aperture nacreous, angled beneath external cords.

Microsculpture (Fig. 46B, C): Vermiform spiral threads not evident on apical whorls; microsculpture between axial pliculae crisply granular; this persisting over much of adult shell, but traces of scratch-like sculpture evident in interstices; in fresh specimens microsculpture generally obscured by relatively thick intritacalx layer and additional superficial encrustations.

Protoconch (Fig. 46A, C): White, not exsert, slightly down-tilted and more or less level with first teleoconch whorl; diameter 260–290 µm; terminal lip straight but with evidence of a small beak-like projection near adapical suture; superficial sculpture well developed, relatively coarse and widely spaced, arranged in irregular axial lines, with no spiral component evident.

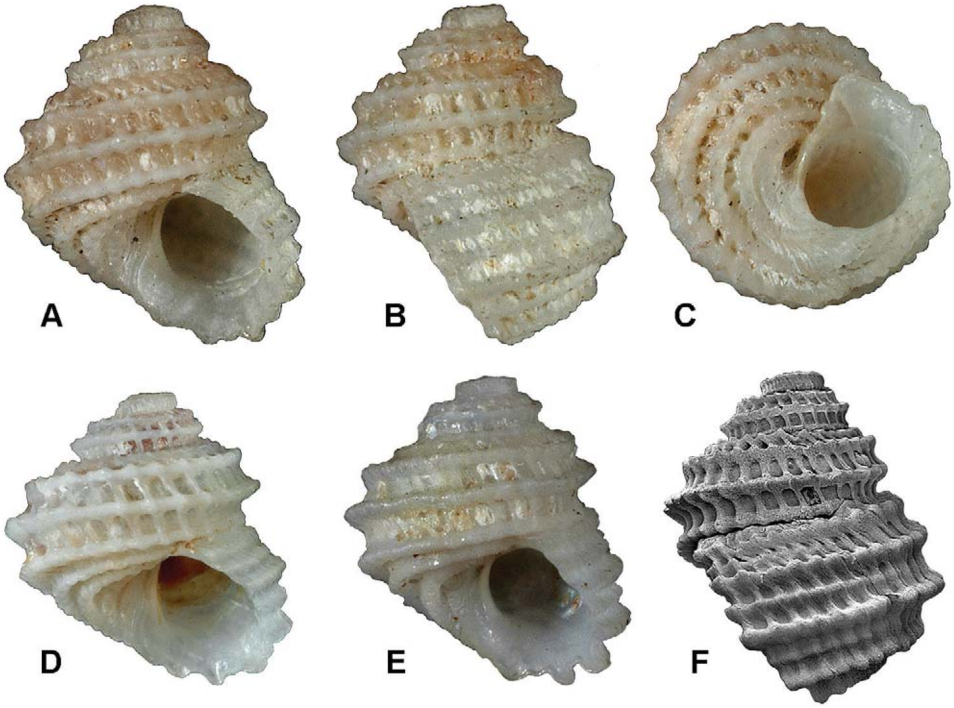

Fig. 45. *Vaceuchelus jayorum* sp. n.: (A–C) holotype, diameter 2.5 mm (M. Jay coll'n, MNHN 24809); (D) depressed specimen, Réunion, diameter 2.4 mm (paratype, M. Jay coll'n, MNHN 24810); (E) Andramara, southern Madagascar, diameter 2.4 mm (paratype, MNHN 24811); (F) side view showing intermediary spiral cords on final part of last adult whorl, SEM, Réunion, diameter 2.35 mm (paratype, M. Jay coll'n, MNHN 24810).

Colour: Shell more or less uniformly white to pale buff; with a dirty white, chalky intritacalx deposit.

Dimensions: Largest specimen, length 2.9 mm, diameter 2.5 mm.

*Operculum*: Like that of *V. natalensis*.

*Radula and external anatomy*: Unknown.

Holotype (Fig. 45A–C): RÉUNION: not further localised (M. Jay coll'n, MNHN 24809).

Paratypes: RÉUNION: Cap la Houssaye (21.01797°S 55.23709°E), -12 m, hand-dredged sand, J. Drivas, 1987 (NMSA K2755/T2959, 3 specimens); not further localised (M. Jay coll'n, MNHN 24810, 35 specimens; NMSA L8467/T2960, 4 specimens; NHMUK 20110385, 1 specimen). MADAGASCAR: Andramara (25.48000°S 44.97167°E), intertidal roche basaltique, dalles sableuses, Exped'n Atimo Vatae, st'n BM10, 2.vi.2010 (MNHN 24811, 2 specimens).

Other material examined: RÉUNION: not further localised (M. Jay coll'n, MNHN). RODRIGUES: Between Anse aux Anglais and Pointe Venus (19.6752°S 63.4313°E), beach-drift, D. Herbert, ix.1991 (NMSA K7825); Grand Baie, near stream (19.67175°S 63.45089°E), beach-drift, D. Herbert, ix.1991 (NMSA L549). MOZAMBIQUE: Inhambane area, off Ponta da Barra lighthouse, 'Stalin Reef' (23.68798°S 35.52566°E), -16 m, dived D. Slater, xi.2003 (D. Slater coll'n).

Distribution and habitat (Fig. 49): Endemic to the tropical south-western Indian Ocean, ranging from the Mascarene Islands, particularly Réunion, to southern Madagascar and central Mozambique. No accurate habitat data available, but probably an inhabitant of near-shore, carbonate substrata and perhaps lagoons.

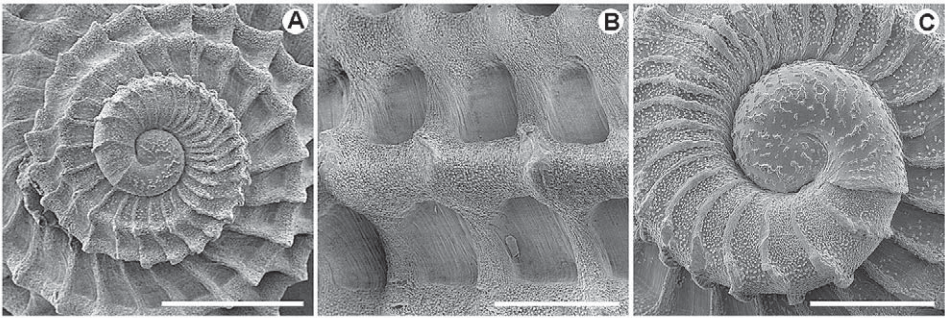

Fig. 46. *Vaceuchelus jayorum* sp. n., Réunion (paratypes, M. Jay coll'n, MNHN 24810): (A) apical whorls showing strong, close-set, axial pliculae on first whorl, bar = 0.5 mm; (B) adult microsculpture, bar = 250 µm; (C) protoconch, bar = 200 µm.

Remarks: This material is confusingly similar to specimens of *V. natalensis* from off-shore habitats, in which the axial pliculae cross the spiral cords to produce a more angularly nodular sculpture. The principle discriminant character of the present material is the appearance of intermediary spiral cords above the periphery of the final quarter of the last adult whorl. Such intermediary cords are never evident in *V. natalensis*. In addition, the axial pliculae on the first teleoconch whorl are considerably more close-set in *V. jayorum* and the intritacalx deposit is more uniformly pale in colour, lacking the greyish axial banding common in *V. natalensis*.

There is also some resemblance to *V. favosus* (Melvill & Standen, 1896), a poorly known species from the Loyalty Islands. However, the figured syntype of that species (MMUM EE.3734; here re-illustrated and designated lectotype, Fig. 70E–G) also lacks intermediary spiral cords in the final quarter of the last adult whorl, and it has a wider umbilicus than any of the south-western Indian Ocean species of *Vaceuchelus*.

### *Vaceuchelus natalensis* (Smith, 1906)

Figs 4K, 6G, 47–49

*Euchelus natalensis*: Smith 1906: 55, pl. 8, fig. 5; Barnard 1963: 266 (in part). Type loc.: Durban, South Africa [H.C. Burnup].
*Vaceuchelus natalensis*: Poppe *et al.* 2006: 47.

Description:

*Shell*: Small, turbiniform; spire height rather variable (L/D=0.90–1.2); teleoconch of up to 3.5 whorls; sculpture strongly cancellate; first whorl initially sculptured only by relatively widely spaced axial pliculae (16–18), but 3 spiral cords develop soon thereafter, one forming shoulder, another level with abapical suture and the third between these, at whorl periphery; cords persist and become progressively stronger with growth; a fourth cord may develop on shoulder during last or penultimate whorl, but otherwise there are no intermediaries; intervals between cords noticeably wider than cords themselves; cords sometimes weakly and rather irregularly granular where crossed by axial pliculae (see notes below); last adult whorl with 22–30 pliculae; pliculae narrower than cords; interstices obliquely quadrate. Base with 4 somewhat more close-set spiral cords, including that level with suture, with a weaker fifth one spiralling into umbilicus;

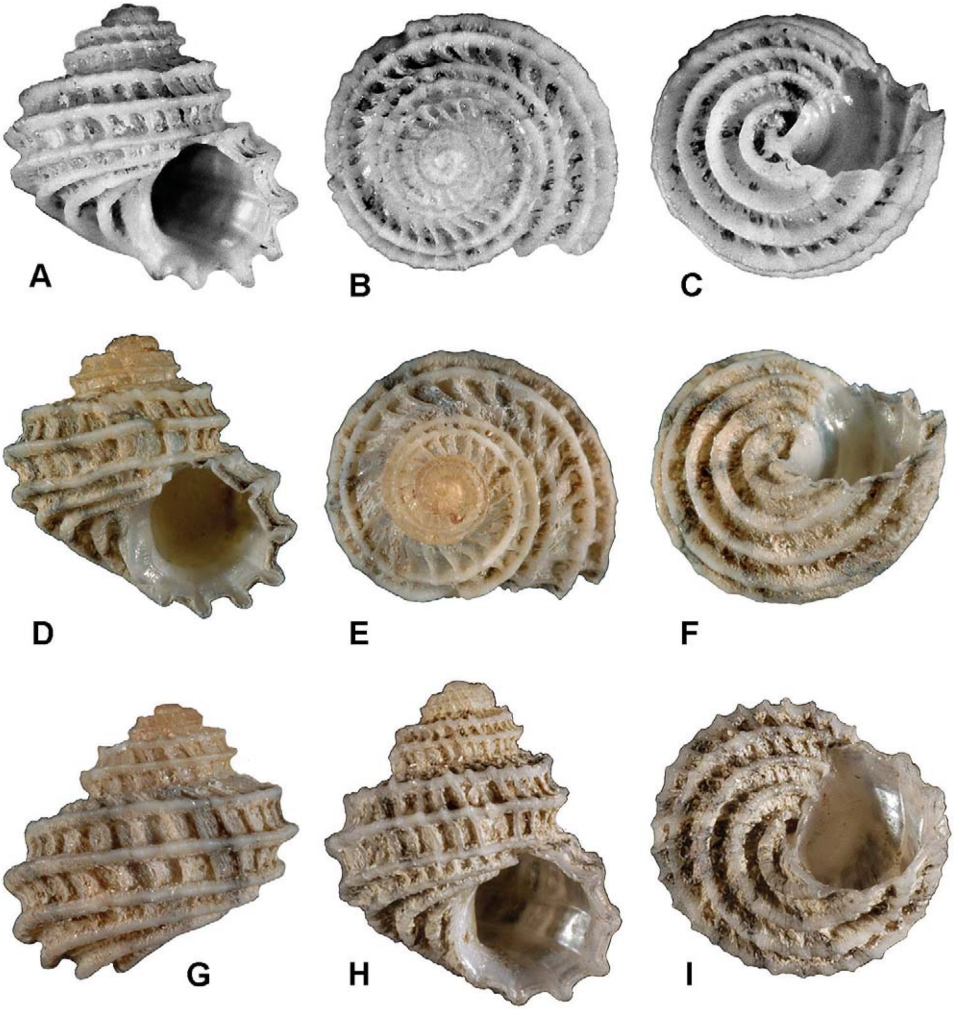

Fig. 47. *Vaceuchelus natalensis* (Smith, 1906): (A–C) lectotype of *Euchelus natalensis* Smith, 1906, diameter 2.9 mm (NMSA T522/1208); (D–G) Widenham, KZN, living, under rocks at LST, diameter 2.9 mm (NMSA W7462); (H–I) elevated specimen, off Umzinto, KZN, living, -84 m, diameter 2.9 mm (NMSA D5428).

umbilicus narrowly patent, partly obscured by reflected columella lip. Peristome oblique; aperture subcircular; columella concave, lacking dentition; outer lip strongly notched at ends of spiral cords, even in the largest specimens; interior of aperture nacreous, lacking internal teeth or spiral ridges, but angled beneath external cords.

Microsculpture (Fig. 48B, C): Vermiform spiral threads not evident on apical whorls, but traces of microscopic granular sculpture present; scratch-like microsculpture weakly evident in sculptural interstices of adult shell, but microsculpture generally obscured by granular intritacalx deposit.

Protoconch (Fig. 48A, C): White, a little exsert and slightly down-tilted; diameter 280–300 µm; lacking an apical beak; terminal lip more or less straight to weakly convex, and slightly flaring; superficial sculpture well developed, arranged in irregular axial lines, with no spiral element evident.

Colour: Shell whitish, living specimens with a dirty buff intritacalx deposit, usually with darker, ashy-grey axial bands, some iridescence in cord intervals; dead shells usually with only traces of intritacalx remaining, mostly in interstices.

Dimensions: Largest specimen, length 3.3 mm, diameter 3.4 mm.

*Operculum* (Fig. 4K): Relatively tightly multispiral throughout.

*Radula* (Fig. 48D, E): Formula ∞+2+1+2+∞; *ca* 60 transverse rows of teeth; transition from lateral to marginal series relatively clear. Rachidian with large trigonal cusp and well-developed hood; cusp with very strong transverse ridge at its base; cutting edge coarsely dentate, central denticle largest, lanceolate, with approx. 4 smaller denticles on each side. Only 2 lateral teeth evident, their cusps spathulate with coarsely and deeply dentate margins. Marginals resembling those of *Herpetopoma,* the inner ones with cusp coarsely pectinate on outer margin; remaining marginals with smaller more finely pectinate cusps, but those at radula margin broader and flatter.

*External anatomy* (Fig. 6G): Head-foot translucent milky-white when alive, snout and neck with some greyish pigmentation. Cephalic lappets present but small and not extending across forehead; right postocular peduncle well developed, similar in size to eyestalk or perhaps larger; right subocular tentacle not evident; neck lobes similar, each with 5 or 6 tentacles of varying size; epipodium posterior to neck lobes with 4 or

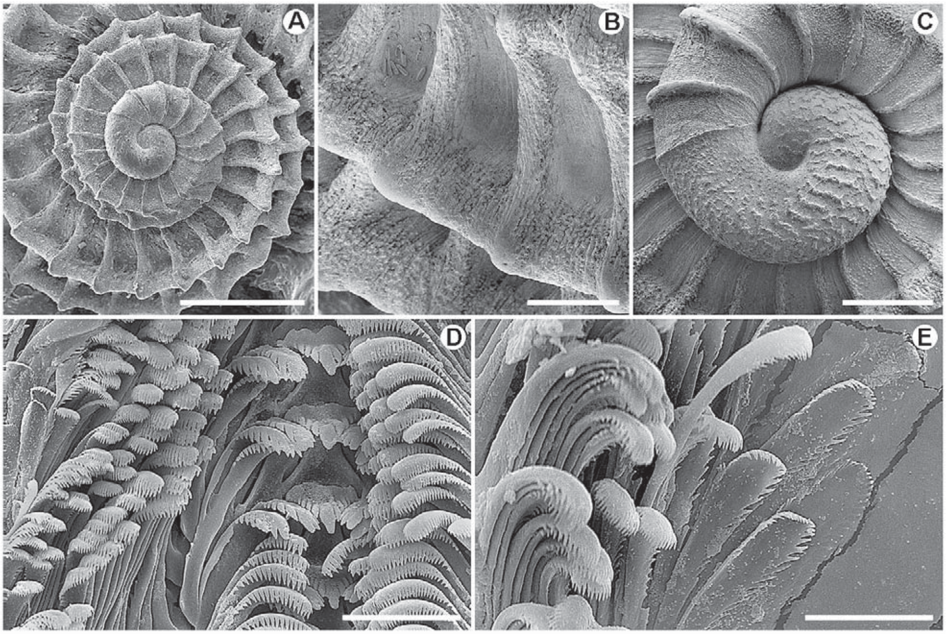

Fig. 48. *Vaceuchelus natalensis* (Smith, 1906): (A) apical whorls showing widely spaced axial pliculae on first whorl, Aliwal Shoal, KZN, bar = 0.5 mm (NMSA S8021); (B) adult microsculpture, Aliwal Shoal, KZN, bar = 100 µm (NMSA S8021); (C) protoconch, off Kosi Bay, KZN, bar = 100 µm (NMSA S2880); (D) radula, central field and inner laterals, Widenham, KZN, bar = 25 µm (NMSA W7462); (E) radula, outer marginal teeth, Widenham, KZN, bar = 10 µm (NMSA W7462).

5 tentacles of varying sizes on each side, with an epipodial sense organ faintly discernable at base of larger ones.

Type material: Lectotype (here designated, Fig. 47A–C) of *Euchelus natalensis* Smith, 1906, in NMSA (1208/T522), length 2.8 mm, diameter 2.9 mm; also three paralectotypes (NMSA W7531/T2642); three further paralectotypes in NHMUK (1906.6.23.18–20). All are fresh specimens, but none is obviously the one originally figured.

Additional material examined (all NMSA unless indicated otherwise): MOZAMBIQUE: Bazaruto Archipelago, Santa Carolina Is. (21.6124°S 35.3399°E), R. Kilburn, ix.1974 (K3929); ditto, south sandbank (21.6124°S 35.3399°E), R. Kilburn, 17.viii.1974 (K1991); Malongane, coral reef 5 km north Ponta do Ouro (26.7983°S 32.8906°E), -15–20 m, hand-dredged sand, D. Herbert, v.1994 (L1653). SOUTH AFRICA: *KwaZulu-Natal*: Kosi Bay, main reef 1–2 km south of estuary (26.9083°S 32.8861°E); -9–17 m, sorted from stone washings, D. Herbert, 12–20.vii.1987 (D9827); ditto, main reef, 1–4 km south of estuary mouth (26.9210°S 32.8861°E), living, -20 m, underwater pump, D. Herbert & R. Broker, 5.v.1990 (S2524); ditto, living, -15 m, stone surfaces, D. Herbert, 4.v.1990 (S2880); off Kosi mouth (26.9333°S 32.9117°E), -50 m, fine sand, shell rubble, *Codium*, dredged NMDP, RV *Meiring Naude*, st'n ZA2, 6.vi.1987 (E1468); between Bhanga Neck and Kosi Bay, reef off marker 13 north near pinnacles (26.93°S 32.90°E), -10–12 m, hand-dredged sand, D. Herbert, 12.v.1990 (S2482, S3106); ditto, -8 m, underwater pump, D. Herbert & K. Bloem, 6.v.1990 (S2769); off Dog Point (27.1083°S 32.8817°E), -70 m, sandstone conglomerate, dredged NMDP, RV *Meiring Naude*, st'n ZC3, 4.vi.1987 (E1736); off Lala Neck (27.2250°S 32.8250°E), -74 m, shells and sand, dredged NMDP, RV *Sardinops*, st'n ZDD3, 8.vi.1990 (S9768); Sodwana Bay, 2–Mile Reef (27.517°S 32.700°E), -10–15 m, sorted from stone washings, D. Herbert & R. Broker, ix.1987 (E740); ditto, -10–15 m, hand-dredged sand, D. Herbert, 30.xii.1990 (S4311); ditto, outer edge of reef, -15–17 m, sorted from stone-washings, D. Herbert, 18–26.x.1986 (D5298); Leadsman Shoal, outer portion (27.80°S 32.62°E), -24–26 m, sorted from stone washings, D. Herbert & NPB, 14.v.1988 (E2673); Leadsman Shoal, Raggie Reef, 1–2 km north of Leven Point (27.80°S 32.62°E), living, -8–12 m, mixed algal & coral reef, D. Herbert & NPB, 15.v.1988 (E6809); NE of Leven Point (27.9167°S 32.6467°E), -250 m, coarse sand, dredged NMDP, RV *Meiring Naude*, st'n ZL5, 9.vi.1988 (S1140); off Leven Point (27.9250°S 32.6083°E), -50–60 m, mud, dredged NMDP, RV *Meiring Naude*, st'n ZL1, 9.vi.1988 (E5873); Umdloti (29.6829°S 31.1127°E), intertidal, under rocks, ix.1974 (J. Marais coll'n 281); Durban (29.850°S 31.017°E), H.C. Burnup (A4564); Durban Bay (29.850°S 31.017°E), shallow dredgings, B.J. Young (E599); Umkomaas (30.2064°S 30.8023°E), living, H.C. Burnup (A4563); Widenham, intertidal rocks (30.216829°S 30.798644°E), low shore spring tide, under large rocks with spaces below, together with arcid and carditid bivalves, leg. D. Herbert & L. Davis, 23.ix.2010 (W7462); Aliwal Shoal (30.2833°S 30.8333°E), D. Herbert & R. Emanuel, 27.xi.1988 (E6189); ditto, -10 m, sand & reef debris, hand-dredged, D. Herbert, 4.iv.1992 (S8222); ditto, -10–20 m, hand-dredged sand, D. Herbert, 30.vi.1991 (S8021); ditto, -14 m, underwater pump, D. Herbert, 2.vi.1991 (S8673); ditto, -16 m, hand-dredged sand, D. Herbert, 26.v.1990 (S5993); ditto, -27 m, in silt from between rocks, G. Smith, don. J. Marais, iii.1988 (E1675, J. Marais coll'n 280); ditto, Cracker Reef, *ca* -23 m, D. Herbert, 30.iv.1989 (E7141); Scottburgh (30.283°S 30.833°E), C.W. Alexander, *ex* W. Falcon coll'n (A4565); Landers Reef off Park Rynie (30.333°S 30.817°E), -29–30 m, sorted from stone washings, D. Herbert, 2.v.1988 (E2251); off Umzinto (30.36°S 30.85°E), living, -84 m, dredged NMDP, RV *Meiring Naude*, st'n X2, 15.viii.1982 (D5428). *Eastern Cape*: Mbotyi (31.45°S 29.73°E), beach drift, R. Kilburn & D. Herbert, v–vi.1985 (C8468); Lwandile/Mdumbi (31.883°S 29.267°E), R. Kilburn & R. Fregona, vii.1981 (C205); Xora River mouth (32.1600°S 28.9974°E), R. Kilburn (7059); off Nthlonyane River (32.2133°S 28.9817°E), -51 m, sandy mud with astrorhizid foraminiferans, dredged NMDP, RV *Meiring Naude*, st'n P7, 19.vi.1982 (E164); Pondoland coast, Mrs A. Filmer, H. Becker coll'n, *ex* Transvaal Mus. 1978 (B1104).

Distribution and habitat (Fig. 49): Southern Mozambique (Bazaruto Archipelago) to just north of the Mbashe River, Eastern Cape, South Africa; from the low intertidal zone of rocky shores to -84 m; in intertidal habitats specimens may be found living at LST under large rocks that are rarely moved by the waves and which have a space beneath them allowing water flow, usually together with arcid and carditid bivalves. I believe Turton's record of the species from Port Alfred, Eastern Cape (Turton 1932) was almost certainly based on material of *V. gemmula*, which Bartsch had earlier mistakenly identified as *V. natalensis*.

Remarks: There is noticeable intraspecific variation in the extent to which the axial pliculae interact with the spiral cords. In intertidal material the interaction is minimal and

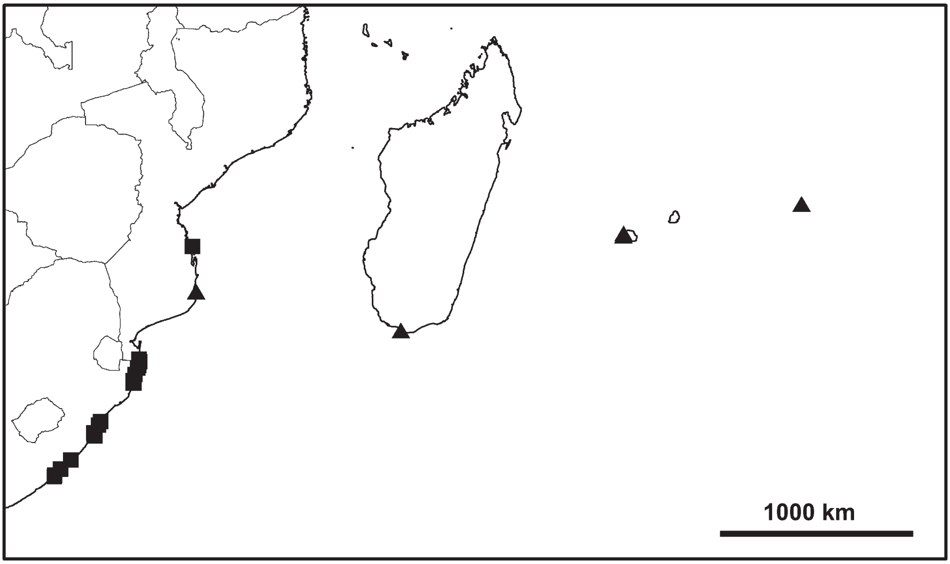

Fig. 49. Distribution of *Vaceuchelus jayorum* (triangles) and *V. natalensis* (squares). Each symbol represents one or more records.

the spiral cords are smooth or at most irregularly undulant. This is the typical condition (Fig. 47A–G). Generally, in specimens from off-shore reefs, however, the axial pliculae are more close-set and they cross the spiral cords, rendering the latter distinctly nodular (Fig. 47H, I). Such specimens closely resemble *V. jayorum* from Réunion, but they do not develop intermediary spiral cords on the last adult whorl. The distinguishing features of *V. gemmula* have been detailed above.

*V. cavernosus* (Sowerby, 1905) from Sri Lanka (Fig. 70A, B) and *V. clathratus* (A. Adams, 1853) from the Philippines (Fig. 70C, D) likewise lack apertural dentition, but are both considerably larger, whereas *V. semilugubris* (below) although equally small, generally has blackish maculations and develops denticles inside the outer lip when mature.

### *Vaceuchelus semilugubris* (Deshayes, 1863)

Figs 4L, 50, 51

*Turbo semilugubris*: Deshayes 1863: 72, pl. 9 [36], figs 9, 10; Martens 1880: 294; Herbert 1996: figs 70, 71 (syntype). Type loc.: Réunion.
*Leptothyra semilugubris*: Pilsbry 1888: 252, pl. 58, fig. 52a; Viader 1937: 55.
*Vaceuchelus semilugubris*: Poppe *et al*. 2006: 47.

Description:

*Shell*: Small, turbiniform, robust; length more or less equal to diameter (L/D=0.92–1.04); teleoconch of approx. 3.5 whorls, but apex usually badly eroded; sculpture cancellate; first whorl strongly shouldered at mid-whorl, almost horizontal above shoulder and vertical below it; shoulder develops into a strong spiral cord at end of whorl, another cord evident at level of abapical suture; axial pliculae do not develop until near end of whorl; this sculpture strengthening during second whorl with an additional cord arising between first cord and adapical suture; these two cords becoming the large peripheral and supra-peripheral cords of last adult whorl; 1–2 additional secondary cords arising above supra-peripheral cord during third whorl; axial pliculae stronger on second and subsequent whorls, prosocline and raised into granules where they cross spiral cords, granules somewhat angular on second whorl, but becoming progressively more rounded and bead-like on subsequent whorls; interstices quadrate; last adult whorl with 25–30 pliculae. Base with 5 spiral cords, the first level with suture, the fifth small and spiralling into umbilicus; umbilicus narrowly patent even in adults. Peristome oblique and nearly tangential, aperture subcircular; columella shallowly concave with a rounded tooth at its base; interior of outer lip of mature individuals subterminally thickened and set with approx. 10 ridge-like denticles, with an additional row of smaller granules just inside lip edge; apertural dentition absent in immature specimens, in these the outer lip is strongly notched at ends of spiral cords; interior nacreous, weakly angled beneath external cords, but labral denticles not extending into aperture as in-running ridges.

Microsculpture (Fig. 51A, B): Juvenile microsculpture comprising irregular vermiform spiral threads; subsequent microsculpture mostly granular, but with traces of scratch-like markings.

Protoconch (Fig. 51C): White, slightly exsert, eroded in most material; diameter *ca* 285 µm; strongly sculptured with an irregular superficial reticulation showing traces of

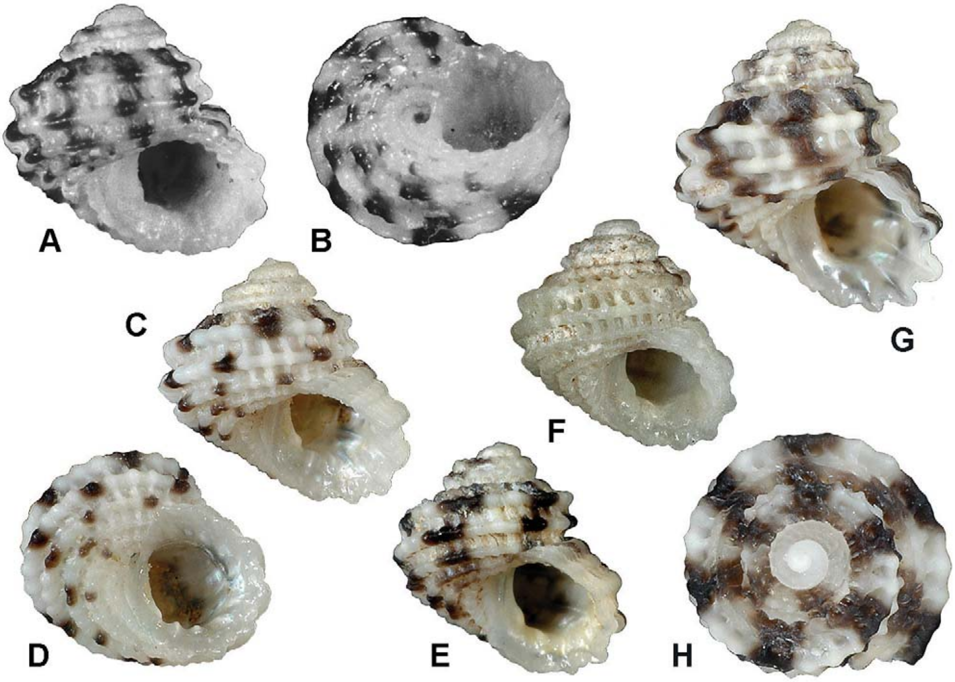

Fig. 50. *Vaceuchelus semilugubris* (Deshayes, 1863): (A, B) lectotype (here designated) of *Turbo semilugubris* Deshayes, 1863, diameter 3.05 mm (MNHN); (C, D) fresh mature specimen, diameter 2.9 mm (M. Jay coll'n, MNHN); (E) finely sculptured specimen, diameter 2.7 mm (M. Jay coll'n, MNHN); (F) finely sculptured specimen almost devoid of black markings, diameter 2.6 mm (M. Jay coll'n, MNHN); (G, H) large, heavily patterned subadult specimen with immature lip and coarse sculpture, diameter 3.1 mm (M. Jay coll'n, MNHN). All specimens from Réunion, but not further localised.

axial alignment, but no spiral element. Terminal lip more or less straight, but perhaps evincing signs of a broken beak-like projection; becoming concave toward abapical suture.

Colour: Shell white, variously patterned with black spots, blotches or axial bands, orientation of pattern prosocline in some specimens, opisthocline in others; markings generally finer on base; pattern fading to brown in old material. Occasional specimens with almost no black markings (Fig. 50F). Coloration of fresh specimens somewhat obscured by dirty buff intritacalx deposit, superficial calcareous encrustations and debris.

Dimensions: Largest specimen, length 3.55 mm, diameter 3.40 mm; smallest specimen with mature apertural dentition, length 2.6 mm, diameter 2.7 mm.

*Operculum* (Fig. 4L): Relatively tightly multispiral throughout.

*Radula* (Fig. 51D, E): Formula ∞+3+1+3+∞; *ca* 50 transverse rows of teeth; transition from lateral to marginal series clear. Rachidian with broad, trigonal cusp, well-developed hood, and a distinct transverse basal ridge; cutting edge with a slender, acuminate central denticle and 2 or 3 progressively smaller, similarly shaped denticles on each side. Lateral teeth all of similar size, their cusps with coarse lateral denticles on both margins (3–5), those on the third lateral particularly strong. Marginals closely resembling those of *Herpetopoma scabriusculum*, the cusps of the inner ones with a strongly pectinate outer margin; outermost marginals shorter and with a slightly dilated, fringed cusp.

*External anatomy*: Only dried material available; evidently chilodontid but insufficient detail evident.

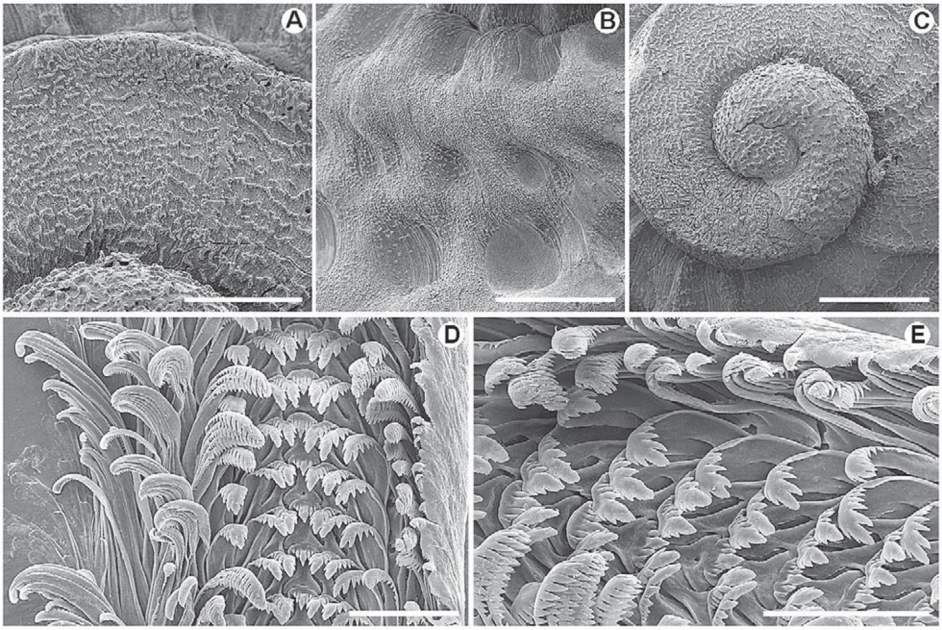

Fig. 51. *Vaceuchelus semilugubris* (Deshayes, 1863), all Réunion, not further localised (M. Jay coll'n, MNHN): (A) juvenile microsculpture, bar = 100 µm; (B) adult microsculpture, bar = 200 µm; (C) protoconch, bar = 250 µm; (D) central field and left marginals, bar = 50 µm; (E) radula, oblique view of right side of central field, bar = 50 µm.

Type material: Two syntypes of *Turbo semilugubris* Deshayes, 1863, in MNHN, the one in better condition is here figured and designated lectotype (MNHN 24658) (Fig. 50A, B), length 3.10 mm, diameter, 3.05 mm.

Other material examined: RÉUNION: not further localised (M. Jay coll'n, MNHN; NMSA G4264, J269); off Cap La Houssaye (21.01797°S 55.23709°E), -12 m, hand-dredged sand, J. Drivas, i.1988 (NMSA K3035).

Distribution and habitat: Known only from the island of Réunion; Jay (2009) recorded it as living under stones at -10–15 m, but noted it to be rare.

Remarks: There appear to have been no published records of this species since its original description. Subsequent mentions of the name are either simple listings (Martens 1880; Viader 1937) or mere translation of the original description (Pilsbry 1888), and there is no evidence of new material having been examined. However, additional samples clearly referable to this species have been found on Réunion, confirming that the original provenance was correct. The occurrence of the species in Mauritius requires confirmation. Pilsbry (1888) and Viader (1937) mentioned this island, but it is not clear whether this was a generalisation or specifically intended to mean Mauritius rather than Réunion. Despite extensive searching for micro-molluscs in beach-drift samples and hand-dredged sand from near-shore reefs on Mauritius (by Kilburn and Herbert), no specimens of *V. semilugubris* have been collected. Nonetheless, it is clearly not common, even on Réunion. Given the proximity of Réunion and Mauritius, it would be surprising if the species did not occur on both islands.

Whether this species should be referred to *Vaceuchelus* or *Herpetopoma* requires further study. I have chosen to refer it to *Vaceuchelus* on account of the shape of the shell and its relatively coarse, cancellate sculpture. The presence of denticles inside the outer lip is a feature common to both *Vaceuchelus* and *Herpetopoma*. However, in the present species there is also a distinct denticle at the base of the columella that delineates a notch (albeit weak) at the junction of the basal and columella lips. This is a feature more typical of *Herpetopoma*.

The species is distinctive amongst small chilodontids of the south-western Indian Ocean on account of its bold, axial colour bands and relatively wide umbilicus. In fresh shells these bands are very dark purplish brown to almost black, but fade to a paler maroon-brown in old and sun-bleached specimens. They are clearly part of the shell, unlike the greyish axial bands seen in fresh material of other species (e.g. *V. natalensis*), which are part of the superficial intritacalx deposit. Rarely, specimens are almost devoid of black markings and may easily be confused with the sympatric *V. jayorum* (above). That species, however, has strong close-set axial pliculae on the first teleoconch whorl, has intermediary spiral cords on the last quarter of the final whorl, and does not develop labral dentition when mature. I suspect *V. semilugubris* may exhibit ecological variation in shell morphology, ranging from typical boldly marked specimens with coarse sculpture, to somewhat smaller specimens with little or no colour pattern and finer sculpture (Fig. 50F). However, since accurate information on habitat is not available, this remains a speculative observation.

## Genus *Perrinia* H. & A. Adams, 1854

*Perrinia*: H. & A. Adams 1854 in 1853–54: 419. Type species: *Monodonta angulifera* A. Adams, 1853, by subsequent designation (Pilsbry 1890 in 1889–90: 15).

Shells of *Perrinia* species are small (length <20 mm) with relatively flat-sided whorls, resulting in a trochiform spire. The suture is frequently strongly indented and the periphery often angular and/or keeled. The apical whorls are sculptured only with axial pliculae and subsequent whorls with both spiral cords and axial pliculae that interact to produce a cancellate or foveolate sculpture (not obviously beaded). The columella has a single, relatively weak tooth or knob near its base, there is no inductural callus shield, the umbilicus is generally closed, and the interior of the outer lip bears spiral ridges that extend deep into the aperture. The juvenile microsculpture is granular and lacks vermiform spiral threads, and the adult microsculpture of close-set, scratch-like, axial marks is well developed.

*Perrinia* has long been regarded as a subgenus of *Turcica* H. & A. Adams, 1854 (type species *Turcica monilifera* A. Adams, 1854, by monotypy), but I consider *Perrinia* species to form a relatively well defined group which can be reasonably easily separated from the much larger *Turcica* s.s. species on account of their smaller size, stouter shells and strong spiral lirae inside the outer lip of the aperture. In the absence of data suggesting otherwise, I therefore accord *Perrinia* full generic status.

It should be noted that Kano *et al*. (2009) have shown that *Turcica* belongs within the Calliotropidae. This may also prove to be the case for *Perrinia* when sequence data become available, but I consider the overall facies of the shell of *Perrinia* to be closer to that of the Chilodontidae and thus maintain it here for the present.

### Key to species of *Perrinia* in the south-western Indian Ocean

1 Shell with broad, low, opisthocline axial ribs ........................................ **angulifera**

– Shell lacking such ribs, axial sculpture restricted to relatively narrow, prosocline pliculae ........................................................................................................2

2 Shell small (length up to 6.0 mm); peripheral spiral cord at most weakly stellate .........................................................................................................**konos**

– Shell larger (length up to 11.0 mm); peripheral spiral cord strongly stellate........... ......................................................................................................... **stellata**

### *Perrinia angulifera* (A. Adams, 1853)

Figs 4M, 5B, 6E, 52–54

*Monodonta angulifera*: A. Adams 1853: 176; Pilsbry 1890 in 1889–90: 416. Type loc.: Puerto Galero, Mindoro Is., Philippines, sandy mud, 6 fath. [-11 m] (Mus. Cuming).

*Tectaria montrouzieri*: Fischer 1878: 212–213; Souverbie & Montrouzier 1879: 31, pl. 3, fig. 6; Herbert 1996: 418, figs 18, 19 [= *M. angulifera* A. Adams, 1853]. Type loc.: Ile Art (New Caledonia).

*Perrinia angulifera*: Smith 1903: 618, pl. 35, fig. 27; Hylleberg & Kilburn 2003: 26; Héros *et al*. 2007: 209.

*Calliostoma anguliferum*: Hidalgo 1904–5: 255.

*Cantharidus pliciferus*: Schepman 1908: 43, pl. 3, fig. 3. Type loc.: *Siboga* st'n 109, Pulu Tongkil, Sulu Archipelago, -13 m, *Lithothamnion* bottom. **Syn. n.**

*Perrinia plicifera*: Poppe *et al.* 2006: 45, pl. 15, fig. 7; Poppe & Tagaro 2008: 180, pl. 35, fig. 5.

*Turcica montrouzieri*: Hedley 1909: 354; Jansen 1996: 10, N° 31.

*Turcica* (*Perrinia*) *angulifera*: Melvill 1928: 98.

*Turcica concinna* [*non* A. Adams, 1863]: Jay 2009.

Description:

*Shell*: Elevated trochiform (L/D=1.24–1.5); apical angle 50–60°; teleoconch of up to 7.5 whorls (apical ones frequently badly eroded or missing); apex truncated; spire whorls somewhat flat-sided, but still retaining a degree of curvature; periphery angular, but not keeled; suture inserted below peripheral angle, level with subperipheral cord creating a narrow channel. First teleoconch whorl sculptured initially only with axial pliculae (±30); 3–4 spiral cords develop during second whorl; cords crossed by crispate axial pliculae; third and subsequent whorls with 5–6 broad, rather uneven spiral cords above and including peripheral one; subsutural cord rendered coronate by well-developed triangular nodules arising from approximately alternate axial pliculae; nodules frequently apically bifid on later whorls; interaction of spiral and axial elements producing a foveolate sculpture with rectangular to D-shaped pits; shell also sculptured by broad, opisthocline (rarely orthocline) ribs, stronger in some specimens than others, 11–15 on last adult whorl; ribs for the most part arising from subsutural coronations (not invariably), strongest at periphery and rendering shell circumference undulant or even weakly stellate (infrequent). Base sculptured by 6–8 spiral cords; cords near umbilicus weaker than those toward periphery; axial pliculae evident in cord intervals, especially that between peripheral and subperipheral cords, weakest and almost obsolete near

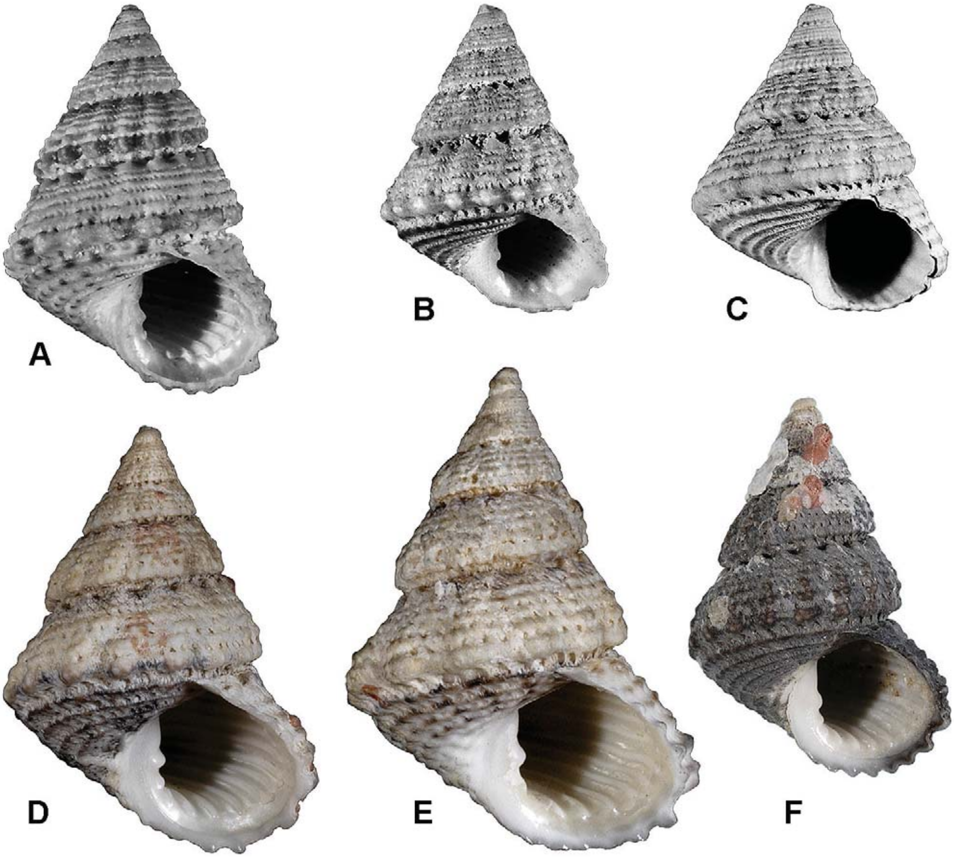

Fig. 52. *Perrinia angulifera* (A. Adams, 1853): (A) lectotype of *Monodonta angulifera* A. Adams, 1853, length 12.9 mm (NHMUK 1968215); (B) holotype of *Tectaria montrouzieri* Fischer, 1878, length 10.2 mm (MHNB); (C) holotype of *Cantharidus pliciferus* Schepman, 1908, length 10.2 mm (ZMA Moll 3.08.028); (D) typical south-western Indian Ocean specimen, off Boteler Point, KZN, length 14.1 mm (NMSA D9209); (E) large specimen, NE of Liefeldt's Rocks, KZN, length 16.0 mm (NMSA E4265); (F) dark specimen, NE of Liefeldt's Rocks, KZN, length 12.5 mm (NMSA E4344).

umbilicus; pliculae interact with cords causing some weak granulation of the latter; umbilicus closed in adults, but patent in very young individuals. Peristome oblique; aperture D-shaped, flattened at parietal and columella lips; columella (at maturity) with a relatively prominent tooth approximately one third of length from basal lip, occasionally also with a very low swelling apical to this; interior of outer lip with up to 16 spiral lirae running into aperture (only in mature shells), those nearest shell axis may terminate on base of columella and appear as small denticles below columella tooth; outer lip prosocline, its margin thin, but becoming thicker internally.

Microsculpture (Fig. 53B, C): Juvenile shell with finely granular microsculpture, vermiform spiral threads not evident; adult shell with well-developed scratch-like microsculpture, which is filled with intritacalx deposit in fresh shells.

Protoconch (Fig. 53A, C): Translucent white; diameter *ca* 260 µm; not projecting above first teleoconch whorl, shell apex thus appearing truncated and somewhat tilted; missing or badly eroded in most specimens; surface sculptured with a fine, irregular granulation; terminal lip strongly angled above mid-whorl.

Colour: Ground colour generally greyish white to pale buff; basal spiral cords commonly marked with brown flecks; some specimens with a reddish or brown spiral band below suture and another at periphery; entire surface covered with off-white, chalky intritacalx deposit. One specimen almost entirely brownish grey, with a dark, ash-grey intritacalx. Most shells encrusted to some degree with other organisms, frequently coralline algae and bryozoans.

Dimensions: Largest NMSA specimen (E4265), length 16.0 mm, diameter 11.6 mm.

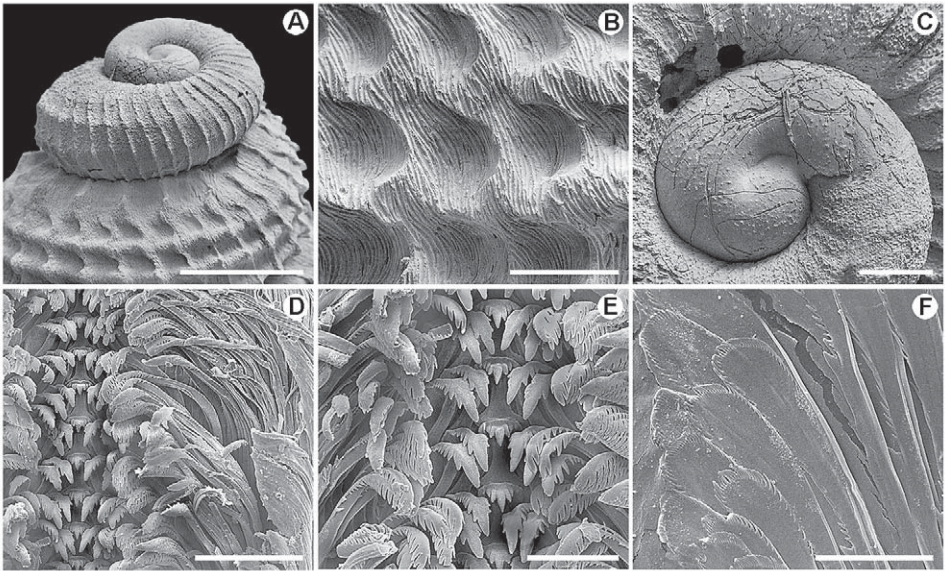

Fig. 53. *Perrinia angulifera* (A. Adams, 1853): (A) tip of spire showing truncated apex, bar = 0.5 mm; (B) adult microsculpture, bar = 200 µm; (C) protoconch with angular projection on terminal lip, bar = 100 µm; (D) radula, central field and right marginals, bar = 100 µm; (E) rachidian, lateral and inner marginal teeth, bar = 50 µm; (F) spathulate outer marginal teeth, bar = 20 µm. (A–C) off Boteler Point, KZN (NMSA E1762); (D–F) NE of Liefeldt's Rocks, KZN (NMSA E4344).

*Operculum* (Fig. 4M): Initially tightly multispiral, but whorls broadening with growth and becoming more openly multispiral.

*Radula* (Fig. 53D–F): Formula ∞+3+1+3+∞, with *ca* 60 transverse rows of teeth; lateral flanges of rachidian well developed creating a distinct hood, cusp with a strong transverse basal ridge, the apex broadly trigonal with stout denticles, a larger, lanceolate median one and 2 or 3 smaller ones on each side. Laterals overlapping extensively, their cusps trigonal and noticeably asymmetrical; central denticle largest, lateral denticles well developed on outer margin, progressively decreasing in size toward tooth shaft; inner margin with fewer denticles. Marginals numerous and slender, cusps of inner ones recurved and coarsely pectinate, outer ones spathulate distally with a feathered edge.

*External anatomy* (Figs 5B, 6E): Body white with pale brownish maculations on sides of foot and underside of epipodium, snout heavily marked (transversely) with dark brown to black. Snout expanded laterally, but not strongly so; free margin of cephalic lappets relatively coarsely divided (2–3 digits); right post-ocular peduncle well developed, arising beside base of eyestalk, somewhat flattened and with a distinct dorsal groove; right subocular tentacle not evident; left neck lobe with numerous tentacles of varying size, right lobe with finely fimbriate margin and approx. 3 tentacles in anterior half; 6 or 7 large epipodial tentacles on each side, with frequent smaller intermediary tentacles of varying size; an indistinct epipodial sense organ present at base of larger epipodial tentacles, none evident under neck lobes.

Type material: Three syntypes of *M. angulifera* A. Adams, 1853, in NHMUK (1968215), the largest is here figured and designated lectotype (Fig. 52A), length 12.9 mm, diameter 8.9 mm. Holotype of *C. pliciferus* Schepman, 1908 (Fig. 52C), in ZMAN (3.08.028). Holotype of *T. montrouzieri* Fischer, 1878 (Fig. 52B), in MHNB (Herbert 1996) and there is an '*ex auctore*' specimen in MNHN, but this has no type status.

Regional material examined (all NMSA unless indicated otherwise): KENYA: Shimoni (4.6482°S 39.3814°E), dredge 1+2, J.D. Taylor (NHMUK). MAURITIUS: off Tombeau Bay (20.1017°S 57.5025°E), -25–25 m, CSIR Water Research (L2724); RÉUNION: off Baie de St-Paul, *Marion-Dufresne* 32, st'n DC85 (21.00°S 55.25°E), -58–70 m, dredged, 1982 (MNHN); off St-Gilles-les-Bains, *Marion-Dufresne* 32, st'n DC56 (21.083°S 55.200°E), -170–225 m, dredged, 1982 (MNHN); off Souris Chaude (21.383°S 55.667°E), -65 m, hand-dredged sand, J. Drivas, 1993 (L548); Réunion, not further localized (M. Jay coll'n, MNHN). RODRIGUES: 160 miles south (21.350°S 65.867°E), *Anton Bruun* 2, st'n 124F (USNM 716607). MOZAMBIQUE: Nacala area, Fernão Veloso Bay (14.4312°S 40.7003°E), -8–10 m, x.1998, C. Fernandes (J. Rosado coll'n); 50 miles SE of Beira (20.5000°S 35.7167°E), -62 m, *Anton Bruun* 8, St'n 400C, IIOE (USNM 718524); off Lacerda lighthouse, 50 km north of Maputo (25.56167°S 32.84472°E), -50–56 m, dredged J. Rosado, v.2010 (J Rosado coll'n); off Ponta Techobanine (26.68132°S 32.95093°E), -68–75 m, dredged J. Rosado, xii.2005 (J. Rosado coll'n). SOUTH AFRICA: *KwaZulu-Natal*: off Kosi Bay (26.8916°S 32.9266°E), -51 m, sand, stones, large algae, dredged NMDP, RV *Sardinops*, st'n ZA48, 4.vi.1990 (S8959); SE of Kosi River mouth (26.9100°S 32.9217°E), living, -50 m, medium sand, algae, dredged NMDP, RV *Meiring Naude*, st'n ZA9, 7.vi.1987 (D6180, D6182); ditto (26.9167°S 32.9300°E), -65 m, sponge, gorgonians, medium sand, dredged NMDP, RV *Meiring Naude*, st'n ZA12, 7.vi.1987 (D8183); ditto (26.9217°S 32.9233°E), living, -50 m, medium sand, rubble, dredged NMDP, RV *Meiring Naude*, st'n ZA11, 7.vi.1987 (D8960); off Boteler Point (27.00°S 32.92°E), -70 m, coral rubble, dredged NMDP, RV *Meiring Naude*, st'n ZB5, 6.vi.1987 (D6382, E1762); ditto (27.013°S 32.905°E), living, -50 m, dead coral rubble, lithothamnion, dredged NMDP, RV *Meiring Naude*, st'n ZB2, 6.vi.1987 (D9209); ditto (27.013°S 32.918°E), -70 m, some coarse sand, some shell rubble, dredged NMDP, RV *Meiring Naude*, st'n ZB4, 6.vi.1987 (D7412); ditto (27.0183°S 32.9200°E), -78 m, coarse sand, dredged NMDP, RV *Meiring Naude*, st'n ZB6, 6.vi.1987 (D7476); NE of Dog Point (27.0800°S 32.8867°E), -56–57 m, sand, lithothamnion pebbles, dredged NMDP, RV *Sardinops*, st'n ZC8, 6.vi.1990 (S5072); ditto (27.08000°S 32.89167°E), living, -65 m, sand, lithothamnion pebbles, dredged NMDP, RV *Sardinops*, st'n ZC9, 7.vi.1990 (S7597); SE of Rocktail Bay (27.2017°S 32.8300°E), living, -60 m, coarse sand, dredged NMDP, RV *Sardinops*, st'n ZD9, 8.vi.1990 (S5250); NE of Liefeldt's Rocks (27.7167°S 32.6650°E), -50 m, lithothamnion, medium sand, dead coral rubble, dredged NMDP, RV *Meiring Naude*, st'n ZJ6, 9.vi.1988 (E4265); ditto (27.72000°S 32.66167°E), living, -50 m, lithothamnion, stones, some coarse sand, dredged NMDP, RV *Meiring Naude*,

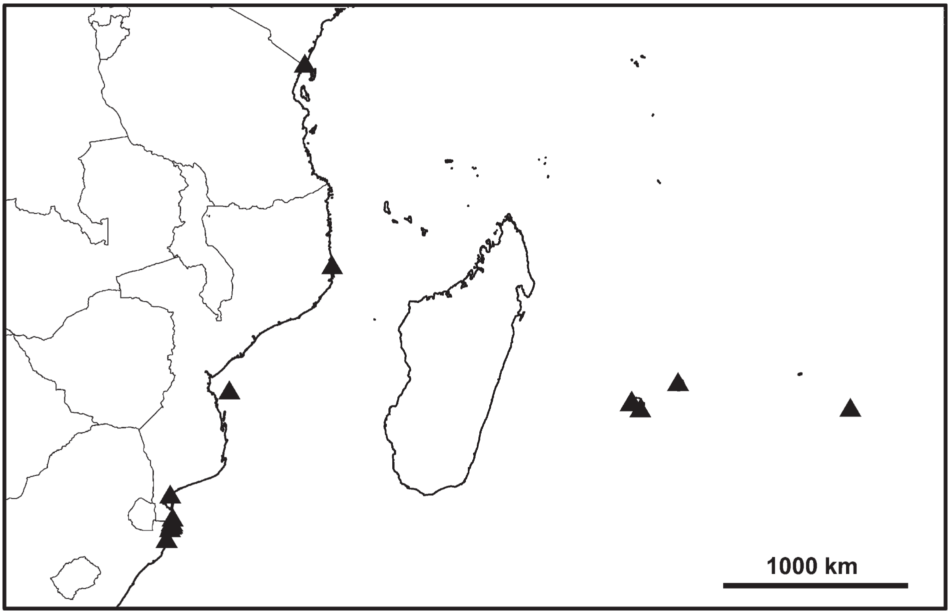

Fig. 54. Distribution of *Perrinia angulifera* in the south-western Indian Ocean. Each triangle represents one or more records.

st'n ZJ1, 8.vi.1988 (E4344); ditto (27.7230°S 32.6633°E), -50 m, medium sand with some stones, dredged NMDP, RV *Meiring Naude*, st'n ZJ5, 9.vi.1988 (E3417).

Other material examined: ARABIAN SEA: Gulf of Oman, Townsend (NMGW). ANDAMAN ISLANDS: Port Blair, Winckworth coll'n (NHMUK). NEW GUINEA: off west side of Lolorua Is., SW of Port Moresby, -13–18 m, Ponder & Colman (AMS); New Britain, J. Brazier (AMS C11849). AUSTRALIA: Flinders Passage, 7(?) fath. [-13 m] Challenger (NHMUK); Gulf of Carpentaria, 10 mls SW of Mapoon, -128 m (AMS); off Murray Is., Torres Strait, -9–15 m, C. Hedley (AMS); east of Banks Is., Torres Strait, -18 m, BMR st'n 522 (AMS); Cape York Peninsula, Albany Passage, 4–14 fath. [-7–26 m], C. Hedley (AMS); ½ ml west of North Direction Is., -36.5 m, Great Barrier Reef Exped'n, dredged, st'n 16, 1929 (AMS); 2 mls NE of west side of Gillet Cay, Swains Reef, southern Great Barrier Reef, 30–40 fath. [-55–73 m] (AMS). NEW CALEDONIA (all ORSTOM, MNHN): Secteur de Poum, st'n 1027 (20°03'S 163°51'E), -29 m; secteur de Poum, st'n 1017 (20°08'S 163°51'E), -21 m; secteur de Nouméa, st'n 56 (22°10'S 166°15'E), -11 m; secteur de Nouméa, st'n 285 (22°24'S 166°26'E), living, -19 m; secteur de Nouméa, st'n 271 (22°15'S 166°21'E), -22 m; secteur de Koumac, st'n 942 (20°37'S 164°13'E), living, -15 m.

Distribution and habitat (Fig. 54): Indo-West Pacific; from SE Asia and northern Australia, to the Andaman Islands, Maldive archipelago (Smith 1903), Mascarene Islands and the continental margin of the western Indian Ocean, from Muscat (Melvill 1928) south to northern South Africa. Off Zululand, this species was dredged, in relative abundance, amongst old coral rubble and pebbles encrusted with *Lithothamnion* growths lying on a substratum of coarse bioclastic sand, at depths of -50–80 m (living specimens -50–65 m). *Cantharidus pliciferus* was also found on a substratum described as a '*Lithothamnion* bottom' (Schepman 1908). In fully tropical areas the bathymetric range evidently extends into shallower water (to -10 m). Deep-water material from Réunion (-170–225 m) comprised only long-dead specimens that probably originated in shallower habitats on the island's steeply shelving coast.

Remarks: South-western Indian Ocean examples of this species generally have fewer (11–15), broader axial ribs than is typical (18 on last adult whorl in NHMUK types) and the axial pliculae between the spirals cords are less close-set. However, in other respects they are indistinguishable and I have little hesitation in referring them to Adams' species. Such small differences are not unexpected in material from such widely separated localities. *Cantharidus pliciferus* Schepman, 1908 from the Sulu Archipelago is simply a subadult specimen of the present species and *Tectaria montrouzieri* Fischer, 1878 from New Caledonia, is a very typical adult (Herbert 1996), albeit rather small.

The broad, opisthocline ribs of this species set it apart from all others of the genus, even those of similar size, e.g. *P. chinensis* (Sowerby, 1888) from Hong Kong (Fig. 71A, B), *P. maculata* (Brazier, 1877) from northern Australia (Fig. 71C, D) and *P. elisa* (Gould, 1849) from Singapore. Amongst local species, *P. konos* is very much smaller and *P. stellata* has a carinate and strongly stellate periphery.

### *Perrinia konos* (Barnard, 1964) **comb. n.**

Figs 4N, 55–57

*Turcica konos*: Barnard 1964: 20, fig. 2f; Kensley 1973: 44, fig. 111. Type loc.: off Umkomaas, KZN south coast, South Africa, 40 fath. [-73 m].

Description:

*Shell*: Small, elevated-trochiform to turriculate (L/D=1.26–1.50); apical angle 55–60°; teleoconch of 6–7 whorls; whorls flat-sided and peripherally angled, peripheral angle marked by a strong keel, base flattened; sutures channelled and inserted below peripheral angulation, spire thus rendered pagodaform; insertion of suture level with subperipheral spiral cord. First teleoconch whorl more or less evenly rounded and sculptured only with strong, evenly spaced, axial pliculae (14–20); peripheral cord (angulation) begins to develop during second whorl, axial pliculae become nodular at angulation; whorls more flat-sided from third whorl onward and with 2 or 3 further spiral cords, one immediately below suture and 1 or 2 between this and peripheral keel; subsutural cord with adapically pointed triangular nodules which project into sutural channel; nodules with a thin lamellate ridge running into suture; middle spiral cord(s) thinner than the other two and at most obsoletely granular where crossed by axial sculpture; peripheral cord becomes keel-like with growth and is rendered stellate in apical view by radiating triangular nodules, 13–20 on body; axial sculpture of prosocline pliculae persists throughout, but pliculae more numerous than either the subsutural or peripheral nodules; whorl surface rendered somewhat cancellate/foveolate by interaction of spiral and axial sculpture. Base with 4 (rarely 5) evenly spaced spiral cords, outer one weakly undulant, others progressively smoother toward columella; interval between peripheral and subperipheral cords deeply concave and forms suture channel in spire whorls; innermost basal spiral very close to columella; umbilicus patent in juveniles, but closed by thickened columella in adults. Aperture subcircular, somewhat flattened in parietal and columellar regions; columella (at maturity) with a bulge-like swelling at its base, rarely forming a distinct tooth; interior of outer lip with up to 11 spiral lirae running into aperture (evident only in fully mature shells), one where basal portion of lip joins columella not enlarged; outer lip prosocline, not obviously thickened; interior nacreous.

Microsculpture (Fig. 56B, C): Initial whorls lacking vermiform spiral microsculpture; later whorls with distinct scratch-like microsculpture.

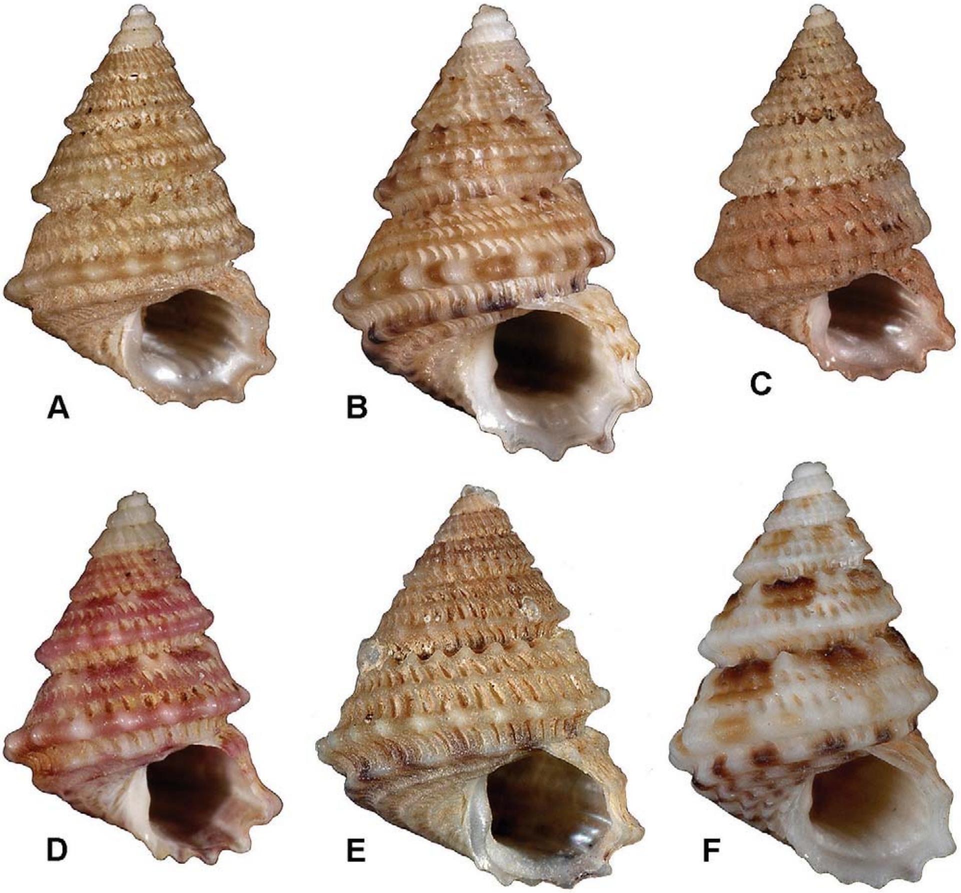

Fig. 55. *Perrinia konos* (Barnard, 1964): (A) typical specimen, off Gobey's Point, KZN, length 5.3 mm (NMSA E1440); (B) specimen with three spiral cords above peripheral keel, off Port Grosvenor, Eastern Cape, length 6.0 mm (NMSA E346); (C) specimen with well developed intritacalx deposit, NE of Gipsy Hill, KZN, length 4.9 mm (NMSA E7462); (D) pink specimen, subadult, off N'tafufu River, Eastern Cape, length 4.9 mm (NMSA E241); (E) broad specimen, Baie Narendry, northern Madagascar, length 5.3 mm (MNHN); (F) boldly patterned specimen, between Lokaro and St Luce, southern Madagascar, length 5.6 mm (MNHN).

Protoconch (Fig. 56A, C): White to translucent white, strongly exsert; diameter 260–280 µm; apical beak scarcely evident; surface evidently smooth; terminal lip roundly angled between mid-whorl and adapical suture.

Colour: Ground colour yellowish white to pale orange, commonly buff; frequently with spots and blotches of a deeper shade beneath suture and at periphery; basal cords often spotted with dark brown; occasional specimens almost entirely pink with deeper pink markings; intritacalx deposit generally cream-yellow, only visible in the freshest specimens; shell frequently encrusted with bryozoans, sponges, tubicolous worms and encrusting Foraminifera.

Dimensions: Attaining length 6.0 mm, diameter 4.2 mm in South Africa, but reaching length 6.2 mm, diameter 4.9 mm in northern Madagascar (MNHN).

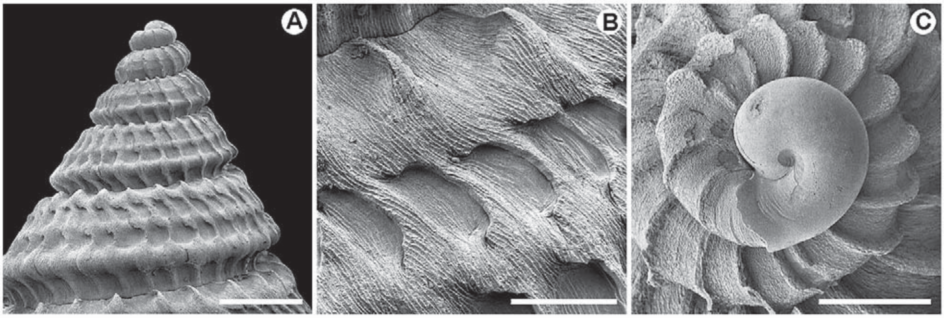

Fig. 56. *Perrinia konos* (Barnard, 1964): (A) apical whorls showing exsert protoconch, off Kwanyana River, Eastern Cape, bar = 0.5 mm (NMSA C5331); (B) adult microsculpture, off Kwanyana River, Eastern Cape, bar = 200 µm (NMSA C5331); (C) protoconch, off Umzinto, KZN, bar = 200 µm (NMSA D5426).

*Operculum* (Fig. 4N): Initially tightly multispiral, but whorls broadening with growth and becoming more openly multispiral.

*Radula*: Formula ∞+3+1+3+∞, with *ca* 70 transverse rows of teeth; similar to that of *P. angulifera* in that the cusp of rachidian is strongly dentate, with a sharply pointed central denticle and several similar but smaller lateral denticles on each side; laterals with a sharply pointed central cusp; marginals very numerous and fine.

*External anatomy*: Little preserved material available, but evidently similar to that of *P. angulifera*.

Type material (four syntypes of *Turcica konos* Barnard, 1964, in SAMC): SOUTH AFRICA: *KwaZulu-Natal*: off Umkomaas, 40 fath. [-73 m] (A9257, 2 adult, 1 immature and 1 broken).

Material examined (all NMSA unless indicated otherwise): MADAGASCAR: West of Cap d'Ambre (12.133°S 48.933°E), -238–249 m, Campagne *Miriky*, dredged, st'n DW3196, 28.vi.2009 (MNHN); west of Nosy Be (13.417°S 47.950°E), -71–158 m, Campagne *Miriky*, dredged, st'n DW3230, 3.vii.2009 (MNHN); in front of Baie Narendry (14.483°S 47.450°E), living, -48–139 m, Campagne *Miriky*, dredged, st'n DW3238, 6.vii.2009 (MNHN); Secteur de Manantenina (24.38333°S 47.53333°E), -154–168 m, Exped'n Atimo Vatae, dredged *Nosy Be 11*, st'n DW3522, 1.v.2010 (MNHN); ditto (24.38333°S 47.51667°E), -200–220 m, Exped'n Atimo Vatae, dredged *Nosy Be 11*, st'n DW3523, 1.v.2010 (MNHN); north of Sainte Luce (24.59833°S 47.53500°E), -80–86 m, Exped'n Atimo Vatae, dredged *Nosy Be 11*, st'n DW3530, 2.v.2010 (MNHN); ditto (24.6567°S 47.5283°E), -86–87 m, Exped'n Atimo Vatae, dredged *Nosy Be 11*, st'n DW3532, 2.v.2010 (MNHN); between Lokaro & Ste Luce (24.8450°S 47.4783°E), -99–101 m, Exped'n Atimo Vatae, dredged *Nosy Be 11*, st'n DW3518, 30.iv.2010 (MNHN); ditto (24.865°S 47.467°E), -80–83 m, Exped'n Atimo Vatae, dredged *Nosy Be 11*, st'n DW3519, 30.iv.2010 (MNHN); south east of Faux-Cap (25.78333°S 46.0333°E), -133–178 m, Exped'n Atimo Vatae, dredged *Nosy Be 11*, st'n CP3620, 15.v.2010 (MNHN). MOZAMBIQUE: NE of Maputo, -65 m, dredged J. Rosado, (D. Slater coll'n); Maputo transect, Campagne Mainbaza, RV *Vizconde de Eza*, dredged, st'n CP3130 (23.883°S 33.117°E), living, -112–127 m, 9.iv.2009 (MNHN); off Maputo, -55–100 m, dredged J. Rosado, 2008 (D. Slater coll'n); off Inhaca Is (26.020°S 33.066°E) -75–125 m, dredged J. Rosado, 2006 (D. Slater coll'n); off Ponta Techobanine (26.68132°S 32.95093°E), -60–115 m, dredged J. Rosado (D. Slater coll'n). SOUTH AFRICA: *KwaZulu-Natal*: off Kosi River Mouth (26.9100°S 32.9433°E), -75 m, coral rubble, sandstone, marine growths, dredged NMDP, RV *Meiring Naude*, st'n ZA13, 7.vi.1987 (D8999); off Black Rock (27.165°S 32.865°E), -150 m, sand, dredged NMDP, RV *Sardinops*, st'n ZCC2, 7.vi.1990 (S5096); off Rocktail Bay (27.1850°S 32.8483°E), -100 m, sand, dredged NMDP, RV *Sardinops*, st'n ZD4, 7.vi.1990 (S5172); off Rocktail Bay (27.19°S 32.85°E), -100 m, sandstone rubble, dredged NMDP, RV *Meiring Naude*, st'n ZD1, 4.vi.1987 (E1419); off Lala Neck (27.2267°S 32.8217°E), -75 m, coarse sand, sandstone, coral, dredged NMDP, RV *Sardinops*, st'n ZDD4, 8.vi.1990 (S3771); off Gobey's Point (27.430°S 32.742°E), living, -55–100 m, sand, shell rubble, dredged NMDP, RV *Meiring Naude*, st'n ZG2, 3.vi.1987 (E1440); Sodwana Bay (27.533°S 32.683°E), -100 m, dredged (A5803); off Jesser Point (27.553°S 32.713°E), living, -85 m, sponge, coral rubble, dredged NMDP, RV *Meiring Naude*, st'n ZH4, 3.vi.1987 (E2936); NE of Gipsy Hill (27.753°S 32.663°E), -110 m, sponge,

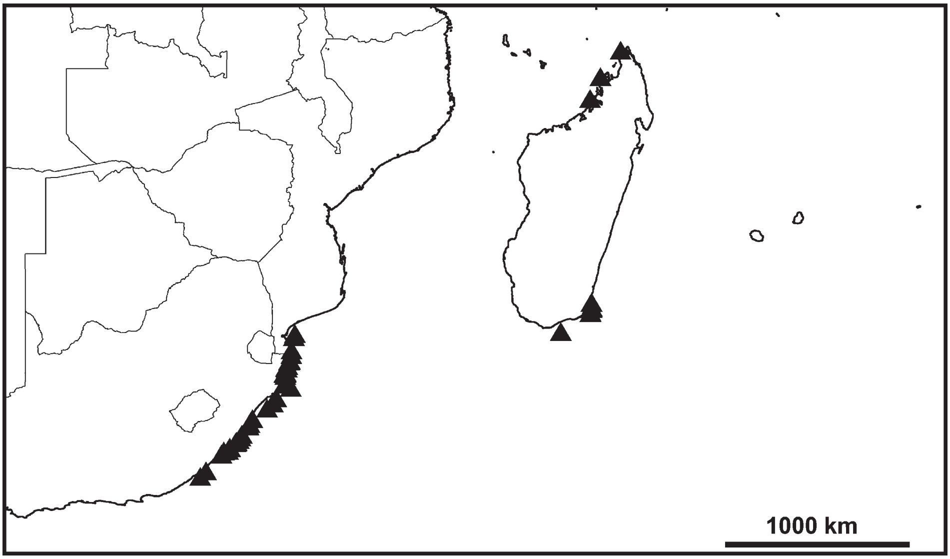

Fig. 57. Distribution of *Perrinia konos*. Each triangle represents one or more records.

stones, dredged NMDP, RV *Meiring Naude*, st'n ZK4, 8.vi.1988 (E7473); ditto (27.773°S 32.657°E), -63–70 m, sand, sandstone, growths, dredged NMDP, RV *Sardinops*, st'n ZK25, 9.vi.1990 (S3476); ditto (27.777°S 32.653°E), -74–87 m, sandstone rocks, slightly muddy sand, dredged NMDP, RV *Sardinops*, st'n ZK23, 9.vi.1990 (E7462, S6370); Leadsman Shoal (27.800°S; 32.616°E), living, -100 m, dredged A.D. Connell, iv.1980 (B4059); off Gipsy Hill (27.8117°S 32.6570°E), -100–125 m, broken shell, dredged NMDP, RV *Meiring Naude*, st'n ZK9, 11.vi.1988 (E3245); ditto (27.828°S 32.637°E), -47–50 m, fine sand, dredged NMDP, RV *Meiring Naude*, st'n ZK1, 8.vi.1988 (S1136); NE of Leven Point (27.917°S 32.647°E), -250 m, coarse sand, dredged NMDP, RV *Meiring Naude*, st'n ZL5, 9.vi.1988 (S1141); SE of Cape Vidal (28.320°S 32.607°E), -110 m, sponge rubble, dredged NMDP, RV *Meiring Naude*, ZM5, 10.vi.1988 (E4907); off St Lucia Lighthouse (28.500°S 32.917°E), -100 m, mud & pebbles, dredged (A5716); Port Durnford–Richard's Bay (29.007°S 32.200°E), -152 m, mud and stones, dredged NMDP, RV *Meiring Naude*, st'n ZQ7, 13.vi.1988 (V3922); off Glenton Reef (29.245°S 32.037°E), -200–210 m, sandy mud, dredged NMDP, RV *Meiring Naude*, st'n ZRR9, 18.vi.1989 (S459); SE of Sheffield Beach (29.5050°S 31.7617°E), -100–105 m, glutinous grey mud, dredged NMDP, RV *Meiring Naude*, st'n XX139, 14.vi.1988 (E5033); off Umlaas Canal (30.018°S 31.053°E), -150 m, coarse sand, numerous spatangoids, pebbles, dredged NMDP, RV *Meiring Naude*, st'n XX70, 9.viii.1985 (E7598); SE of Green Point (30.250°S 30.905°E), living, -100 m, fine sand & rubble, dredged NMDP, RV *Meiring Naude*, st'n XX92, 8.vii.1986 (D5989); off Umzinto (30.36°S 30.85°E), -84 m, dredged NMDP, RV *Meiring Naude*, st'n X2, 15.vii.1982 (D5426); off Park Rynie (30.375°S 30.855°E), -136 m, sponge rubble, dredged NMDP, RV *Meiring Naude*, 5.iii.1981 (B3889); ditto, living, -110 m, sponge rubble, dredged R. Kilburn, 2.iii.1981 (W7457); ditto, 100 m, sand and sponge rubble, dredged NMDP, RV *Meiring Naude*, 4.iii.1981 (B3719); off Port Shepstone (30.775°S 30.538°E), -70 m, eroded shell & rubble, dredged NMDP, RV *Meiring Naude*, 4.iii.1981 (B3655); off Margate (30.91°S 30.47°E), -100–110 m, sponge, dredged NMDP, RV *Meiring Naude*, st'n X6, 22,vii.1982 (B8786); off Trafalgar (31.020°S 30.382°E), -120 m, sand, sponge, dredged NMDP, RV *Meiring Naude*, st'n X4, 22.vii.1982 (B8866); off Mpahlana River (31.118°S 30.280°E), living, -100 m, sponge rubble, dredged NMDP, RV *Meiring Naude*, st'n XX3, 15.vi.1983 (C5248); between Mpahlana & Umyameni rivers (31.14°S 30.27°E), -100 m, sponge rubble, dredged NMDP, RV *Meiring Naude*, st'n XX8, 15.vi.1983 (C5378). *Eastern Cape*: off Mtamvuna River (31.1483°S; 30.2617°E), -111 m, sponge, dredged NMDP, RV *Meiring Naude*, st'n A14, 18.viii.1981 (E278, E870); ditto (31.15°S 30.27°E), -137 m, rocks, sponge, dredged NMDP, RV *Meiring Naude*, st'n A16, 18.viii.1981 (E6994); off Kwanyana River (31.183°S 30.223°E), -100 m, sponge rubble, dredged NMDP, RV *Meiring Naude*, st'n XX10, 15.vi.1983 (C5331,C5484); off Port Grosvenor (31.4083°S 29.9500°E), -80 m, lithothamnion sheets, dredged NMDP, RV *Meiring Naude*, st'n D20, 16.viii.1981 (E217, E6978); ditto (31.41°S 29.95°E), living, -80 m, worn coral nodules, dredged NMDP, RV *Meiring Naude*, st'n D17, 16.viii.1981 (E177, E346); ditto (31.4360°S 29.9516°E), -100–115 m, sand, some mud, solitary coral, shells, dredged NMDP, RV *Meiring Naude*, st'n D3, viii.1981 (C1333); off Mbotyi (31.550°S 29.863°E), -200 m, sandstone slabs, coarse sand, dredged NMDP, RV *Meiring Naude*, st'n F13, 4.vii.1986 (C9755); off N'tafufu River (31.578°S 29.662°E), -50 m, mud, sand, dredged NMDP, RV *Meiring Naude*, st'n H6, 14.viii.1981 (E241); off Mgazi River (31.738°S 29.537°E), -250 m, muddy sand, dredged NMDP, RV *Meiring Naude*, st'n J11, 4.vii.1985 (E7423); off Qora River (32.557°S 28.800°E), -100 m, coarse sand, some sponge rubble, dredged NMDP, RV *Meiring Naude*, st'n U6, 14.vi.1983 (C5189); off Kei River (32.822°S 28.520°E), -138 m, coarse sand, dredged NMDP, RV *Meiring Naude*, st'n Z4, 13.vi.1983 (C5116).

Distribution and habitat (Fig. 57): South-western Indian Ocean; from northern Madagascar to Mozambique, extending south to the Great Kei River, Eastern Cape, South Africa; -47–250 m, living specimens -55–110 m, on varied substrata, but usually associated with sponge and coral rubble.

Remarks: Distinctive amongst local species on account of its small size and turriculate profile. Specimens from Madagascar often rather broad and with a more coarsely stellate peripheral cord. *Perrinia angulifera* (A. Adams, 1853) has a similar elevated-trochiform spire, but is less pagodaform and much larger (length up to 16 mm). The most similar sympatric species is *P. stellata* (A. Adams, 1864), but that also generally attains a larger size (length up to 9.6 mm in south-eastern Africa) and has a much more strongly stellate periphery and stronger basal cords.

Schepman (1908) described a number of new species of this genus (placed as a subgenus of *Calliostoma*) from Indonesia, two of which, *P. squamocarinata* and *P. nigromaculata*, resemble the present taxon. *P. squamocarinata* (syntype examined, ZMAN 3.08.084, Fig. 71E, F) (additional figures provided by Poppe *et al*. (2006) and Poppe & Tagaro (2008)) differs in having stronger granules on the spiral cords above the peripheral keel on the last adult whorl, and the base retains an umbilicus (albeit small) and has five granular spiral cords (usually only four in *P. konos*) with strong axial pliculae in their intervals. *P. nigromaculata* (holotype examined, ZMAN 3.08.087, figured by Poppe *et al*. 2006) is less strongly keeled than *P. konos* and is larger (length *ca* 10 mm), has finer, more numerous spiral cords and a much more prominent tooth at the base of the columella (additional figures provided by Tsuchida & Ikebe (1990), Tsuchida & Kurozumi (1992), Poppe *et al*. (2006) and Poppe & Tagaro (2008)). Also from the Philippines, the recently described *Perrinia cecileae* Poppe, Tagaro & Dekker, 2006 has a similar elevated conical profile and is of a similar size, but it has more numerous spiral cords above the periphery, a weaker peripheral keel on the spire whorls, and much stronger columella teeth. *Turcica* (*Perrinia*) *morrisoni* Ladd, 1966 from the Miocene and Recent of the Marshall Islands is more depressed, has a more granular sculpture and fewer, stronger peripheral stellations.

## *Perrinia stellata* (A. Adams, 1864)

### Figs 4O, 58–60

*Turcica stellata*: A. Adams 1864*a*: 508; Pilsbry 1890 in 1889–90: 418, pl. 67, fig. 77; Yen 1942: 177, pl. 11, fig. 11 (holotype); Mastaller 1979: 31; Smythe 1979: 64; *idem* 1882: 39; Glayzer *et al*. 1984: 318. Type loc.: China Seas (Cuming) [erroneous, here emended to the Gulf of Suez].

*Tectaria armata*: Issel 1869: 192, 289, pl. 2, fig. 7; Moazzo 1939: 183. Type loc.: Gulf of Suez, Red Sea.

*Euchelus* (*Perrinia*) *stellata*: MacAndrew 1870: 443.

*Turcica* (*Perrinia*) *stellata*: Melvill & Standen 1901: 351; Tomlin 1927: 298 [=*Tectaria armata* Issel, 1869]; Melvill 1928: 98; Lamy 1938: 82, fig. 9; Biggs 1973: 350; Kilburn 1977: 176.

*Calliostoma stellatum*: Hidalgo 1904–5: 255.

*Tectarius armatus*: Sturany 1903: 263, 278.

*Turcica* (*Turcica*) *stellata*: Bisacchi 1931: 182.

*Perrinia stellata*: Kendall & Skipwith 1969: 855; Bosch *et al*. 1995: 33, fig. 28; Hoenselaar & Dekker 1998: 199; Rusmore-Villaume 2008: 20; Zuschin *et al*. 2009: 99, pl. 9, figs 5–7; Bandel 2010: 470, fig. 15d–f.

## Description:

*Shell*: Elevated-trochiform to turriculate (L/D=1.10–1.65); apical angle 42–63°; teleoconch of up to 8 whorls; whorls flat-sided and periphery angular, marked by strong, stellate, keel-like spiral cord, below which is a distinct supra-sutural sulcus. First teleoconch whorl rounded and sculptured only with close-set, curved, axial pliculae (±35); weak spiral cords develop toward end of second whorl; supra-sutural cord rapidly strengthening during third and subsequent whorls, and developing characteristic squamose, stellate projections; projections becoming fewer and larger with growth (±15 on last adult whorl); uppermost cord also strengthens, but to a lesser extent and becomes coronated by apically orientated, scale-like granules; these 1.5–2 times as numerous as peripheral projections; interval between peripheral cord/keel and abapical suture progressively deeper and more channelled with growth; development of remaining spirals between adapical suture and periphery variable, sometimes distinct, sometimes obsolete; axial sculpture becoming less obvious with growth; apical whorls (not first) somewhat cancellate, becoming more foveolate with elongate D-shaped pits on later whorls; pliculae in supra-sutural sulcus

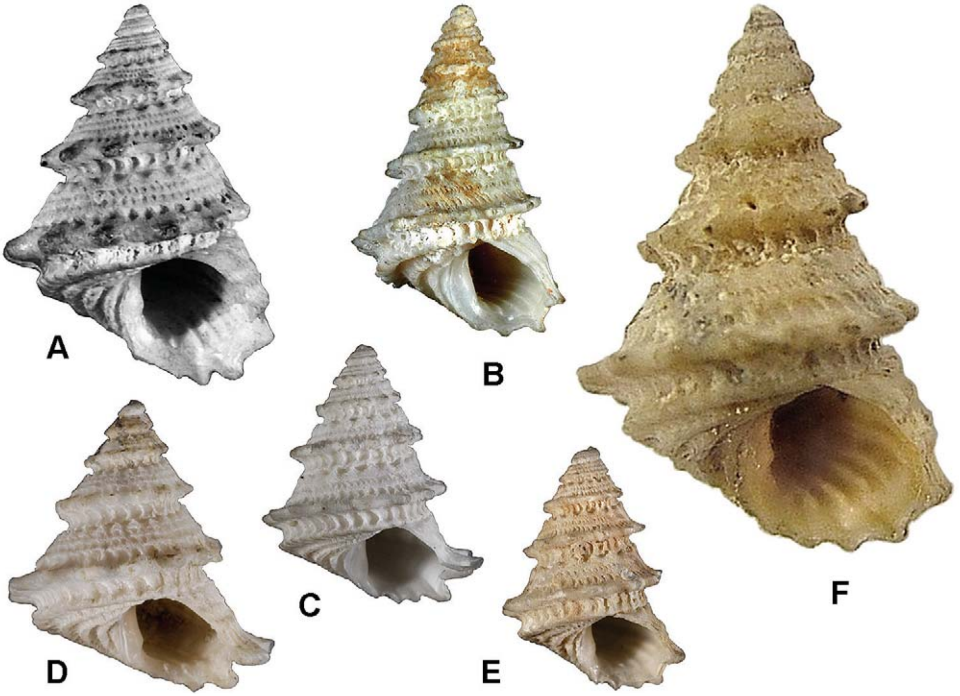

Fig. 58. *Perrinia stellata* (A. Adams, 1864): (A) holotype of *Turcica stellata* A. Adams, 1864, length 10.9 mm (NHMUK 1968214); (B) narrow specimen, NE of Liefeldt's Rocks, KZN, length 9.6 mm (NMSA E4264); (C) subadult specimen, Mozambique Is., length 8.0 mm (NMSA G7930); (D) broad specimen, Hurghada, Egypt, length 8.25 mm (NMSA L376); (E) small adult specimen, off Mission Rocks, KZN, length 6.9 mm (NMSA E7530); (F) holotype of *Tectaria armata* Issel, 1869, length 15.5 mm (MCSNG, photo courtesy of Maria Tavano).

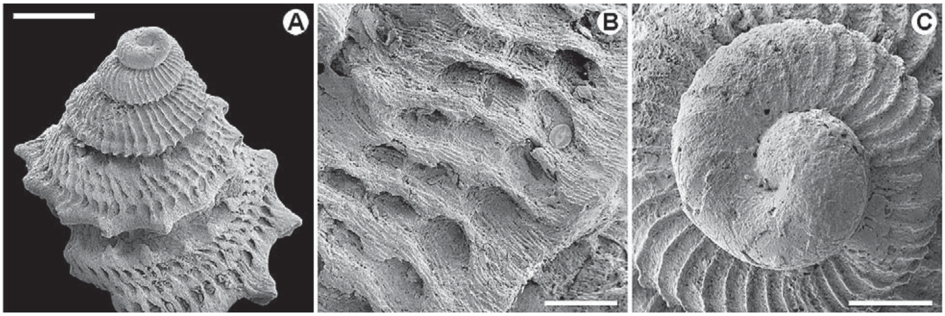

Fig. 59. *Perrinia stellata* (A. Adams, 1864), off Mission Rocks, KZN (NMSA E7530): (A) juvenile shell whorls showing exsert protoconch and close-set axial pliculae on earliest teleoconch whorls, bar = 0.5 mm; (B) adult microsculpture, bar = 100 µm; (C) protoconch, bar = 100 µm.

usually stronger and less close-set than those above peripheral keel. Base with 4 well-defined spiral cords and a fifth adjacent to columella; outermost cord strongest and frequently set with scale-like granules, in large specimens the other basal cords may also be somewhat granular; umbilicus closed. Peristome oblique; aperture D-shaped; columella more or less straight, a single weak tooth or rounded bulge present at its base in mature specimens; outer lip strongly notched at ends of peripheral and basal cords, particularly in subadults; interior of outer lip weakly thickened with in-running ridges at maturity, but most local material somewhat subadult in this respect; interior of aperture nacreous, angled beneath peripheral cord.

Microsculpture (Fig. 59B, C): Initial whorls somewhat worn in all available material, but evidently lacking vermiform spiral microsculpture; later whorls with distinct scratch-like microsculpture.

Protoconch (Fig. 59A, C): Apex missing or heavily encrusted in most specimens; protoconch remaining only in some juveniles and rather worn even in these; translucent white; diameter *ca* 260 µm; moderately exsert; terminal lip roundly angled between mid-whorl and apical suture; superficial sculpture eroded in all available material.

Colour: Shell milky-white, fresh specimens with a cream to dirty buff intritacalx deposit, often with broad, dark greyish axial bands, particularly in juveniles. Many specimens with heavy, whitish or pinkish coralline encrustation.

Dimensions: Largest specimen (holotype of *Tectaria armata*), length 15.5 mm. South-east African specimens develop mature apertural features at a smaller size than those from the north-western Indian Ocean and Red Sea, and never attain such a large size (largest southern African specimen, length 9.6 mm).

*Operculum* (Fig. 4O): Initially tightly multispiral, but whorls broadening with growth and becoming more openly multispiral, although somewhat less so than in *P. angulifera* and *P. konos*.

*Radula*: Unknown.

*External anatomy*: Like that of *P. angulifera*; only small specimens available, but no clear differences are apparent.

Type material: Holotype of *Turcica stellata* A. Adams, 1864 (Fig. 58A), in NHMUK (1968214). Holotype of *Tectaria armata* Issel, 1869 (Fig. 58F), in MCSNG.

Regional material examined (all NMSA unless indicated otherwise): KENYA: Shimoni (4.6482°S 39.3814°E), dredge 1+2, J.D. Taylor (NHMUK); ditto, dredge 6, J.D. Taylor (NHMUK); ditto (4.6536°S 39.3799°E), dredged in channel between mainland and Wasini Is., <12 fath. [-22 m], coral sand, J.D. Taylor (NHMUK); Kichangani, Shimoni, from broken fish traps, J.D. Taylor (NHMUK). TANZANIA: Entrance to Dar-es-Salaam harbour, -7.3 m, W. Rudman (AMS). MADAGASCAR: Banc du Leven, NW of Madagascar (12.533°S 47.667°E), -35–150 m, Benthedi Exped'n, st'n 5, dredged, 1977 (MNHN). MOZAMBIQUE: Mozambique Is. (15.03°S 40.73°E), R. Kilburn, ix.1974 (G7930); Bazaruto Archipelago, 0.5 miles west of Santa Carolina Is. (21.619°S 35.332°E), 3 fath. [-5.5 m], sand and shell debris, dredged, P. & E. Roscoe, 8.i.1976 (G7096); off Ponta da Barra lighthouse, 'Office Reef' (23.7869°S 35.5410°E), -24 m, dived, xi.2003 (D. Slater coll'n); off Lacerda Lighthouse (25.56167°S 32.84472°E), -52–55 m, dredged, vi.2010 (J. Rosado coll'n); NE of Maputo, -65 m, dredged J. Rosado, ii.2010 (D. Slater coll'n); off Ponta Techobanine (26.68132°S 32.95093°E), -60 m, dredged J. Rosado, xii.2005 (D. Slater coll'n). SOUTH AFRICA: *KwaZulu-Natal*: off Kosi Bay (26.905°S 32.925°E), living, -45 m, sand, stones and large algae, dredged NMDP, RV *Sardinops*, st'n ZA49, 4.vi.1990 (S8937); Kosi Bay, main reef, 1–4 km south of estuary mouth (26.9210°S 32.8861°E), -18 m, underwater pump, D. Herbert & K. Bloem, 6.v.1990 (S2260); ditto, living, -20–22 m, underwater pump, D. Herbert & K. Bloem, 5.v.1990 (S1985); SE of Kosi River Mouth (26.9217°S 32.9183°E), living, -50 m, algae, shells, dredged NMDP, RV *Meiring Naude*, st'n ZA20, 8.vi.1987 (E1364); off Boteler Point (27.0083°S 32.9117°E), -50 m, dead coral rubble and lithothamnion, dredged NMDP, RV *Meiring Naude*, st'n ZB7, 6.vi.1987 (D7437); off Hully Point (27.3367°S 32.7700°E), -30–40 m, fine muddy sand, dredged NMDP, RV *Meiring Naude*, st'n ZF7, 5.vi.1987 (E2904); off Sodwana Bay (27.553°S 32.686°E), -50 m, shell and coral sand with foraminiferans, dredged CSIR Water Research (A5849); ditto, -46 m, sediment at base of drop-off in canyon, dredged UND Marine Geoscience Unit, 7.xi.1992 (V2629); NE of Liefeldt's Rocks (27.7167°S 32.6650°E), -50 m, lithothamnion, medium sand, dead coral rubble, dredged NMDP, RV *Meiring Naude*, st'n ZJ6, 9.vi.1988 (E4264); SE of Mission Rocks (28.2917°S 32.5433°E), -50 m, old coral rubble, lithothamnion, dredged NMDP, RV *Meiring Naude*, st'n ZN1, 10.vi.1988 (E7350); Aliwal Shoal, off Scottburgh (30.2833°S 30.8333°E), *ca* -14 m, underwater pump, D. Herbert, 2.vi.1991 (S8689); Lander's Reef, off Park Rynie (30.3333°S 30.8166°E), -34 m, sand, D. Herbert, 2.vi.1991 (S6010).

Other material examined: PERSIAN GULF: Khor-al-Bazm, Abu Dhabi, H.E.J. Biggs (NMSA G6968 and NHMUK); Dabai [Dubai] R. Winckworth (NHMUK). GULF OF OMAN: Jask, Iran, R. Winckworth (NHMUK). PAKISTAN: Mekran Coast, V.W. MacAndrew (NHMUK). RED SEA: Suez, J.J. Walker and R. MacAndrew (NHMUK); Suez Canal, living, Cambridge University Exped'n (NHMUK 1928.3.30.236); Great Bitter Lake, Suez, living, dredged at -9 m, muddy sediment with coarse sand covered thickly by *Sargassum*, C. Beets (H. Dekker coll'n, large specimens); Nuweiba, Sinai, beach, J. Wise (AMS); Eilat, north beach, H. Kurutz & J. Wise (AMS); Gulf of Aqaba, Dahab, south side of Ras el Kura, sand beach, coral reef, reef flat (H. Dekker coll'n); Hurghada, Egypt, R. Kilburn (NMSA L376); 16 km S of Hurghada, Egypt, sandy beach stones, dead coral, coral reef (H. Dekker coll'n). GULF OF ADEN: Aden, H. Burnup coll'n (NMSA G4296).

Distribution and habitat (Fig. 60): Persian Gulf, Gulf of Oman, Arabian Sea, Red Sea, Suez Canal and East Africa south to the KwaZulu-Natal south coast (Scottburgh area); living material collected from -18–50 m in South Africa, but probably also occurring in shallower water in truly tropical areas; available data on habitat preferences is inconclusive. A record from Zambales in the Philippines (Hidalgo 1904–05) requires confirmation.

Remarks: A characteristic species though somewhat variable in size and shell proportions. The only local species with which it might be confused is *P. konos*, but that species is smaller, never has such strongly developed peripheral projections, has weaker basal cords and more widely spaced axial pliculae on the apical whorls. *Turcica* (*Perrinia*) *morrisoni* Ladd, 1966 from the Marshall Islands, is smaller, less elevated and has much more obvious dentition inside the outer lip.

Tomlin (1927) followed by Lamy (1938) synonymised *Tectaria armata* Issel, 1869 from the Red Sea, with the present species. The figure of the holotype here provided (Fig. 58F) indicates that this was fully justified. Tomlin (1927) also questioned the validity of the original Cumingian locality data, China Seas. This is a notoriously vague locality which should be rejected in view of the known inaccuracy of the provenance attached

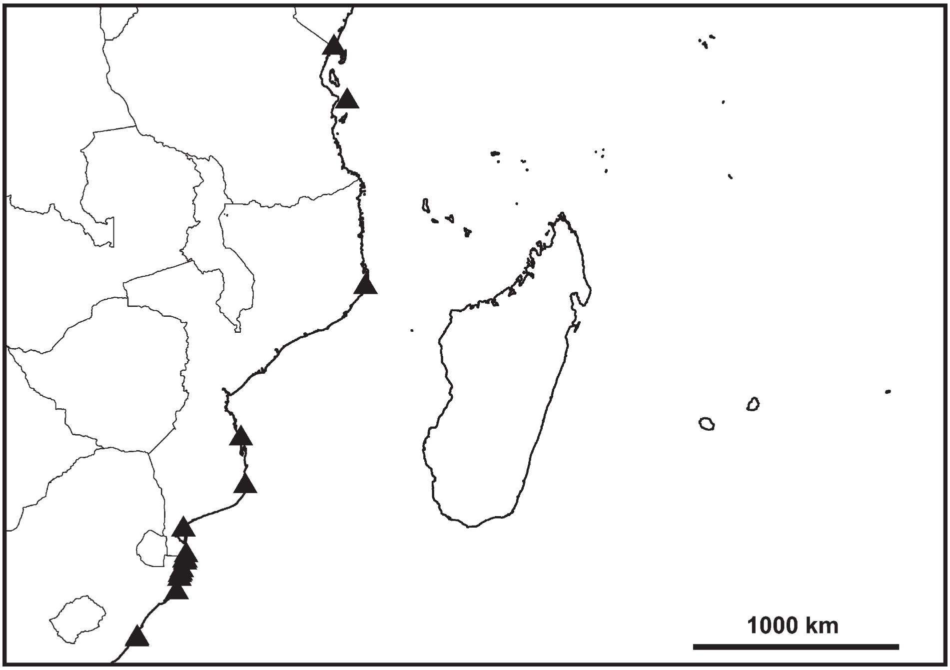

Fig. 60. Distribution of *Perrinia stellata* in the south-western Indian Ocean. Each triangle represents one or more records.

to much Cuming material. With the exception of one unconfirmed record from the Philippines (Hidalgo 1904–05), the species has been recorded subsequently only from the western Indian Ocean. I here emend the type locality to be the Gulf of Suez.

### Genus **Pholidotrope** gen. n.

Etymology: From Greek *pholidotos* (scaly) and *trope* (a turn); in reference to the scale-like sculpture on the spiral cords. Gender feminine.

Type species: *Pholidotrope gloriosa* sp. n.

Diagnosis: Shell small, profile conical with narrowly indented suture; suture level with subperipheral cord; sculpture coarsely cancellate with scale-like projections on spiral cords; columella with a single basal tooth; interior of outer lip thickened and set with ridge-like denticles, that nearest columella largest and separated from basal columella tooth by a U-shaped notch; denticles do not extend into aperture as in-running ridges; umbilical and parietal region covered by glossy inductural callus shield; aperture obliquely tangential to base of last adult whorl; outer lip with low subterminal external varix; protoconch exsert.

Remarks: *Pholidotrope* resembles *Clypeostoma* in possessing a well developed basal callus shield, but differs in being smaller, having a more conical profile, coarser sculpture, only one tooth on the columella and a subterminal external varix behind the outer lip. It also resembles *Mirachelus* Woodring, 1928 from the western Atlantic and eastern Pacific, but species of that genus lack an expanded basal callus and a subterminal external labral varix. *Perrinia* likewise lacks both these features, and in addition its aperture is spirally corded within and the dentition at the base of the columella is weaker.

### **Pholidotrope gloriosa** sp. n.

Figs 61, 62

Etymology: From Latin *gloriosa* (famous, glorious); in reference to Îles Glorieuses, near which the type material was collected.

Description:

*Shell*: Trochiform, small, spire conical, base somewhat flattened (L/D=1.18); teleoconch of 5.5 whorls; initial whorls rounded, becoming more flat-sided with growth; suture narrowly indented; sculpture of spiral cords and lamellate axial pliculae; first whorl sculptured only by relatively widely spaced axial pliculae (13), second whorl with 16 axial pliculae and 2 developing spiral cords; third whorl with 17 axial pliculae and a third spiral cord developing at shoulder; fourth and fifth whorls with 3 strong spiral cords and 18 and 19 axial pliculae respectively; cords and pliculae subequal in strength, their intersections produced into scale-like nodules, those on shoulder cord somewhat more rounded; suture level with subperipheral cord; cord intervals wider than cords themselves, that between peripheral and subperipheral cord deep. Base with 4 spiral cords, progressively weaker toward centre; umbilicus narrowly patent in juvenile, but umbilical and parietal regions covered by a thin, smooth inductural callus spreading from aperture at maturity. Peristome markedly oblique, more or less in one tangential plane; aperture D-shaped; columella more or less straight, but with a distinct, roundly trigonal tooth near its base; outer lip internally thickened, its edge flaring outward; inner thickening with 10 ridge-like denticles, that nearest columella largest, creating a U-shaped notch between it and columella tooth; interior of aperture nacreous, labral denticles not extending internally as in-running spiral ridges; exterior of outer lip subterminally thickened by a low collabral varix.

Microsculpture (Fig. 62A, B): Early whorls with close-set, microscopic granules, vermiform spiral threads not evident; fine, prosocline, scratch-like marks on later whorls.

Protoconch (Fig. 62C): White, globose and distinctly exsert, diameter *ca* 280 μm; surface worn, but with evidence of a fine, flocculent microsculpture; terminal lip convex.

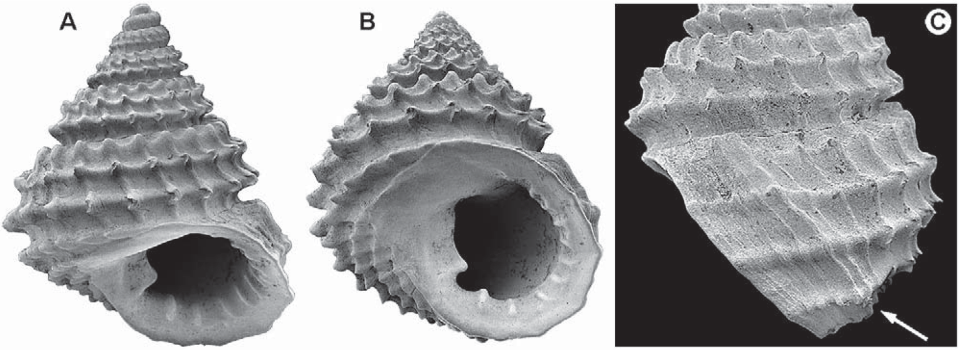

Fig. 61. *Pholidotrope gloriosa* sp. n., holotype (MNHN): (A) apertural view, length 4.7 mm; (B) oblique basal view into aperture; (C) side view showing subterminal external varix (arrow).

Fig. 62. *Pholidotrope gloriosa* sp. n., holotype: (A) granular juvenile microsculpture; (B) fine scratch-like microsculpture on last adult whorl; (C) protoconch. Bars all = 100 µm.

Colour: White.

Dimensions: Holotype, length 4.7 mm, diameter 3.9 mm.

*Operculum, radula and external anatomy*: Unknown.

Holotype: MADAGASCAR: NW of Madagascar, west of Banc du Leven (12.53°S 47.67°E), -35–150 m, Benthedi Exped'n, st'n 5, dredged, 1977 (MNHN 24656).

Paratype: MADAGASCAR: NW of Madagascar, west of Îles Glorieuses (11.487°S 47.303°E), -250 m, rock dredge, Benthedi Exped'n, st'n 8, dredged, 19.iii.1977 (MNHN 24657).

Distribution and habitat: Known only from off north-western Madagascar, -35–250 m, presumably on rocky substrata.

Remarks: The small size and conical profile of *Pholidotrope gloriosa* renders it distinctive amongst south-western Indian Ocean chilodontids. The only similar species, *Perrinia konos*, is more elevated, less coarsely sculptured and has less well-developed dentition at the base of the columella.

## Genus *Granata* Cotton, 1957

*Granata*: Cotton 1957: 126. Type species: *Stomatella imbricata* Lamarck, 1816, by original designation.

Nomenclatural remarks: Cotton (1957), believing *Stomatella auricula* Lamarck, 1816 to be the type species of *Stomatella* Lamarck, 1816[3], proposed a new generic taxon, *Granata*, for *Stomatella imbricata* Lamarck, 1816. However, there have been differing opinions concerning the type species designation for *Stomatella*. Early workers such as Thiele (1924, 1929) and Wenz (1938), following Gray (1847) and Pilsbry (1890 in 1890–91), believed it to be *S. imbricata* and, recognising the true affinities of that species, placed *Stomatella* near *Euchelus* and *Danilia*. In contrast, most recent authors (e.g. Keen 1960; Hickman & McLean 1990) have followed Cotton (1957) who observed that Anton had designated *Stomatella auricula* as the type species of *Stomatella*, in his

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[3] Although Lamarck (1816) is traditionally cited as the author of *Stomatella*, the genus has recently been credited to Bowdich (1822) (Bouchet & Rocroi 2005). This stems from the fact that Lamarck's plate of *Stomatia* and *Stomatella* in his *Tableau Encyclopédique* (Lamarck 1816: pl. 450) has no associated legend and thus no species are listed under these names and it is not evident which figures he considered to belong to the respective genera. The legend is taken to have been eventually published in 1827 (Evenhuis 2003). Prior to this, however, Lamarck clarified his concept of these genera in his *Histoire naturelle des animaux sans vertèbres* (Lamarck 1822; April), where he described a number of species, but this was predated by a publication in which Bowdich (1822; February) discussed *Stomatella*, citing and illustrating a single species, *Stomatella imbricata*, thus suggesting that Bowdich was the first to validly propose the genus. However, in reallity a legend was published in 1816 for the *Stomatia* and *Stomatella* plate in the

*Verzeichniss der Conchylien* (Anton 1838, but cited as 1839), and that this pre-dated Gray's (1847) more widely known designation of *S. imbricata*. Macpherson and Gabriel (1962) claimed that no such designation existed in the *Verzeichniss der Conchylien* and believed *Granata* to be an 'absolute [objective] synonym' of *Stomatella*. Iredale and McMichael (1962) listed *S. imbricata* as the 'logotype' (type species by subsequent designation) of *Stomatella*, citing Dujardin in *Dictionnaire Universel d' Histoire Naturelle* (d'Orbigny 1839–1849) and giving a date of '*ante* 1845'. The most recent analysis of the dates of publication for the various volumes and livraisons of d'Orbigny's *Dictionnaire* (Evenhuis 1990), however, gives the date for volume 12, livraison 133, pages 1–64 (entries *Stellion* to *Strombides* in the dictionary, *Stomatella* on p. 47) as 9 September 1848.

Examination of Anton's *Verzeichniss* shows that a type designation is in fact present, though somewhat concealed. In the introductory pages to this work, Anton stated "…*den Gattungen* (*deren typusart mit Versalbuchstaben gedruckt ist*)" ["…the genera (whose type species are printed in capital letters)"] (Anton 1838: vi) and entry 1222 under *Stomatella* is printed "LUTEA = St. auricula Lam. = Patella lutea L.". However, since *Stomatella lutea* was not one of the nominal species originally included by Lamarck (1916) in *Stomatella*, it is not eligible for subsequent designation as the type species (ICZN 1999: Art. 69.1). This not withstanding, since Anton clearly indicated that he considered *Patella lutea* to be a synonym of *Stomatella auricula*, which was one of the species originally included in *Stomatella*, this is to be considered a valid fixation of the latter species as the type species of the genus (ICZN 1999: Art. 69.2.2). Dated 1838 (Cernohorsky 1978*a*), it is evidently the earliest designation available. Like Anton, Lamarck himself considered *Patella lutea* and *Stomatella auricula* to be synonymous (Lamarck 1822: 210), though Pilsbry (1890 in 1890–91) believed *P. lutea* to be an unidentifiable entity.

Remarks: Hickman (1998) believed *Granata* to be a monotypic genus endemic to the southern half of Australia. However, I follow other recent authors (e.g. Sasaki 2000; Poppe *et al*. 2006) in referring additional auriform chilodontids to this genus. While these may not be as depressed and haliotiform as the type species, they almost certainly belong to the same lineage. With these taxa included in *Granata*, it is evident that the genus is widely distributed in the Indo-West Pacific. In addition to being conchologically similar, *G. sulcifera*, like *G. imbricata*, has an enlarged right hypobranchial gland and secretes a noxious white mucus when irritated, and has a similar radula morphology.

The relationship of *Granata* and *Stomatolina* Iredale, 1937 (type species *Stomatella rufescens* Gray, 1847, by original designation) needs to be further investigated. Both stomatelline and chilodontid taxa have been referred to *Stomatolina*. Although the matter could be easily resolved by examination of the radula and external anatomy, the difficulty lies in obtaining reliably identified specimens of *S. rufescens*. On the evidence available

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*Tableau Encyclopédique*, in a 16-page "*Liste des objets représentés dans les planches de cette livraison*" that is unfortunately lacking in many sets of the work (Evenhuis & Petit 2003; Petit 2011). The author of *Stomatella* is thus indeed Lamarck (1816). This superficially trivial nomenclatural fact is of considerable significance, for had Bowdich (1822) been the first to validly propose the *Stomatella*, then its type species would (by monotypy) be *Stomatella imbricata* and not *Stomatella auricula*. This in turn would mean that the trochid subfamily currently known as the Stomatellinae ought no longer be known by that name, and the Stomatellinae/idea would in fact be an earlier name for the Chilodontidae. Fortunately such is not the case, but I document the matter to provide clarification.

(Iredale 1937), it seems more probable that *Stomatolina* is stomatelline, perhaps close to *Pseudostomatella* Thiele, 1924.

Though perhaps related to *Granata*, species of *Hybochelus* Pilsbry, 1890 (type species *Stomatella cancellata* Krauss, 1848, by original designation) differ in having a less expanded last adult whorl, an open umbilicus (typically) which is bordered by somewhat stronger cords, and an operculum which almost completely closes the aperture (pers. observ. *Hybochelus mysticus* (Pilsbry, 1890)). The genus occupies conchological morphospace somewhat intermediate between that of typical *Euchelus* and *Granata*. As indicated earlier (see *Excluded taxa*, p. 398), Krauss's *Stomatella cancellata* is an extralimital species and is not included in this revision.

### Key to species of *Granata* in the south-western Indian Ocean

1 Aperture very broad, ratio of maximum:minimum aperture diameter 1.25–1.40; cream patterned with reddish to reddish brown spots that remain distinct on last adult whorl; axial sculpture of rather coarse, regular, crispate pliculae.... **cumingii**

– Aperture not as broad, ratio of maximum:minimum aperture diameter 1.04–1.16; initially with purplish to greyish brown spots, becoming more densely pigmented on last adult whorl; axial sculpture of rather uneven growth-lines........... **sulcifera**

### *Granata cumingii* (A. Adams, 1854) **comb. n.**

Figs 63–65

*Stomatella cumingii*: A. Adams 1854*a*: 834, pl. clxxv, fig. 38; *idem* 1854b: 74; Sowerby 1874: pl. v, fig. 32; Pilsbry 1890 in 1890–91: 13, pl. 52, fig. 67. Type loc.: none originally given; here designated to be tropical East Africa.

*Stomatia cumingii*: Chenu 1959 in 1959–62: 364, fig. 2709.

This species is similar to *Granata sulcifera* (below) and does not warrant a full redescription. It differs most obviously in shape and colour, having a distinctly more elongate

Fig. 63. *Granata cumingii* (A. Adams, 1854): holotype of *Stomatella cumingii* A. Adams, 1854, maximum diameter 31.1 mm (NHMUK 1968201).

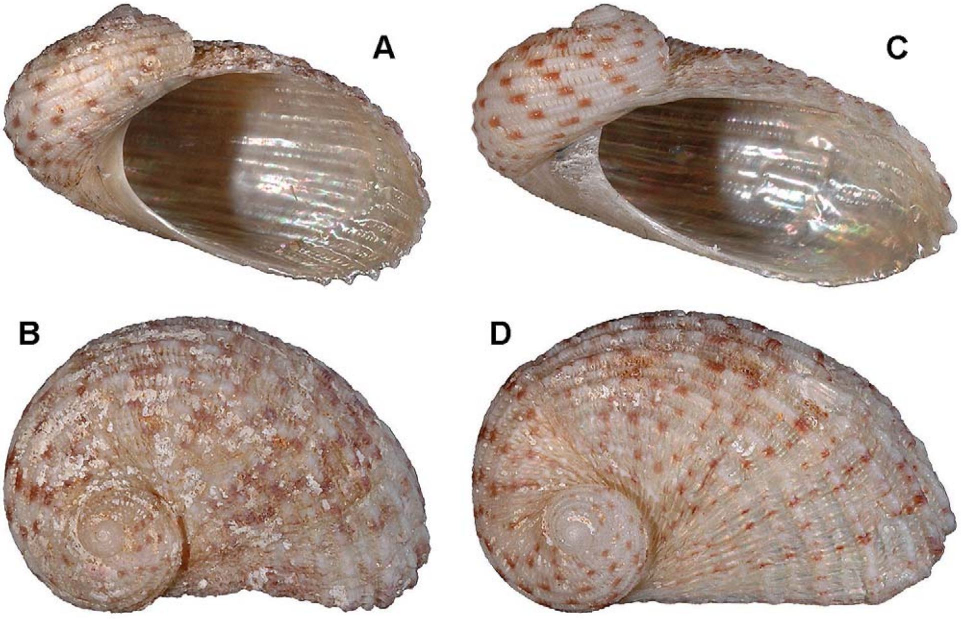

Fig. 64. *Granata cumingii* (A. Adams, 1854): (A, B) Conducia Bay, northern Mozambique, maximum diameter 18.2 mm (NMSA L1440); (C, D) Kikambala, Kenya, maximum diameter 20.7 mm (NMSA F8740).

aperture (ratio of maximum: minimum aperture diameter 1.25–1.40 in *G. cumingii* compared with 1.04–1.16 in *G. sulcifera*) and a more consistent colour pattern of reddish or reddish brown spots on a cream ground that remain distinct even on the last adult whorl. In addition, the sculpture of *G. cumingii* is somewhat coarser, the axial pliculae more crispate and regular, and the interstices more obviously iridescent. Although smaller, the three specimens listed below, are almost identical with the holotype and are undoubtedly conspecific therewith.

Besides mention in late nineteenth century iconographies (Sowerby 1874; Pilsbry 1890 in 1890–91), this species seems not to have been discussed in the literature subsequent to its original description. No locality data accompanied the holotype and, until now, the provenance of the species has remained unknown. *Granata lyrata* (Pilsbry, 1890), from Japan, which is also reportedly more strongly sculptured than *G. sulcifera* (Sasaki 2000), as a less elongate aperture and has greyish rather than reddish maculations.

*Microsculpture*: Similar to that of *G. sulcifera*.

*Protoconch*: Missing in all available specimens.

*Operculum*: Oligospiral; like that of *G. sulcifera*.

*Radula*: Unknown.

*External anatomy*: Only one, badly contracted specimen available, but evidently similar to that of *G. sulcifera*.

Type material: Holotype of *Stomatella cumingii* A. Adams, 1854, in NHMUK (1968201), maximum diameter 31.1 mm, height 19.8 mm (Fig. 63); provenance unknown.

Other material examined: KENYA: Kikambala (3.828°S 39.829°E), B. Hooper, don. A. Jenner, iii.1972 (NMSA F8740). MOZAMBIQUE: Conducia Bay (14.9128°S 40.7178°E), living, on rock on muddy bottom above

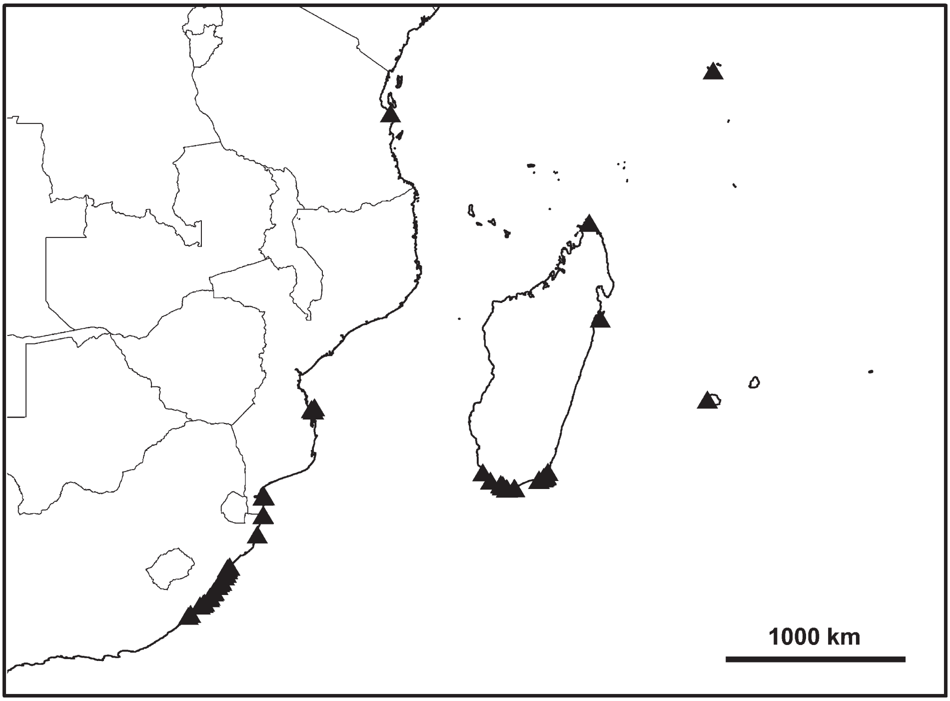

Fig. 65. Distribution of *Granata* species in the south-western Indian Ocean. *Granata cumingii* (circles) and *G. sulcifera* (triangles). Each symbol represents one or more records.

LST, K. Grosch, ix.1976 (NMSA L1440). MADAGASCAR: Secteur de Lavanono (25.48333°S 44.93167°E), -14–18 m, tombant calcaire avec surplombs, Exped'n Atimo Vatae, st'n BS04, 30.v.2010 (MNHN).

Distribution and habitat (Fig. 65): Known only from the tropical western Indian Ocean, from southern Kenya and northern Mozambique to southern Madagascar; has been found living intertidally, on a rock on a muddy substratum, near low water.

### *Granata sulcifera* (Lamarck, 1822)

Figs 4C, 6D, 65–67

*Stomatella sulcifera*: Lamarck 1822: 210, N° 3; Delessert 1841: pl. 33, fig. 3a, b; Krauss 1848: 93; A. Adams 1850: 30; 1854*a*: 833, pl. clxxiv, fig. 3; H. Adams & A. Adams 1854 in 1853–54: 435, 1858: pl. 49, fig. 8b, c (operculum); Brazier 1877: 46; Pilsbry 1890 in 1890–91: 11, pl. 52, fig. 59; Sowerby 1892: 46; Melvill & Standen 1895: 126; 1899: 178; 1901: 345; Hidalgo 1904–5: 259; Couturier 1907: 171; Hedley 1907: 478; 1909: 353; Schwartz 1910: 115; Dautzenberg 1929: 337 [543]; 1932: 79; Dautzenberg & Bouge 1933: 410; Mermod & Binder 1963: 136, fig. 206; Davies 1972: 253; Smythe 1982: 40, pl. 1e; Glayzer *et al.* 1984: 318; Kilburn & Rippey 1982: 42, pl. 9, fig. 5. Type loc.: '*les mers de la Nouvelle-Hollande*' (Australia).

*Stomatella articulata*: A. Adams 1850: 30; 1854*a*: 834, pl. clxxiv, fig. 2; Pilsbry 1990 in 1890–91: 13, pl. 52, fig. 43; Sowerby 1874: pl. iv, fig. 22; Sowerby 1892: 46; Schwartz 1910: 115; Dautzenberg 1932: 79; Barnard 1951: 117, pl. xiv, fig. 17; 1963: 244, fig. 12b (radula); Paes da Franca 1960: 55, pl. 1, fig. 7; Macnae & Kalk 1969: 37, 118, 127; Kensley 1973: 44, fig. 108. Type loc.: '*In insulis Pacificis*', but also given as 'Australia; Lord Hood's Is. [Tuamotu], South Seas, on the pearl oyster' [Cuming].

*Stomatella elegans* [*non* Gray, 1847]: Biggs & Grantier 1960: 387; Bosch & Bosch 1982: 37.

*Stomatella* (*Stomatella*) *sulcifera*: Kilburn 1972: 394 [= *S. articulata*].

?*Hybochelus* (*Granata*) *sulcifera*: Habe 1964: 11, pl. 4, fig. 16.

*Granata sulcifera*: Bosch *et al*. 1995: 32, fig. 27; Jansen 1996: 8, Nº 25; Sasaki 2000: 55, Nº 9; Poppe *et al*. 2006: 33, pl. 12, fig. 4; Poppe & Tagaro 2008: 172, pl. 31, fig. 54, 6.

not *Stomatella sulcifera*: A. Adams 1854*a*: 833, pl. clxxiv, fig. 3; Chenu 1859 in 1859–62: 363, fig. 2703; Sowerby 1874: pl. ii, fig. 11. The figures in these works depict a shell with bold axial bands (cf. Kilburn 1972).

### Description:

*Shell*: Depressed turbiniform to auriform (L/D=0.74–0.90), last adult whorl expanding rapidly; teleoconch of up to 4 whorls; suture indented but not channelled, level with peripheral cord on spire whorls but descending below this near aperture; first teleoconch whorl initially more or less smooth, 3–4 spiral cords develop toward end of whorl; second whorl with 4–5 cords and further cords arising by intercalation with growth on subsequent whorls; end of penultimate whorl with 4–6 first-order cords; intervals between cords wider than cords themselves and usually with a weaker intermediary lira (frequently more than one near end of last adult whorl); axial pliculae develop during second and third whorls; pliculae initially rather regular and producing somewhat cancellate sculpture (second whorl), becoming finer, more close-set and irregular with growth; last adult whorl also with strong, irregular growth-lines; upper cords granular, those nearer periphery smoother. Base similarly sculptured, but cords lower; umbilicus lacking; aperture large, ovate; maximum:minimum aperture diameter 1.04–1.16; columella nacreous and lacking denticles, strongly concave, its junction with basal lip scarcely delimited; interior of outer lip not obviously thickened and lacking denticles

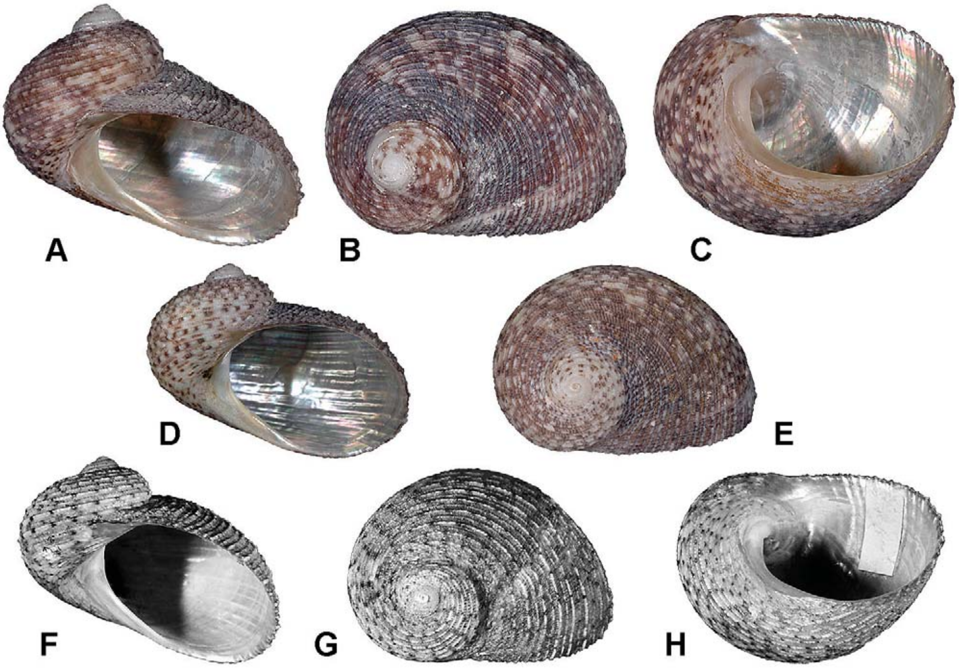

Fig. 66. *Granata sulcifera* (Lamarck, 1822): (A–C) Santa Carolina Is., Bazaruto Archipelago, Mozambique, maximum diameter 21.5 mm (NMSA J9645); (D, E) specimen with spotted colour pattern, Durban Bay, maximum diameter 18.8 mm (NMSA 5708); (F–H) lectotype of *Stomatella articulata* A. Adams, 1850, maximum diameter 19.0 mm (NHMUK 1968113).

or ridges; interior of aperture highly nacreous when fresh, with weak anglulations underlying external cords.

Microsculpture: Vermiform spiral threads not evident on juvenile shell, but surface of early whorls generally worn; later whorls with fine scratch-like axial microsculpture (Fig. 67A).

Protoconch (Fig. 67B): White, diameter 250–270 µm; usually missing, damaged or badly eroded; protrudes slightly above first teleoconch whorl; sculptured with a coarsely flocculent sculpture with some traces of spiral threads (perhaps resembling that of *Clypeostoma salpinx* when fresh); apex weakly beaked; terminal lip with a well-developed projection just above mid-whorl, angular in some specimens rounded in others.

Colour: Initially whitish, with dark purplish or greyish brown spots appearing on cords during third whorl; subsequent whorls spotted, blotched or washed with similar

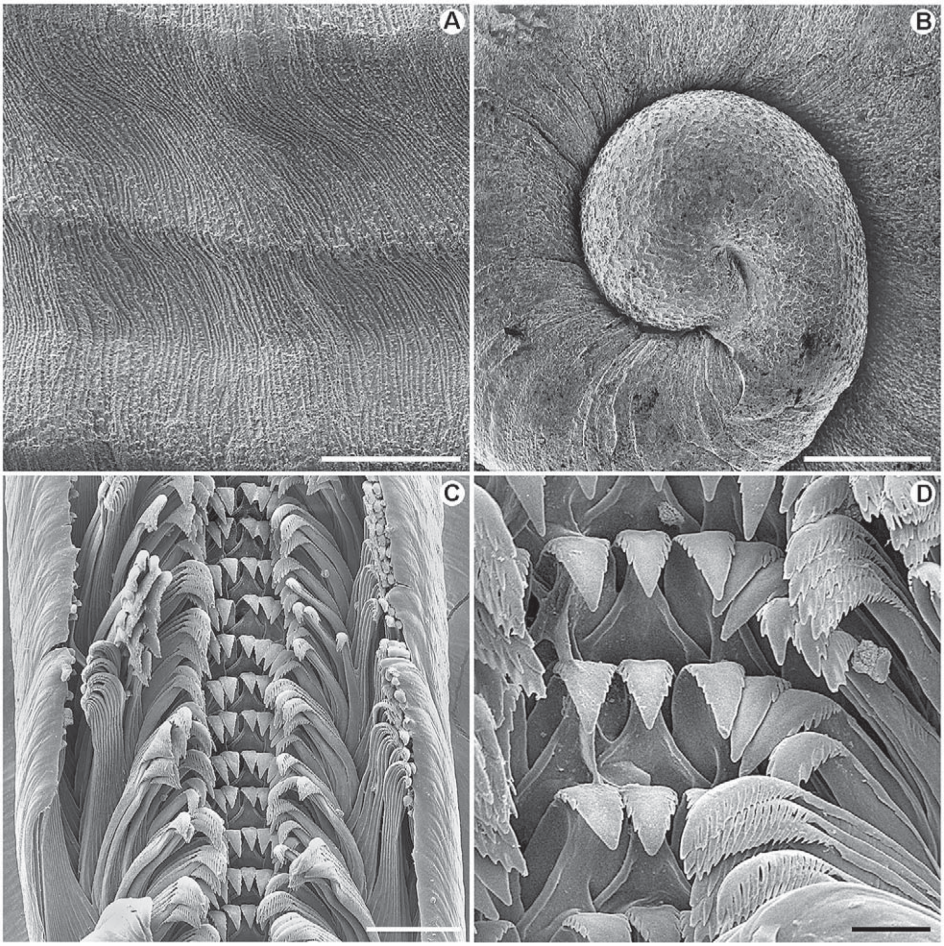

Fig. 67. *Granata sulcifera* (Lamarck, 1822): (A) scratch-like adult microsculpture, Inhaca Is., southern Mozambique, bar = 100 µm (NMSA L1437); (B) protoconch, Mtwalume, KZN, bar = 100 µm (NMSA B8666); (C, D) radula, Santa Carolina Is., central Mozambique, bars = 100 µm and 25 µm respectively (NMSA K3084).

shades, last whorl sometimes heavily so; in living specimens coloration frequently obscured by a dirty brownish periostracal layer.

Dimensions: Largest specimen, maximum diameter 21.6 mm, height 19.2 mm.

*Operculum* (Fig. 4C): Oligospiral; somewhat thicker than in other chilodontid genera; maximum diameter approx. half maximum diameter of aperture; frequently damaged.

*Radula* (Fig. 67C, D): Formula $\infty$+(3–4)+1+(3–4)+$\infty$, with 90–100 transverse rows of teeth; rachidian relatively weakly hooded, cusp acutely trigonal with margins serrated by lateral denticles. Lateral teeth overlapping extensively, their cusps similar to that of rachidian, but slightly asymmetrical and a little larger; whether the fourth tooth should be considered a lateral or a marginal is debateable (Barnard (1963) likewise observed a gradual transition from laterals to inner marginals). Remaining marginals numerous, longer and more slender, with recurved, pectinate cusps. In terms of its general form this radula is similar to that of the type species, *G. imbricata*, but in that species the tooth cusps are finer and more elongate (Hickman & McLean 1990; Hickman 1998).

*External anatomy* (Fig. 6D): General body colour yellowish white, epipodium paler with a few scattered black blotches, also on sides of the foot; cephalic tentacles, forehead and snout usually with grey-brown to black pigmentation. Cephalic lappets, neck lobes and epipodial fold well developed, forming an almost continuous sensory skirt around aperture margin, as in other auriform vetigastropods (e.g. *Haliotis* spp.). Cephalic lappets moderately broad with close-set, stubby processes on free margin; snout laterally expanded; post-ocular peduncle present on right (in both sexes), arising from posterior base of right eyestalk; peduncle with a longitudinal dorsal groove evident in some specimens; a smaller subocular tentacle emerging from ventral base of right eyestalk (illustrated also in *G. lyrata* by Kano 2008: fig. 4). Neck lobes originate beneath eyestalks, overlapping snout flanges, and extend posteriorly for approximately half length of animal; free margin of both lobes microscopically fimbriate with micropapillate tentacles of 2 or 3 sizes emerging from beneath margin; more numerous on left lobe than right; neck lobes narrowing posteriorly and merge seamlessly with epipodial fold. Edge of epipodial fold set almost throughout with epipodial tentacles of varying size, their number depending upon animal size (approx. 10 major epipodial tentacles on each side in large specimens, with numerous smaller intermediaries). An epipodial sense organ is present at base of most of the larger epipodial tentacles, but usually small and indistinct; none evident below neck lobes.

Type material: Holotype of *Stomatella sulcifera* Lamarck, 1822, in MHNG, "Nouv. Hollande", figured by Mermod & Binder (1963: fig. 206) and Poppe *et al*. (2006: fig. 26). Three syntypes of *Stomatella articulata* A. Adams, 1850, in NHMUK (1968113), one here illustrated and designated lectotype, maximum diameter 19.0 mm, height, 15.5 mm (Fig. 66F–H).

Regional material examined (selected, all NMSA unless indicated otherwise): TANZANIA: Dar-es-Salaam (6.7805°S 39.3104°E), I.F. Lambert (F8571). MOZAMBIQUE: Bazaruto Is., north reef (21.5197°S 35.4915°E), E. Roscoe, 1.xii.1974 (9647); Santa Carolina Is., Bay north of Battleship Rock (21.6187°S 35.3371°E), found under dead coral by itself, instead of in a colony, E. Roscoe (G2100); Santa Carolina Is., west bay (21.6187°S 35.3371°E), E. Roscoe, 1969–1973 (G99, J9645, J9646, J9648); ditto, living, R. Kilburn, 21.viii.1974 (K3084; L2695); Bazaruto Is., Ponta Gengareme (21.6638°S 35.4313°E), E. Roscoe, 1972–1974 (G2168, J9644); Inhaca Is., living, vii.1969 (L1437); ditto, bay west of lighthouse at Cabo Inhaca (25.9741°S 32.9778°E), living, under stones at low water, R. Kilburn & D. Herbert, x.1993 (L1442); ditto, sheltered west coast (26.0093°S 32.9075°E), living, under rock and dead coral blocks at low water, R. Kilburn & D. Herbert, x.1993 (L1446). MADAGSACAR: Pointe Barrow (25.20333°S 44.32167°E), -4 m, Exped'n Atimo Vatae, st'n TA31, 28.v.2010 (MNHN); secteur du Cap Malaimpioka (25.3650°S 44.8367°E), living, -10–17 m, sable et algues, Exped'n Atimo Vatae, st'n BP36, 8.vi.2010 (MNHN);

secteur de Lavanono (25.440°S 44.935°E), living, -14–18 m, tombant calcaire avec surplombs, Exped'n Atimo Vatae, st'n BS03, 29.v.2010 (MNHN); NW Rocher de l'Albatros (25.4700°S 44.9400°E), living, -12–14 m, fond rocheux et cailloux, Exped'n Atimo Vatae, st'n BB01, 25.v.2010 (MNHN); Ambatomainty (25.4383°S 44.9417°E), living, intertidal platier a galets basaltiques, Exped'n Atimo Vatae, st'n BM03, 25.v.2010 (MNHN); Ambatobe, pres Soamanitse (25.4567°S 44.9567°E), living, rochers et sable grossier, Exped'n Atimo Vatae, st'n BM02, v–vi.2010 (MNHN); Ambatobe, Bavarama (25.465°S 44.960°E), living, intertidal platier a galets basaltiques, Exped'n Atimo Vatae, st'n BM06, 28–29.v.2010 (MNHN); Andramara (25.48000°S 44.97167°E), living, intertidal roche basaltique, dalles sableuses, Exped'n Atimo Vatae, st'n BM10, 2.vi.2010 (MNHN); Cap Sainte Marie (25.58167°S 45.12667°E), living, -15 m, dalles sableuses et blocs, Exped'n Atimo Vatae, st'n BV20, 10.vi.2010 (MNHN); Cap Sainte Marie (25.6050°S 45.1617°E), intertidal platier calcaire, Exped'n Atimo Vatae, st'n BM16, 10.vi.2010 (MNHN); Faux-Cap (25.5700°S 45.53167°E), -1–10 m, piscine de sable fin, protegée, Exped'n Atimo Vatae, st'n BV09, 4.vi.2010 (MNHN); entrée Est Baie des Galions (25.155°S 46.755°E), living, -10 m, brossage sur rares cailloux, Exped'n Atimo Vatae, st'n TB10, 11.v.2010 (MNHN); Cap Ranavalona (25.0717°S 46.9617°E), living, intertidal platier gréseux et algues, Exped'n Atimo Vatae, st'n TM02, 27.iv.2010 (MNHN); Plage Libanona (25.0417°S 46.9950°E), -4–5 m, fond rocheux corallien, Exped'n Atimo Vatae, st'n TB07, 9.v.2010 (MNHN); Cap d'Antsirabe (25.0433°S 46.9967°E), living, intertidal platier rocheux, Exped'n Atimo Vatae, st'n TM 14, 6.v.2010 (MNHN); Plage Monseigneur (25.0350°S 46.9983°E), living, intertidal platier rocheux avec algues, Exped'n Atimo Vatae, st'n TM01, iv–v.2010 (MNHN); Pointe Flacourt (25.025°S 47.000°E), living, -2–4 m, rochers dans sable, Exped'n Atimo Vatae, st'n TB13, 15.v.2010 (MNHN); Port de Fort Dauphin (25.0267°S 47.0000°E), living, -2–4 m, cailloux sur sable, Exped'n Atimo Vatae, st'n TV21, 15.v.2010 (MNHN); Pointe Evatra, crique (24.9683°S 47.1017°E), living, -3–8 m, fond rocheux et gazon d'algues, Exped'n Atimo Vatae, st'n TR05, 30.iv.2010 (MNHN); sud de la Baie de Lokaro (24.9500°S 47.1067°E), -5–6 m, limon et sable sur roche, Exped'n Atimo Vatae, st'n TV11, 6.v.2010 (MNHN); Ilot de Lokaro (24.9417°S 47.1183°E), intertidal sable, mode battu, Exped'n Atimo Vatae, st'n TM05, 30.iv.2010 (MNHN); Sainte Luce, sud Ilot Souillac (24.76333°S 47.20667°E), living, -4–7 m, Exped'n Atimo Vatae, st'n TA37, 5–6.vi.2010 (MNHN). RÉUNION: Not further localised (M. Jay coll'n, MNHN). SOUTH AFRICA: *KwaZulu-Natal*: Between Bhanga Neck and Kosi Bay, reef off marker 13 north (26.93°S 32.90°E), living, -9–14 m, D. Herbert & F. Wiercx *et al*. dived, 7&12.v.1990 (S1674); Leadsman Shoal, Raggie Reef, 1–2km North of Leven Point (27.90°S 32.62°E), -9–14 m, mixed algal and coral reef, D. Herbert & NPB, dived, 13.v.1998 (E2520); Umhlali (29.50°S 31.23°E), H. Burnup coll'n (8655); Umhlali, Thompson's Bay, Charles Pool (29.5229°S 31.2278°E), R. & E. Kilburn, J. Marais 1972–1979 (9332, 9517, B6720, S9043); Tongaat (29.583°S 31.133°E), H. Burnup coll'n (6369); Umdloti (29.6760°S 31.1158°E), W. Falcon coll'n (6366, 8656); Umdloti (29.6829°S 31.1127°E), rocky intertidal zone, low shore pools D. Herbert, L. Davis & T. Nangammbi, 27.ii.2005 (W2790); Durban (29.85°S 31.02°E), H. Burnup coll'n (6370); ditto, W. Falcon coll'n (A4558); ditto. S. Fenwick (A2009); ditto, R. Kilburn (5708, B5676); Durban Bay (29.8742°S 31.0559°E), dredgings B.J. Young, don. xi.1976–1979 (A5187, B2306, B2307); Durban, Vetch's pier (29.866975°S 31.052026°E), living, R. & E. Kilburn, 6.iv.1970 (V3925); Durban area, Reunion Rocks (29.9860°S 30.9648°E), living, rocky intertidal zone, D. Herbert, 19.iii.2003 (W546); Isipingo tidal pool and adjacent rocks (29.9996°S 30.9476°E), R. Kilburn, D. Herbert & R. Fregona, 25.iii.1985 (9023, D609); Widenham, intertidal rocks (30.216829°S 30. 798644°E), low shore spring tide, living under large rocks with spaces below, together with arcid and carditid bivalves, leg. D. Herbert & L. Davis, 23.ix.2010 (W7463); Aliwal Shoal, off Scottburgh (30.2833°S 30.8333°E), -14–20 m, D. Herbert, dived, 25.x.1992 (S7972); ditto, -25–27 m, hand-dredged sand and reef debris, D. Herbert, 4.iv.1992 (S7160); ditto, -10–20 m, hand-dredged sand, D. Herbert, 30.vi.1991 (S8016); Park Rynie, Rocky Bay (30.3364°S 30.7353°E), J. Marais (S9056); Mtwalume (30.4833°S 30.6333°E), living, intertidal rock pools, R. Kilburn & D. Herbert, 12.viii.1984 (B8666, V3927); Port Shepstone (30.75°S 30.45°E), H. Burnup coll'n (A4556, A4557); Port Shepstone area, Shelly Beach (30.817°S 31.658°E), W.G. Rump, ii.1930 (6367); Port Edward area, Leisure Bay (31.0214°S 30.2485°E), J.P. Marais (S9042). *Eastern Cape*: Pondoland Coast, A. Filmer, *ex* Transvaal Mus. 1978, H. Becker coll'n (B6845); Mzamba (31.08°S 30.20°E), beach drift, J. P. Marais, iv.1992 (S8342); ditto, R. Kilburn & D. Herbert, 12–30.v.1986 (D2953); between Mzamba and Mtentu Rivers, don. J. Stannard, vii.1988 (E5989); Msikaba Is., north side (31.3248°S 29.9682°E), R. Kilburn *et al*., viii.1983 (C5503); Port Grosvenor (31.38°S 29.90°E), R. Kilburn, 30.iv.1976 (A4852); Mbotyi (31.465°S 29.736°E), living, R. Kilburn & D. Herbert, v–vi.1985 (C8270); Mbotyi east (31.4588°S 29.7484°E), sheltered bay, loose rocks and crevices, fine silt, large pool behind reef, R. Kilburn & J. McKay, 26–27.iv.1976 (A5263); Lwandile/Mdumbi (31.883°S 29.266°E), R. Kilburn & R. Fregona, vii.1981 (C31); Coffee Bay (31.98°S 29.15°E), W. Tyson, *ex* Albany Mus. 1980 (B5565).

Other material examined: PERSIAN GULF: not further localised, Lebour (NMSA H6196). PAKISTAN: Karachi, R. Winckworth (NHMUK). INDIA: Mannar, R. Winckworth (NHMUK); Gulf of Mannar, Tuticorin, Koswari Is. (8.8704°N: 78.2255°E), beach-drift, R. Kilburn, 12.x.2000 (NMSA L5243). SEYCHELLES: Cerf Is., R.C. Wood (NMSA J7964). AUSTRALIA: Lizard Is., Queensland, J.D. Taylor (NHMUK).

Literature records: MADAGASCAR: Diego-Suarez [Antsiranana] (12.267°S 49.283°E), Decary (Dautzenberg 1932); Île Ste-Marie, entre l'Île aux Nattes et Ilampy (17.071°S 49.836°E) (Dautzenberg 1929); Lambetabe [Lambelabe] (24.783°S 43.933°E) (Dautzenberg 1929); Faux-Cap (25.567°S 45.517°E), Decary (Dautzenberg 1932); Cap Ste-Marie (25.599°S 45.137°E), Decary (Dautzenberg 1932, as *Stomatella articulata*).

Distribution and habitat (Fig. 65): Indo-West Pacific; from Japan (Sasaki 2000) and the Tuamotu Archipelago (Couturier 1907) in the east, to the eastern seaboard of Africa, extending south to the northern Eastern Cape (Coffee Bay, 32.00°S); common in the low intertidal and shallow subtidal down to -18 m (empty shells to -45 m), living specimens most often found under stones and dead coral blocks, sometimes in small groups, in both sheltered and somewhat exposed habitats; often where the rock rests on muddy sand and where conditions are somewhat anoxic (Kilburn 1972; Kilburn & Rippey 1982, and pers. observ.). Shells of living specimens frequently encrusted with tubes of spirorbid polychaetes, sometimes heavily so.

Remarks: *Granata sulcifera* is the only chilodontid species commonly found living intertidally in southern Africa and is easily recognised by its low spire and rapidly expanding last adult whorl. *Vaceuchelus gemmula* and *V. natalensis* may also be found intertidally in South Africa, but are less frequently encountered, and are probably often overlooked on account of their small size.

*Granata elegans* (Gray, 1847) from north-eastern Australia, *G. lyrata* (Pilsbry, 1890) (not *Stomatia lirata* A. Adams, 1850 – a species of *Pseudostomatella*) from Japan, and *G. maculata* (Quoy & Gaimard, 1834), described from Vanikoro Is., need to be examined for comparison as potential synonyms, but *G. sulcifera* predates all. Much museum material identified as *G. elegans* is in fact referable to *G. sulcifera*, and so probably are some literature references (e.g. Bosch & Bosch 1982); unfortunately the whereabouts of the type material of Gray's species is unknown. *G. lyrata* reportedly differs from *G. sulcifera* in having a less rapidly expanding last adult whorl and in being more strongly sculptured (Sasaki 2000).

This species has also been recorded from Pleistocene shorelines in the southern and eastern Cape, South Africa (Schwarz 1910; Barnard 1962; Davies 1972). Although such a range extension would have been quite possible during warmer interglacial periods, these records require confirmation since there may well have been confusion with the somewhat similar *Pseudostomatella orbiculata* (A. Adams, 1850), which is not uncommon in raised beach deposits in the Algoa Bay–Mossel Bay area (Kilburn & Tankard 1975). The same may also apply to Sowerby's (1892) record of *Stomatella articulata* from the Bairstow collection (i.e. Port Elizabeth).

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Deep-water material was collected off Mozambique on board RV *Vizconde de Eza* during the MAINBAZA cruise, a joint effort of MNHN and Instituto Español de Oceanografia (IOE), and off Madagascar in 2009–2010 on board FV *Miriky* and FV *Nosy Be 11* owned by the Société des Pêcheries de Nosy Be (Groupe Unima); further material was collected intertidally and by diving in south Madagascar during Expedition ATIMO VATAE. These Mozambique-Madagascar expeditions (2009–2010) were funded by the Total Foundation, Prince Albert II of Monaco Foundation, and Stavros Niarchos Foundation, and were conducted by the MNHN and Pro-Natura International (PNI) as part of their "*Our Planet Reviewed*" programme (PI Philippe Bouchet). In addition, two earlier cruises yielded further chilodontid lots in the MNHN: BENTHEDI cruise, conducted in 1977 on board RV *Noroit* in the northern part of the Mozambique Channel (PI Bernard Thomassin); and

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## REFERENCES

Adams, A. 1850. An arrangement of Stomatellidae, including the characters of a new genus, and of several new species. *Proceedings of the Zoological Society of London* **18**: 29–40.

———1853 [1851]. Contributions towards a monograph of the Trochidae, a family of gasteropodous Mollusca. *Proceedings of the Zoological Society of London* **19**: 150–192.

———1854*a*. Monograph of Stomatellinae, a sub-family of Trochidae. Pp. 827–846, pls 173–175. *In*: Sowerby, G.B. 1842–87. *Thesaurus conchyliorum*. Vol. 2. London: Sowerby.

———1854*b* [1853]. Descriptions of new shells from the collection of H. Cuming, Esq. *Proceedings of the Zoological Society of London* **21**: 69–74.

———1864*a* [1863]. Descriptions of a new genus and of twelve new species of Mollusca. *Proceedings of the Zoological Society of London* **31**: 506–509.

———1864*b*. Notes on some molluscan animals from the seas of China and Japan. *Annals and Magazine of Natural History*, *Series 3* **13**: 140–144.

Adams, H. & Adams, A. 1853–1854. The genera of Recent Mollusca; arranged according to their organisation. Vol. 1. London: John van Voorst, pp. i–xl, 1–484.

———1858. The genera of Recent Mollusca; arranged according to their organisation. Vol. 3 [plates]. London: John van Voorst, pls 1–138.

Aimassi, G. & Ferrero Mortara, E. 1983. Osservazioni paleoecologiche e biostratigrafiche su una malacofauna pliocenica dell'Astigiano (Buttigliera d'Asti). *Bolletino Malacologico* **19** (9–12): 177–206.

Aktipis, S.W. & Giribet, G. 2012. Testing relationships among the vetigastropod taxa: a molecular approach. *Journal of Molluscan Studies* **78**: 12–27.

Alf, A., Maestrati, P. & Bouchet, P. 2010. New species of *Bolma* (Mollusca: Vetigastropoda: Turbinidae) from the tropical deep sea. *Nautilus* **124** (2): 93–99.

Anton, H.E. 1838. *Verzeichniss der Conchylien welche sich in der Sammlung von Hermann Eduard Anton befinden*. Halle: Eduard Anton, pp. i–xvi, 1–110. [For date of publication see Cernohorsky (1978*a*).]

Bandel, K. 1982. Morphologie und Bildung der frühontogenetischen Gehäuse bei conchiferen Mollusken. *Facies* **7**: 1–198.

———2009. The slit bearing nacreous Archaeogastropoda of the Triassic tropical reefs in the St Cassian Formation with evaluation of the taxonomic value of the selenizone. *Berliner Paläontologische Abhandlungen* **10**: 5–47.

———2010. Relationships of the Triassic Eucycloidea Koken, 1897 (Mollusca, Gastropoda) to modern genera such as *Pagodatrochus*, *Calliotropis* and *Euchelus*, based on morphology of the early shell. *Bulletin of Geosciences* **85** (3): 435–486.

Barnard, K.H. 1951. *A beginner's guide to South African shells*. Cape Town: Maskew Miller, pp. i–ii, 1–215.

———1962. Revised list of South African late Tertiary and Pleistocene marine Mollusca. *Transactions of the Royal Society of South Africa* **36** (4): 179–196.

———1963. Contributions to the knowledge of South African marine Mollusca. Part IV. Gastropoda: Prosobranchiata: Rhipidoglossa, Docoglossa. Tectibranchiata. Polyplacophora. Solenogastres. Scaphopoda. *Annals of the South African Museum* **47** (2): 201–360.

———1964. The work of the s.s. *Pieter Faure* in Natal waters, with special reference to the Crustacea and Mollusca; with description of new species of Mollusca from Natal. *Annals of the Natal Museum* **16**: 9–29.

Bartsch, P. 1915. Report on the Turton collection of South African marine mollusks with additional notes on other South African shells contained in the United States National Museum. *Bulletin of the United States National Museum* **91**: i–xii, 1–305, pls 1–54.

Beu, A.G. & Climo, F.M. 1974. Mollusca from a Recent coral community in Palliser Bay, Cook Strait. *New Zealand Journal of Marine and Freshwater Research* **8** (2): 307–332.

Beu, A.G. & Raine, J.I. 2009. Revised descriptions of New Zealand Cenozoic Mollusca from Beu and Maxwell (1990). *GNS Science miscellaneous series no. 27*. (http://www.gns.cri.nz/static/Mollusca; accessed 17/08/2012)

Biggs, H.E.J. 1973. The marine Mollusca of the Trucial Coast Persian Gulf. *Bulletin of the British Museum of Natural History* (*Zoology*) **24** (8): 343–421.

Biggs, H.E.J. & Grantier, L.L. 1960. A preliminary list of the marine Mollusca of Ras Tanura, Persian Gulf. *Journal of Conchology* **24** (11): 387–392.

Bisacchi, J. 1931. Alcuni *Trochus* del Mar Rosso. *Annali del Museo Civico di Storia Naturale Giacomo Doria di Genova* **55**: 176–182.

Bosch, D. & Bosch, E. 1982. *Seashells of Oman*. London: Longman, pp. 1–206.

Bosch, D.T, Dance, S.P., Moolenbeek, R.G. & Oliver, P.G. 1995. *Seashells of Eastern Arabia*. Abu Dhabi, Dubai and London: Motivate Publishing, pp. 1–296.

Bouchet, P., Frýda, J., Hausdorf, B., Ponder, W., Valdes, A. & Warén, A. 2005. Working classification of the Gastropoda. Part 2 (pp. 240–284). *In*: Bouchet, P. & Rocroi, J.-P. Classification and nomenclator of gastropod families. *Malacologia* **47** (1–2): 1–397.

Bouchet, P. & Rocroi, J.-P. 2005. Nomenclator of gastropod family-group names. Part 1 (pp. 5–239). *In*: Classification and nomenclator of gastropod families. *Malacologia* **47** (1–2): 1–397.

Bowdich, T.E. 1822. *Elements of Conchology, including the fossil genera and animals. Part 1. Univalves*. London: Treuttel & Würtz, pp. i–xiii, 14–75 plus index; pls i–xix.

Brazier, J. 1877. Continuation of the Mollusca collected during the "Chevert" Expedition. *Proceedings of the Linnean Society of New South Wales* **2** (1): 46–53.

Brusina, S. 1865. Conchiglie Dalmate inedite. *Verhandlungen der kaizerlich-königlichen zoologisch-botanischen Gesellschaft in Wien* **15**: 3–42.

———1866. *Contribuzione pella fauna dei molluschi Dalmati*. Vienna: Imperiale e Reale Societa Zoologico-Botanica di Vienna, pp. 1–134, pl. 1.

Cabezas, P., Macpherson, E. & Machordom, A. 2010. Taxonomic revision of the genus *Paramunida* Baba, 1988 (Crustacea: Decapoda: Galatheidae): a morphological and molecular approach. *Zootaxa* **2712**: 1–60.

Cantraine, F. 1835. Diagnoses ou descriptions succinctes de quelques espèces nouvelles de mollusques qui feront partie de l'ouvrage: Malacologie méditerranéenne et litorale…. *Bulletin de l'Académie Royale des Sciences et Belle-lettres de Bruxelles* **2** (11): 380–401.

Cernohorsky, W.O. 1978*a*. The date of publication of Anton's "Verzeichnis der Conchylien". *Veliger* **20** (3): 299.

———1978*b*. *Tropical Pacific marine shells*. Sydney: Pacific Publications, pp. 1–352.

Chang, C.-K. 2003. Small mollusks from Lutao, Taiwan. Chapter VII, Part 2. Trochidae and its allied families. *Internet Hawaiian Shell News*, March 2003.

Chenu, J.C. 1859–62. *Manuel de conchyliologie et de paléontologie conchyliologique*. Paris: Victor Masson. Vol. 1 (1859), pp. i–vii, 1–508; Vol. 2 (1862), pp. 1–327.

Cossmann, M. 1918. *Essais de Paléoconchologie comparée*. Vol. 11. Paris: Cossmann, pp. 1–388, pls 1–11.

Costa, O.G. 1861. *Microdoride mediterranea o descrizione de poco ben conosciuti od affatto ignoti viventi minuti e micoscropici [*sic*] del Mediterraneo*. Vol. 1. Napoli: Stamperia dell'Iride, pp. 1–xviii, 1–80, 13 pls (i, ia–xii).

Cotton, B.C. 1946. Australian beaded top shells. *South Australian Naturalist, Adelaide* **23** (3): 6–8.

———1957. Records of uncommon South Australian molluscs. *Records of the South Australian Museum* **8**: 117–130, pl. 6.

———1959. South Australian Mollusca: Archaeogastropoda. *Handbook of the Flora and Fauna of South Australia*. Adelaide: Government Printer, pp. 1–449.

Couturier, M. 1907. Étude sur les mollusques gastropodes recueillis par M. L.-G. Seurat dans les archipels de Tahiti, Paumotu et Gambier. *Journal de Conchyliologie* **55**: 123–178.

Crocetta, F. & Spanu, M. 2008. Molluscs associated with the Sardinian deep water population of *Corallium rubrum* (Linné, 1758). *Mediterranean Marine Science* **9** (2): 65–85.

Crosse, H. 1863. Descriptions d'espèces nouvelles de l'archipel calédonien. *Journal de Conchyliologie* **11**: 178–181.

Dall, W.H. 1889. Notes on the soft parts of *Trochus infundibulum* Watson with an account of a remarkable sexual modification of the epipodium, hitherto undescribed in Mollusca. *Nautilus* **3** (1): 2–4.

———1927. Notes on the genera of Costa's Microdoride. *Nautilus* **40** (4): 134.

Dance, S.P. 1986. *A history of shell collecting*. Leiden: E.J. Brill & W. Backhuys, pp. i–xv, 1–265, pls 1–32.

Dautzenberg, P. 1929. Contribution a l'étude de la faune de Madagascar. Mollusca II, Mollusca marina testacea. *Faunes des colonies Français* **3** (4): 115–430 (321–636).

———1932. Mollusques testacés marins de Madagascar supplement. *Journal de Conchyliologie* **76**: 5–119.

Dautzenberg, P. & Bouge, J.-L. 1933. Les mollusques testacés marins des éstablissements Français de l'Océanie. *Journal de Conchyliologie* **33**: 41–104, 145–326, 351–469.

Davies, O. 1972. Pleistocene shorelines in the southern and south-eastern Cape Province (Part 2). *Annals of the Natal Museum* **21** (2): 225–279.

Delessert, B. 1841. *Recueil de coquilles décrites par Lamarck dans son Histoire naturelle des Animaux sans vertèbres et non encore figurées*. Paris: Fortin, Masson et Cie, pp. 1–92, 40 pls.

Deshayes, G.P. 1863. *Catalogue des mollusques de l'ile de la Réunion* (*Bourbon*). Annexe E. *In*: Maillard, L. 'Notes sur l'isle de La Réunion'. Paris: Dentu, pp. 1–4, 1–144, pls 1–14.

De Simone, A. & Kosuge, S. 2010. On the molluscan species landing accompany with the harvest of precious coral fisheries operated in the Mediterranean Sea (1). *Bulletin of the Institute of Malacology, Tokyo* **3** (10): 157–162.

d'Orbigny, A. 1842–1843. *Paléontologie Française. Description zoologique et géologique de tous les animaux mollusques et rayonnés fossils de France. Terrains crétacés*. Vol. 2, Gasteropoda. Paris: Arthus Bertrand, pp. 1–456, plus atlas of plates, pls 149–256. [pp. 1–80, 1842; pp. 81–456, 1843]

d'Orbigny, C.V.D., ed. 1839–1849. *Dictionnaire universel d'histoire naturelle*.... 13 volumes + 3 atlases. Paris: C. Renard.

Drivas, J. & Jay, M. 1988. *Coquillages de La Réunion et de l'ile Maurice*. Singapore: Times Editions, pp. 1–159.

Duch, T.M. 1969. Spawning and development in the trochid gastropod *Euchelus gemmatus* (Gould, 1841) [*sic*] in the Hawaiian Islands. *Veliger* **11** (4): 415–427.

Duncan, F.M. 1937. On the dates of publication of the society's 'Proceedings' 1859–1926. With an appendix containing the dates of publication of the 'Proceedings' 1830–1858, compiled by the late F.H. Waterhouse, and of the 'Transactions' 1833–1869, by the late Henry Peavot, originally published in PZS 1893, 1913. *Proceedings of the Zoological Society of London, Series A* **107**: 71–84.

Engl, W. & Rolán, E. 2009. Two new species of *Putzeysia* (Prosobranchia, Chilodontidae) from the Canary Islands. *Iberus* **27** (2): 93–98.

Evenhuis, N.L. 1990. Dating the livraisons and volumes of d'Orbigny's *Dictionnaire Universel d'Histoire Naturelle*. *Bishop Museum Occasional Papers* **30**: 219–225.

———2003. Dating and publication of the of *Encyclopédie Méthodique* (1782–1832), with special reference to the parts of the *Histoire Naturelle* and details on the *Histoire Naturelles des Insectes*. *Zootaxa* **166**: 1–48.

Evenhuis, N.L. & Petit, R.E. 2003. Corrections and additions to the dating of the "*Histoire Naturelle des Vers*" and the *Tableau Encyclopédie* (*vers, coquilles, mollusques et polypiers*) portions of the *Encyclopédie Méthodique*. *Zootaxa* **207**: 1–4.

Fischer, P. 1875–1880. Genres *Calcar, Trochus*, *Xenophora*, *Tectarius* et *Risella*. *In*: Kiener, L.C. *Spécies général et iconographie des coquilles vivantes*.... Vol. 11. Paris: J.-B. Baillère et fils, pp. 1–96, 1875; 97–144, 1876; 145–240, 1877; 241–336, 1878 (*Calcar* and *Trochus*); pp. 337–463, 1879–80 (*Xenophora*, *Tectarius* and *Risella*); Index 464–480.

———1878. Diagnoses molluscorum novorum. *Journal de Conchyliologie* **26**: 211–213.

Fraussen, K. & Rosado, J. 2011. The *Cantharus* group (Gastropoda: Buccinidae) on the Almirante Leite Bank (Mozambique) with description of two new species and one new genus. *Novapex* **12** (3–4): 73–79.

Fretter, V. & Graham, A. 1994. *British prosobranch molluscs, their functional anatomy and ecology*. Revised and updated edition. London: Ray Society, pp. i–xix, 1–820.

Fukuda, H. 1993. Marine Gastropoda (Mollusca) of the Ogasawara (Bonin) Islands. Part 1: Archaeogastropoda and Neotaenioglossa. *Ogasawara Research* **19**: 1–86.

Gardner, N.W. 1975. *Herpetopoma* – our beaded top shells. *Poirieria* **7** (6): 121–125.

Giannuzzi-Savelli, R., Pusateri, F., Palmeri, A. & Ebreo, C. 1994. *Atlante delle Conchiglie Marine del Mediterraneo*. Vol. 1 (Archaeogastropoda). Rome: Edizioni de 'La Conchiglia', pp. 1–125.

Glayzer, B.A., Glayzer, D.T. & Smythe, K.R. 1984. The marine Mollusca of Kuwait, Arabian Gulf. *Journal of Conchology* **31** (5): 311–330.

Gmelin, J.F. 1791. *In*: Linnaeus, C. *Systema Naturae*.... 13th ed. Vol. 1, part 6. Leipzig: Georg Emanuel Beer, pp. 2225–3910.

Gould, A.A. 1846–50. Shells collected by the United States Exploring Expedition under the command of Charles Wilkes. *Proceedings of the Boston Society of Natural History* **2–3**: [See Johnson (1964) for pagination and dating of the various parts of this work.]

———1852. Mollusca and shells. Vol. 12. *In*: *United States Exploring Expedition during the years 1839–1842 under the command of Charles Wilkes U.S.N.* Boston, pp. i–xv, 1–510.

———1862. *Otia Conchologica: descriptions of shells and mollusks from 1839 to 1862*. Boston: Gould & Lincoln, pp. i–iv, 1–256.

Graham, A. 1988. *Molluscs: prosobranch and pyramidellid gastropods. Keys and notes for the identification of the species.* Synopses of the British Fauna No 2 (2nd ed.). Leiden: E.J. Brill & W. Backhuys for Linnean Society of London, pp. i–viii, 1–662.

Gray, J.E. 1847. Guide to the Recent Mollusca, their synomymies and types. *Proceedings of the Zoological Society of London* **15**: 129–219.

Guidastri, R., Melone, G. & Taviani, M. 1984. Systematic position of "*Trochus" wiseri* Calcara (Prosobranchia: Trochidae). *Archiv für Molluskenkunde* **114** (4/6): 125–136.

Habe, T. 1964. *Shells of the western Pacific in colour*. Osaka: Hoikusha Publishing Co., Ltd.

Hedley, C. 1899. The Mollusca of Funafuti. Part 1. – Gasteropoda. *Memoirs of the Australian Museum* **3** (7): 397–488.

———1907. The Mollusca of Mast Head Reef, Capricorn group, Queensland. Part 2. *Proceedings of the Linnean Society of New South Wales* **32**: 476–513.

———1909. Catalogue of the marine Mollusca of Queensland. *Australian Association for the Advancement of Science* **12**: 343–371.

Herbert, D.G. 1987. Revision of the Solariellinae (Mollusca: Prosobranchia: Trochidae) in southern Africa. *Annals of the Natal Museum* **28** (2): 283–382.

———1992. Revision of the Umboniinae in southern Africa and Mozambique (Mollusca: Gastropoda: Trochidae). *Annals of the Natal Museum* **33** (2): 379–459.

———1993. Revision of the Trochinae, tribe Trochini (Mollusca: Prosobranchia: Trochidae) in southern Africa. *Annals of the Natal Museum* **34** (2): 239–308.

———1996. A critical review of the trochoidean types in the Muséum d'Histoire Naturelle, Bordeaux (Mollusca: Gastropoda). *Bulletin du Muséum national d'Histoire naturelle, Paris*, *Series 4* **18** (section A) (3–4): 409–445.

———1998. Revision of the genus *Calliotrochus* Fischer, 1879 (Gastropoda: Trochoidea). *Invertebrate Taxonomy* **12**: 545–565.

Herbert, D.G. & Bouchet, P. 2011. CHILODONTIDAE Macalister, 1876 (Ciliophora), CHILODONTINAE Eigenmann, 1910 (Pisces, Characiformes), and CHILODONTINAE Wenz, 1938 (Mollusca, Gastropoda): proposed resolution of homonymy between family-group names. *Bulletin of Zoological Nomenclature* **68** (3): 175–179.

Herbert, D.G. & Warén, A. 1999. South African Mollusca described by Ferdinand Krauss, their current status and notes on type material housed in the Naturhistoriska Riksmuseet, Stockholm. *Annals of the Natal Museum* **40**: 205–243.

Héros, V., Lozouet, P., Maestrati, P., Cosel, R. von, Brabant, D. & Bouchet, P. 2007. Mollusca of New Caledonia. *In*: Payri, C.E. & Richer de Forges, B. eds, *Compendium of marine species of New Caledonia*, Doc. Sci. Tech. 117, seconde édition, Nouméa: Institut de recherche pour le développement, pp. 199–254.

Herrmannsen, A.N. 1846–1847. *Index generum malacozoorum primordia.* Cassell: T. Fischer. Vol. 1: Part 1: 1–104 [1846]; Part 2: 105–232 [1846]; Part 3: 233–360 [1847]; Part 4: 361–488 [1847]; Part 5: 489–637 [1847].

Hickman, C.S. 1981. Selective deposit feeding by the deep-sea archaeogastropod *Bathybembix aeola*. *Marine Ecology Progress Series* **6**: 339–342.

———1998. Superfamily Trochoidea. Pp. 671–690. *In*: Beesley, P.L., Ross, G.J.B. & Wells, A. eds, *Mollusca: The Southern Synthesis. Fauna of Australia.* Vol. 5. Part B. Melbourne: CSIRO Publishing, pp. i–viii, 565–1234.

Hickman, C.S. & McLean, J.H. 1990. Systematic revision and suprageneric classification of trochacean gastropods. *Science series, Natural History Museum of Los Angeles County* **35**: 1–169.

Hidalgo, J.G. 1904–1905. *Catalogo de los moluscos testáceos de las islas Filipinas, Joló y Marianas. I.– Moluscos marinos*. Madrid: Real Academia de Ciencias Exactas, Fiscias y Naturales, pp. i–xvi, 1–408.

Higo, S., Callomon, P. & Goto, Y. 1999. *Catalogue and bibliography of the marine shell-bearing Mollusca of Japan. Gastropoda, Bivalvia, Polyplacophora, Scaphopoda*. Osaka: Elle, pp. 1–749.

Hirase, S. & Taki, I. 1954. *Illustrated handbook of shells in natural colors from the Japanese islands and adjacent territory*. Tokyo: Maruzen Co. Ltd.

Hoenselaar, H.J. & Dekker, H. 1998. Molluscs of the Great Bitter Lake, Suez Canal, Egypt, collected by C. Beets in 1950. *Basteria* **62**: 197–214.

Høisæter, T. & Geiger, D.L. 2011. Species of *Anatoma* (Gastropoda: Anatomidae) in Norwegian and adjacent waters, with description of two new species. *Nautilus* **125** (3): 89–112.

Hutton, F.F. 1883. Notes on some branchiate Gastropoda. *Transactions of the New Zealand Institute* **15**: 118–131, pls 13–16.

Hylleberg, J. & Kilburn, R.N. 2003. Marine molluscs of Vietnam: annotations, voucher material and species in need of verification. *Phuket Marine Biological Center Special Publication* **28**: 1–300.

International Commission on Zoological Nomenclature (ICZN). 1999. *International Code of Zoological Nomenclature*. 4th ed. London: International Trust for Zoological Nomenclature, pp. i–xxix, 1–306.

Iredale, T. 1929. Queensland molluscan notes I. *Memoires of the Queensland Museum* **9**: 261–297.

———1937. Middleton and Elizabeth Reefs, south Pacific Ocean. *Australian Zoologist* **8** (4): 232–261.

Iredale, T. & McMichael, D.F. 1962. A reference list of the marine Mollusca of New South Wales. *Australian Museum Sydney, Memoir* **11**: 1–109.

Issel, A. 1869. *Malacologia del Mar Rosso ricerche zoologiche e paleontologiche*. Pisa: Editori della Biblioteca Malacologica, i–xi, 1–388, pls 1–5.

Jansen, P. 1996. *An illustrated and annotated checklist of the Australian Trochidae. Part 1. Eucyclinae and Margaritinae*. Townsville: Jansen, pp. 1–16.

Jay, M. 2009. Mollusques de l'île de la Réunion. Version 23 March, 2009 http://vieoceane.free.fr/mollusques/intro_mollusque.htm [accessed 17/08/2012]

Johnson, R.I. 1964. *The Recent Mollusca of Augustus Addison Gould*. Washington: Smithsonian Institution, pp. 1–182, pls 1–42.

———1994. Types of shelled Indo-Pacific mollusks described by W.H. Pease. *Bulletin of the Museum of Comparative Zoology, Harvard* **154** (1): 1–61.

Kaicher, S.D. 1990. *Card Catalogue of world shells*. Pack № 56, Trochidae V. St Petersburg, Florida: Kaicher.

Kano, Y. 2008. Vetigastropod phylogeny and a new concept of Seguenzioidea: independent evolution of copulatory organs in the deep-sea habitats. *Zoologica Scripta* **37**: 1–21.

Kano, Y., Chikyu, E. & Warén, A. 2009. Morphological, ecological and molecular characterization of the enigmatic planispiral snail genus *Adeuomphalus* (Vetigastropoda: Seguenzioidea). *Journal of Molluscan Studies* **75**: 397–418.

Kay, E.A. 1965. Marine molluscs in the Cuming collection, British Museum (Natural History) described by William Harper Pease. *Bulletin of the British Musem* (*Natural History*)*, Zoology* **Suppl. 1**: 1–96, pls 1–14.

———1979. *Hawaiian marine shells: reef and shore fauna of Hawaii. Section 4*: *Mollusca*. Bernice P. Bishop Museum, special publication **64** (4): i–xviii, 1–652.

Keen, A.M. 1960. *In*: Moore, R.C., ed., *Treatise on Invertebrate Paleontology. Part I. Mollusca 1*. Boulder, Colorado: Geological Society of America and University of Kansas, pp. i–xxiii, 1–351.

Kendall, C.G. & Skipwith, P.A. D'E. 1969. Holocene shallow-water carbonate and evaporite sediments of Khor al Bazam, Abu Dhabi, southwest Persian Gulf. *American Association of Petroleum Geologists Bulletin* **53** (4): 841–869.

Kensley, B. 1973. *Sea-shells of southern Africa. Gastropods*. Cape Town: Maskew Miller, pp. 1–236.

Kilburn, R.N. 1972. Taxonomic notes on South African marine Mollusca (2), with the description of new species and subspecies of *Conus*, *Nassarius*, *Vexillum* and *Demoulia*. *Annals of the Natal Museum* **21** (2): 391–437.

———1977. Taxonomic studies on the marine Mollusca of southern Africa and Mozambique. Part 1. *Annals of the Natal Museum* **23** (1): 173–214.

Kilburn, R.N. & Rippey, E. 1982. *Sea shells of southern Africa*. Johannesburg: Macmillan, pp. 1–249.

Kilburn, R.N. & Tankard, A.J. 1975. Pleistocene mollucs from the west and south coasts of the Cape Province, South Africa. *Annals of the South African Museum* **67** (6): 183–226.

Kirk, T.W. 1882. Decriptions of new shells. *Transactions of the New Zealand Institute* **14**: 282–283.

Kollmann, H.A. 2005. Révision critique de la paléontologie française d'Alcide d'Orbigny [sous la direction de J.-C. Fischer]. Vol. 3, Gastropodes Crétacés. Leiden: Backhuys, pp. 1–239.

Komai, T. & Chan, T.-Y. 2010. Two new pandalid shrimps and the discovery of the second specimen of the rare hippolytid shrimp *Leontocaris bulga* Taylor & Poore, 1998 (Crustacea, Decapoda) from the Mozambique MAINBAZA cruise. *Zoosystema* **32** (4): 625–641.

KOSUGE, S. & CHINO, M. 1998. Report on the small to micro sized shells from Philippines (1). *Bulletin of the Institute of Malacology, Tokyo* **3** (5): 77–81, pls 25–26.

KRAUSS, F. 1848. *Die südafrikanischen Mollusken. Ein Beitrag zur Kenntniss des Kap- und Natallandes und zur geographischen Verbreitung derselben, mit Beschreibung und Abbildung der neuen Arten*. Stuttgart: Ebner & Seubert, pp. i–ii, 1–140, pls 1–6.

LADD, H.S. 1966. Chitons and gastropods (Haliotidae through Adeorbidae) from the western Pacific islands. *United States Geological Survey Professional Paper* **531**: 1–98, pls 1–16.

———1982. Cenozoic fossil mollusks from western Pacific islands; gastropods (Eulimidae and Volutidae through Terebridae). *United States Geological Survey Professional Paper* **1117**: 1–100, pls 1–41.

LAMARCK, [J.B.P.A.]. 1816. *Tableau encyclopédique et méthodique des trois règnes de la nature*. Paris: V. Agasse. Part 23 [Livraison 84], pls 391–488, et liste des objets représentés dans les planches de cette livraison, pp. 1–16.

———1822. *Histoire naturelle des animaux sans vertèbres*. Tome 6, partie 2. Paris: Verdière, pp. 1–232.

LAMY, E. 1938. Mission Robert Ph. Dollfus en Egypte. VII. Mollusca testacea. *Mémoires de l'Institut d'Egypte* **37**: 1–89.

LANDAU, B., MARQUET, R. & GRIGIS, M. 2003. The Early Pliocene Gastropoda (Mollusca) of Estepona, southern Spain. Part 1: Vetigastropoda. *Palaeontos* **3**: 1–87.

LIMA, G.M. & LUTZ, R.A. 1990. The relationship of larval shell morphology to mode of development in marine prosobranch gastropods. *Journal of the Marine Biological Association, U.K.* **70**: 611–637.

LUQUE, A.A., GEIGER, D.L. & ROLÁN, W. 2011. A revision of the genus *Satondella* Bandel, 1998 (Gastropoda, Scissurellidae). *Molluscan Research* **31** (1): 1–14.

MACANDREW, R. 1870. Report on the testaceous Mollusca obtained during a dredging excursion in the Gulf of Suez in the months of February and March 1869. *Annals and Magazine of Natural History, Series 4* **6**: 429–450.

MACNAE, W. & KALK, M. 1969. *A natural history of Inhaca Island Moçambique*. Revised edition. Johannesburg: Witwatersrand University Press, pp. i–vi, 1–163, pls 1–11.

MACPHERSON, J.H. & GABRIEL, C.J. 1962. *Marine molluscs of Victoria.* National Museum of Victoria, Handbook Nº 2. Melbourne: Melbourne University Press, pp. i–xv, 1–475.

MARSHALL, B.A. 1979. The Trochidae and Turbinidae of the Kermadec Ridge (Mollusca: Gastropoda). *New Zealand Journal of Zooology* **6** (4): 521–552.

———1983. Recent and Tertiary Seguenziidae (Mollusca: Gastropoda) from the New Zealand region. *New Zealand Journal of Zooology* **10**: 235–262.

———1991. Mollusca Gastropoda: Seguenziidae from New Caledonia and the Loyalty Islands. *In*: Crosnier, A. & Bouchet, P., eds, Résultats des Campagnes MUSORSTOM, Vol. 7. *Mémoires du Muséum National d'Histoire Naturelle, Paris* **150**: 41–109.

———1995. Calliostomatidae (Gastropoda: Trochoidea) from New Caledonia, the Loyalty Islands, and the northern Lord Howe Rise. *In*: Bouchet, P., ed., Résultats des Campagnes MUSORSTOM, Vol. 14. *Mémoires du Muséum National d'Histoire Naturelle, Paris* **167**: 381–458.

MARTENS, E. VON. 1880. Mollusken. *In*: Möbius, K. *Beiträge zur Meeresfauna der Insel Mauritius und der Seychellen*. Berlin: Gutmann, pp. 181–352, pls 19–22.

MASTALLER, M. 1979. *Beiträge zur faunistik und ökologie der Mollusken und Echinodermen in der Korallenriffen bei Aqaba, Rotes Meer*. PhD dissertation. Bochum: Ruhr-Universität, pp. 1–344.

MCGHIE, H.A. 2008. Catalogue of type specimens of molluscs in the collection of the Manchester Museum, the University of Manchester, UK. *ZooKeys* **4**: 1–46.

MCLEAN, J.H. 1970. New species of tropical eastern Pacific Gastropoda. *Malacological Review* **2**: 115–130.

———1981. The Galapagos Rift limpet *Neomphalus*: relevance to understanding the evolution of a major Paleozoic–Mesozoic radiation. *Malacologia* **21** (1–2): 291–336.

———1982. Importance of gill structure in trochacean classification. *Western Society of Malacologists, Annual Report* **14**: 11.

———1984. *Agathodonta nortoni*, new species: living member of a Lower Cretaceous trochid genus. *Nautilus* **98** (3): 121–123.

MELVILL, J.C. 1909. Report on the marine Mollusca obtained by Mr J. Stanley Gardiner F.R.S., among the islands of the Indian Ocean in 1905. *Transactions of the Linnean Society of London, Series 2* **13**: 65–138, pl. 5.

———1918. Descriptions of thirty-four new species of marine Mollusca from the Persian Gulf, Gulf of Oman, and Arabian Sea, collected by Mr F.W. Townsend. *Annals and Magazine of Natural History, Series 9* **1**: 137–158.

———1928. The marine Mollusca of the Persian Gulf, Gulf of Oman, and North Arabian Sea, as evidenced mainly through the collections of Captain F.W. Townsend. 1893–1914. – Addenda, corrigenda, and emendanda. *Proceedings of the Malacological Society of London* **18**: 93–117.

Melvill, J.C. & Standen, R. 1895. Notes on a collection of shells from Lifu and Uvea, Loyalty Islands, formed by the Rev. James and Mrs Hadfield, with a list of species. Part 1. *Journal of Conchology* **8**: 84–132.

———1896. Notes on a collection of shells from Lifu and Uvea, Loyalty Islands, formed by the Rev. James and Mrs Hadfield, with a list of species. Part 2. *Journal of Conchology* **8**: 273–315.

———1899. Report on the marine Mollusca obtained during the first expedition of Prof. A.C. Haddon to the Torres Straits, in 1888–89. *Journal of the Linnean Society of London, Zoology* **27**: 150–206.

———1901. The Mollusca of the Persian Gulf, Gulf of Oman and Arabian Sea, as evidenced mainly through the collections of Mr F.W. Townsend, 1893–1900; with descriptions of new species. *Proceedings of the Zoological Society of London* **1901**: 327–460.

Melvill, J.C. & Sykes, E.R. 1897. Notes on a collection of marine shells from the Andaman Islands, with description of new species. *Proceedings of the Malacological Society of London* **2**: 164–172.

Mermod, G. & Binder, E. 1963. Les types de la collection Lamarck au Museum de Geneve. Mollusques vivants. Part 5. *Revue Suisse de Zoologie* **70** (7): 127–172.

Millard, V. 1997. Classification of Mollusca. Cape Town: V. Millard, pp. 1–544.

Moazzo, P.G. 1939. Mollusques testacés marins du Canal de Suez. *Mémoires de l'Institut d'Egypte* **38**: 1–283.

Monterosato, T., M. di. 1884. *Nomenclatura generica e specifca do alcune conchiglie Mediterranee*. Palermo: Virzi, pp. 1–152.

Moolenbeek, R.G. & Faber, M.J. 1989. The genus *Euchelus* (Prosobranchia: Trochidae) in the West Indies. *In*: *Studies in honour of Dr P.W. Hummelinck*. № 123. Amsterdam: Foundation for Scientific Research in Surinam and the Netherlands Antilles, pp. 217–226.

Neubert, E. 1998. Six new species of marine gastropods from the Red Sea and Gulf of Aden. *Fauna of Arabia* **17**: 463–472.

Nevill, G. & Nevill, H. 1869. Descriptions of marine Gastropoda from Ceylon, etc. *Journal of the Asiatic Society of Bengal* **38** (2): 157–164.

Odhner, N.H.J. 1917. Results of Dr E. Mjöberg's Swedish scientific expeditions to Australia 1910–1913. XVII. Mollusca. *Kungliga Svenska Vetenskapsakademiens Handlingar* **52** (16): 1–115, pls 1–3.

Olsson, A.A. 1971. Biological results of the University of Miami deep-sea expeditions. 77. Mollusks from the Gulf of Panama collected by R/V *John Elliott Pillsbury*, 1967. *Bulletin of Marine Science* **21** (1): 35–92.

Orr Maes, V. 1967. The littoral marine mollusks of Cocos-Keeling Islands (Indian Ocean). *Proceedings of the Academy of Natural Sciences, Philadelphia* **119** (4): 93–217, pls 1–26.

Paes da Franca, M. de L. 1960. Sobre uma colecção malacológica recolhida na ilha da Inhaca (Moçambique). Estudos de Biologia Maritima. *Memórias da Junta de Investigações do Ultramar*, *Segunda Série* **15**: 43–102, pls 1–29.

Palazzi, S. & Villari, A. 2001 (2000). Molluschi e Brachiopodi delle grotte sottomarine del Taorminese. *La Conchiglia* **32** (Suppl. 297): 1–56.

Pease, W.H. 1861 (1860). Descriptions of forty-seven new species of shells from the Sandwich Islands, in the collection of Hugh Cuming, Esq. *Proceedings of the Zoological Society of London* **28**: 431–438.

Petit, R.E. 2011. Reprint of Lamarck's "Liste des objets". *Conchologia Ingrata* **3**: 1–18.

Philippi, R.A. 1846–1855. Die Kreiselschnecken oder Trochoideen, *Trochus*. *In*: Martini, F.H.W. & Chemnitz, J.H. *Systematisches Conchylien-Cabinet*. 2nd edition. Küster, H.C. ed., Band 2, Abtheilung 3. Nürnberg: Bauer & Raspe, pp. 1–372, pls 1–49.

———1847. Versuch einer systematischen Eintheilung des Geschlechtes *Trochus*. *Zeitschrift für Malakzoologie* **4**: 17–24.

Piani, P. 1980. Catalogo dei molluschi conchiferi viventi nel Mediterraneo. *Bolletino Malacologico* **16** (5–6): 113–224.

Pilsbry, H.A. 1888. Turbinidae. *In*: Tryon, G.W. *Manual of Conchology*. Series 1. Vol. 10, Part 2. Philadelphia: Academy of Natural Sciences, pp. 161–290, pls 37–64.

———1889–90. Trochidae. *In*: Tryon, G.W. *Manual of Conchology*. Series 1. Vol. 11. Philadelphia: Academy of Natural Sciences, pp. 1–519, pls 1–67. [1–208, pls 1–50, 1889; 209–519, pls 51–67, 1990.]

———1890. Trochidae, new and old. *Proceedings of the Academy of Natural Sciences, Philadelphia* **42**: 343–344.

———1890–91. Stomatellidae, Scissurellidae, Pleurotomariidae, Haliotidae, Scutellinidae, Addisoniidae, Cocculinidae, Fissurellidae. *In*: Tryon, G.W. *Manual of Conchology*. Series 1. Vol. 12. Philadelphia: Academy of Natural Sciences, pp. 1–323, pls 1–64. [1–192, pls 1–45, 1890; 193–323, pls 46–64, 1891.]

———1921 (1920). Marine mollusks of Hawaii XIV–XV. *Proceedings of the Academy of Natural Sciences of Philadelphia* **72** (3): 360–382.

Ponder, W.F. & Stanbury, P.J. 1972. Type specimens in the Macleay Museum, University of Sydney. VI. Molluscs. *Proceedings of the Linnean Society of New South Wales* **97**: 42–55.

Poppe, G.T. & Goto, Y. 1991. *European Seashells. Vol. 1. Polyplacophora, Caudofoveata, Solenogastra, Gastropoda*. Wiesbaden: Christa Hemmen, pp. 1–352.

Poppe, G.T. & Tagaro, S.P. 2008. Chilodontidae. *In*: Poppe, G.T., *Philippine marine molluscs*. Vol. 1. Hackenheim, Germany: ConchBooks, pp. 1–759.

Poppe, G.T., Tagaro, S.P. & Dekker, H. 2006. The Seguenziidae, Chilodontidae, Trochidae, Calliostomatidae and Solariellidae of the Philippine Islands. *Visaya* **Suppl. 2**: 3–228.

Powell, A.W.B. 1979. *New Zealand Mollusca: marine, land and freshwater shells*. Auckland: Collins, pp. i–xiv, 1–500.

Quinn, J.F. 1979. Biological results of the University of Miami deep-sea expeditions. 130. The systematics and zoogeography of the gastropod family Trochidae collected in the Straits of Florida and its approaches. *Malacologia* **19** (1): 1–62.

———1983. A revision of the Seguenziacea Verrill, 1884 (Gastropoda : Prosobranchia). I. Summary and evaluation of the superfamily. *Proceedings of the Biological Society of Washington* **96** (4): 725–757.

Reeve, L. 1857–1858. Descriptions of seven new shells from the collection of the Hon. Sir David Barclay, of Port Louis, Mauritius. *Proceedings of the Zoological Society of London* **25** [1857]: 207–210. [The first part of this paper (pp. 207–208) was published in 1857 and the last part (pp. 209–210) in 1858 fide Duncan (1937)]

Rennie, J.V.L. 1930. New Lamellibranchia and Gastropoda from the Upper Cretaceous of Pondoland (with an appendix on some species from the Cretaceous of Zululand). *Annals of the South African Museum* **28**: 159–260.

Richer de Forges, B. 2010. Majoid crabs from the Mozambique Channel with the description of a new species of *Oxypleurodon* Miers, 1886 (Decapoda, Brachyura). *In*: Fransen, C. *et al*., eds, *Studies on Malacostraca, Lipke Bijdeley Holthuis Memorial Volume*. *Crustaceana Monographs* **14**: 645–653.

Rolán, E. 2005. *Malacological fauna from the Cape Verde archipelago. Part 1, Polyplacophora and Gastropoda*. Hackenheim: ConchBooks, pp. 1–455.

Rusmore-Villaume, M.L. 2008. *Seashells of the Egyptian Red Sea: The illustrated handbook*. Cairo: American University in Cairo Press, pp. i–xii, 1–307.

Sasaki, T. 1998. Comparative anatomy and phylogeny of the Recent Archaeogastropoda (Mollusca: Gastropoda). *University Museum, University of Tokyo, Bulletin* **38**: 1–223.

———2000. Trochidae. Pp. 55–83. *In*: Okutani, T., ed., *Marine mollusks in Japan*. Tokyo: Tokai University Press, pp. i–xlvii, 1–1175.

Scaperrotta, M., Bartolini, S. & Bogi, C. 2009. *Accrescimenti: stadi di accrescimento dei molluschi marini del Mediterraneo*. Vol. 1. Ancona: L'informatore Piceno, pp. 1–168, 121 pls.

Schepman, M.M. 1908. The Prosobranchia of the "Siboga" Expedition. Part 1. Rhipidoglossa and Docoglossa, with an appendix by Prof. R. Bergh. *Siboga Expeditie 1899–1990*. Vol. 49a, Part 1. Leiden: E.J. Brill, pp. 1–107, pls 1–9.

Schwarz, E.L.H. 1910. The Pleistocene deposits of Port Elizabeth. *Transactions of the Geological Society of South Africa* **12**: 112–118.

Sherborn, C.D. & Palmer, T.S. 1899. Dates of Charles d'Orbigny's 'Dictionnaire Universel d'Histoire Naturelle' 1839–1849. *Annals and Magazine of Natural History*, *Series 7* **3**: 350–352.

Shirley, J. 1911. Additions to the marine Mollusca of Queensland. *Proceedings of the Royal Society of Queensland* **23** (1): 93–102.

Smith, E.A. 1876. A list of marine shells, chiefly from the Solomon Islands, with descriptions of several new species. *Journal of the Linnean Society of London, Zoology* **12**: 535–562.

———1897. Notes on some type-specimens in the British Museum. *Proceedings of the Malacological Society of London* **2**: 229–232.

———1903. *In*: Stanley Gardiner, J., ed., *Fauna and geography of the Maldive and Laccadive archipelagoes*. Vol. 2: Marine Mollusca. Cambridge: Cambridge University Press, pp. 589–630, pls 35–36.

———1906. On South African marine Mollusca, with descriptions of new species. *Annals of the Natal Government Museum* **1** (1): 19–71.

Smriglio, C., Mariottini, P. & Gravina, F. 1989. Molluschi del Mar Tirreno centrale: ritrovamento di *Putzeysia wiseri* (Calcara, 1842), *Ischnochiton vanbellei* Kaas, 1985 e *Neopilina zografi* (Dautzenberg & Fischer, 1896). Contributo VI. *Bollettino Malacologico* **25**: 125–132.

Smythe, K.R. 1979. The marine Mollusca of the United Arab Emirates, Arabian Gulf. *Journal of Conchology* **30**: 57–80.

———1982. *Seashells of the Arabian Gulf.* London: George Allen & Unwin, pp. 1–123, pls 1–20.

Solem, A. 1953. Marine and fresh-water mollusks of the Solomon Islands. *Fieldiana: Zoology* **34** (22): 213–227.

———1958. Marine mollusks from Bouganiville and Florida, Solomon Islands. *Fieldiana: Zoology* **39** (20): 213–226.

Souverbie, S.-M. & Montrouzier, X. 1879. Description d'espèces nouvelles de l'Archipel Calédonien. *Journal de Conchyliologie* **27**: 25–34.

Sowerby, G.B. 1874. Monograph of the genus *Stomatella*. *In*: Reeve, L.A. 1843–78. *Conchologica Iconica*, Vol. 19. London: Lovell Reeve.

———1892. *Marine Shells of South Africa*. London: Sowerby, pp. i–iv, 1–89.

———1897. *Appendix to the Marine Shells of South Africa*. London: Sowerby, pp. 1–42.

Spadini, V. 1986. Contributo alla conoscenza dei Trochidae (Gastropoda: Archaeogastropoda) del Senese: Specie nuove o pocco conosciute. *Bolletino Malacologico* **22** (1–4): 85–90.

Spencer, H.G., Willan, R.C., Marshall, B.A. & Murray, T.J. 2002 [updated 2011]. *Checklist of the Recent Mollusca described from the New Zealand Exclusive Economic Zone*. http://www.molluscs.otago.ac.nz/index.html [accessed 17/08/2012].

Spencer, H.G., Marshall, B.A. & Willan, R.C. 2009. Recent Mollusca. *In*: Gordon, D.P., ed., *New Zealand inventory of biodiversity.* 1. Kingdom Animalia: Radiata, Lophotrochozoa, Deuterostomia. Christchurch: Canterbury University Press, pp. 196–219.

Springsteen, F.J. & Leobrera, F.M. 1986. *Shells of the Philippines*. Manila: Carfell Seashell Museum, pp. 1–377.

Sturany, R. 1903. Expedition S.M. Schiff 'Pola' in das Rothe Meer, nördliche und südliche hälfte, 1895/96 und 1897/8. Zoologische Ergebnisse xxiii. Gastropoden des Rothen Meeeres. *Denkschriften der Kaiserlichen Akademie der Wissenschaften, Wien* **74**: 219–283.

Taylor, J.D. & Glover, E.A. 2004. Diversity and distribution of subtidal benthic molluscs from the Dampier Archipelago, Western Australia; results of the 1999 dredging survey (DA2/99). *Records of the Western Australian Museum,* suppl. **66**: 247–291.

Thiele, J. 1917. Marine und litorale Mollusken von Madagascar, den Comoren und Ostafrika (Sammlung Voeltzkow 1903–05). *In*: Voeltzkow, A. Reise in Ostafrika in den Jahre 1903–1904. Wissenschaftliche Ergebnisse. Band III, Systematische Arbeiten, Heft 5. Stuttgart: E. Schweizerbart'sche Verlagsbuchhandlung, pp. 561–564.

———1924. Revision des Systems der Trochacea. *Mitteilungen aus dem Zoologischen Museum in Berlin* **11** (1): 47–74.

———1929. *Handbuch der systematischen Weichtierkunde*. Band. 1, Teil 1. Jena: Fischer, pp. 1–376.

Tomlin, J.R. le B. 1927. Zoological results of the Cambridge Expedition to the Suez Canal, 1924. Report on the Mollusca (Amphineura, Gastropoda, Scaphopoda, Pelecypoda). *Transactions of the Zoological Society of London* **32**: 291–319.

Trew, A. 1987. *James Cosmo Melvill's new molluscan names*. Cardiff: National Museum of Wales, pp. 1–84.

Troschel, F.H. 1879. *Das Gebiss der Schnecken zur Begründung einer natürlichen Classification*. Band 2, Lieferung 6. Berlin: Nicolaische Verlagsbuchhandlung, pp. 217–246, pls xxi–xxiv.

Tsuchida, E. & Ikebe, S. 1990. Some mollusks dredged from the submarine bank Zenisu near the Izu-Shichto Islands. *Nankiseibutu* **32** (2): 59–64.

Tsuchida, E. & Kurozumi, T. 1992. Three trochid gastropods dredged from Kerama Archipelago, Okinawa Prefecture. *Chiribotan* **23** (1): 19–23.

———1996. Noteworthy molluscs dredged by the R/V Tansei-Mariu near Okino-Yama Bank off Boso Peninsula, central Japan. *Journal of the Natural History Museum and Institute, Chiba* **4** (1): 33–49.

Turton, W.H. 1932. *The marine shells of Port Alfred, South Africa*. London: Oxford University Press, pp. i–xvi, 1–331, pls 1–70.

Vaught, K.C. 1989. *A classification of the living Mollusca*. Melbourne, Florida: American Malacologists Inc., pp. i–xii, 1–189.

Verrill, A.E. & Bush, K.J. 1900. Additions to the marine Mollusca of the Bermudas. *Transactions of the Connecticut Academy of Sciences* **10** (2): 513–544.

Viader, R. 1937. Revised catalogue of the testaceous Mollusca of Mauritius and its dependencies. *Mauritius Institute Bulletin* **1** (2): i–xiii, 1–111, plus map.

Vilvens, C. 2001. Description of a new species of *Agathodonta* (Gastropoda: Trochidae: Eucyclinae: Chilodontini) from Indonesia and the Philippine Islands. *Novapex* **2** (2): 57–60.

Vilvens, C. & Héros, V. 2003. Description of *Herpetopoma eboreum* n. sp. (Gastropoda: Trochidae: Eucyclinae: Chilodontini) from New Caledonia. *Novapex* **4** (2–3): 61–65.

———2005. New species and new records of *Danilia* (Gastropoda: Chilodontidae) from the western Pacific. *Novapex* **6** (3): 53–64.

Walsby, J. & Morton, J. 1982. *Marine molluscs. Part 1. Amphineura, Archaeogastropoda and Pulmonata*. (Cape Rodney to Okatari Point marine reserve). Auckland: University of Auckland, Leigh Marine Laboratory, pp. i–iv, 1–89.

Warén, A. 1991. New and little known "skeneimorph" gastropods from the Mediterranean Sea and the adjacent Atlantic Ocean. *Bollettino Malacologico* **27** (10–12): 149–248.

Warén, A., Bengston, S., Goffredi, S.K. & Van Dover, C.L. 2003. A hot-vent gastropod with iron sulfide dermal sclerites. *Science* **302**: 1007.

Warén, A. & Bouchet, P. 1988. A new species of Vanikoridae from the western Mediterranean, with remarks on the northeast Atlantic species of the family. *Bollettino Malacologico* **24** (5–8): 73–100.

———1993. New records, species, genera, and a new family of gastropods from hydrothermal vents and hydrocarbon seeps. *Zoologica Scripta* **22** (1): 1–90.

Wells, F.E. & Slack-Smith, S.M. 1986. Part IV. Molluscs. *In*: Berry, P.F., ed., *Faunal surveys of the Rowley Shoals. Scott Reef and Seringapatam Reef, north-western Australia*. *Records of the Western Australian Museum* **Suppl. 25**: 41–57.

Wenz, W. 1938. Gastropoda. Allgemeiner Teil und Prosobranchia. Prosobranchia 2. *In*: *Handbuch der Paläozoologie*. Band 6, Teil 1. Berlin: Gebrüder Borntraeger, pp. 241–480.

Williams, S.T., Karube, S. & Ozawa, T. 2008. Molecular systematics of Vetigastropoda: Trochidae, Turbinidae and Trochoidea redefined. *Zoologica Scripta* **37**: 483–506.

Williams, S.T., Donald, K.M., Spencer, H.G. & Nakano, T. 2010. Molecular systematics of the marine gastropod families Trochidae and Calliostomatidae (Mollusca: Superfamily Trochoidea). *Molecular Phylogenetics and Evolution* **54**: 783–809.

Wilson, B. 1993. *Australian Marine Shells, Prosobranch Gastropods.* Vol. 1. Kallaroo, W. Australia: Odyssey, pp. 1–408.

Yen, T.-C. 1942. A review of Chinese gastropods in the British Museum. *Proceedings of the Malacological Society of London* **24**: 170–289.

Zuschin, M., Janssen, R. & Baal, C. 2009. Gastropods and their habitats from the northern Red Sea (Egypt: Safaga). Part 1: Patellogastropoda, Vetigastropoda and Cycloneritimorpha. *Annalen des Naturhistorischen Museums in Wien* **11A**: 73–158.

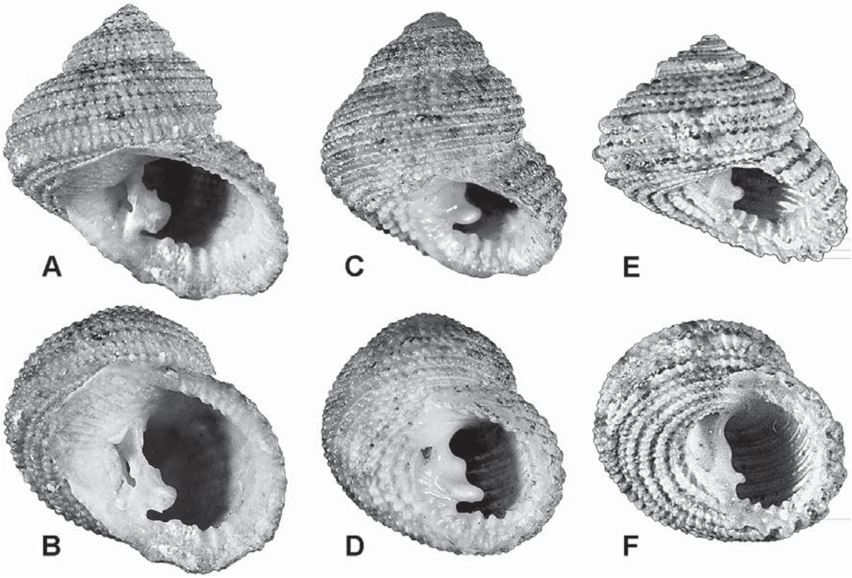

Fig. 68. *Ascetostoma* and *Herpetopoma* species examined for comparison: (A, B) *Euchelus ringens* Schepman, 1908, holotype, Sulu Archipelago, Indonesia, length 7.8 mm, diameter 7.5 mm [not length 7.5 mm, diameter 8.0 mm as given by Schepman] (ZMAN 3.08.092); (C, D) *Clanculus crassilabrum* Sowerby, 1905, one of three syntypes, specimen marked with an X, Sri Lanka, length 7.0 mm, diameter 6.4 mm (NHMUK 1905.10.23.41–43); (E, F) *Monodonta exasperata* A. Adams, 1853, one of four syntypes, Sibonga Is. [Cebu], Philippines, length 6.0 mm, diameter 6.5 mm (NMHUK 196875).

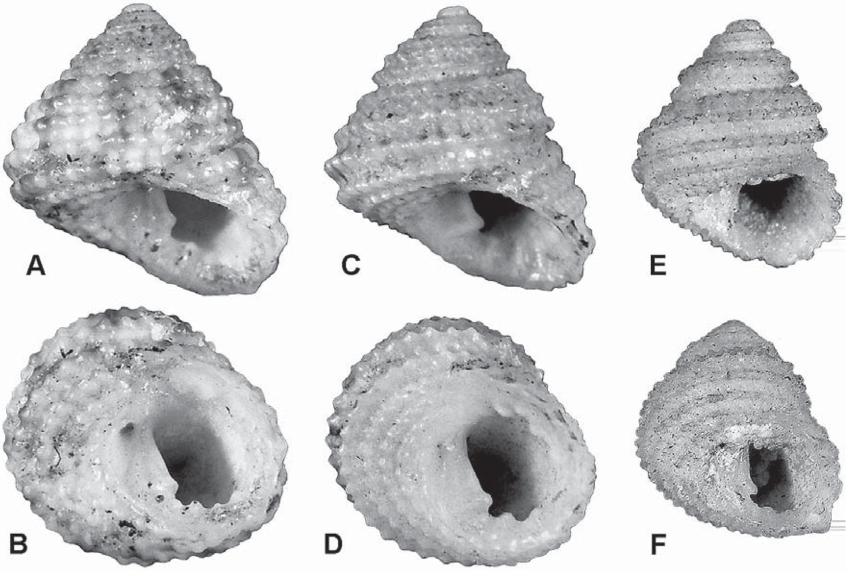

Fig. 69. *Herpetopoma* species examined for comparison: (A, B) *Euchelus corrugatus* Pease, 1861, lectotype (designated Kay 1965: 58), Sandwich Islands [Hawaii], length 3.8 mm, diameter 3.7 mm (NHMUK 1962821); (C, D) *Euchelus fimbriatus* Pease, 1861, holotype, Sandwich Islands [Hawaii], length 3.7 mm, diameter 3.6 mm (NHMUK 1962823); (E, F) *Diloma verruca* Gould, 1861, lectotype (designated Johnson 1964: 167), Coral Seas, China, length 3.2, diameter 2.7 mm (USNM 420).

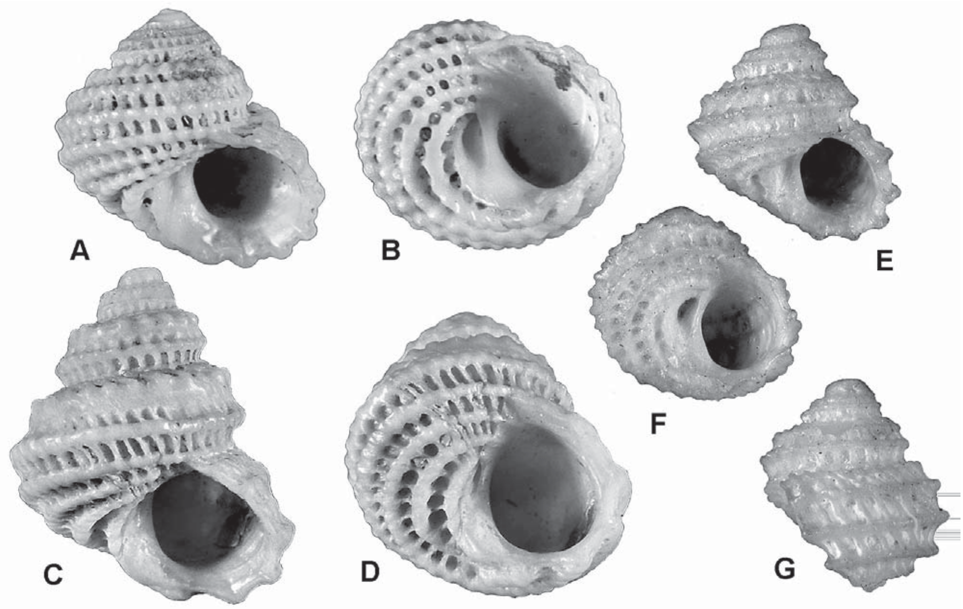

Fig. 70. *Vaceuchelus* species examined for comparison: (A, B) *Euchelus cavernosus* Sowerby, 1905, one of three syntypes, specimen marked with an X, Sri Lanka, length 7.2 mm, diameter 7.0 mm (NHMUK 1905.10.23.6–8); (C, D) *Monodonta clathrata* A. Adams, 1853, one of three syntypes, Bohol, Philippines, length 9.3 mm, diameter 7.8 mm (NHMUK 196868); (E–G) *Euchelus favosus* Melvill & Standen, 1896, figured syntype (here designated as lectotype) length 2.63 mm, diameter 2.60 mm (MMUM EE.3734, McGhie 2008). Not to scale, E–G enlarged relative to A–D.

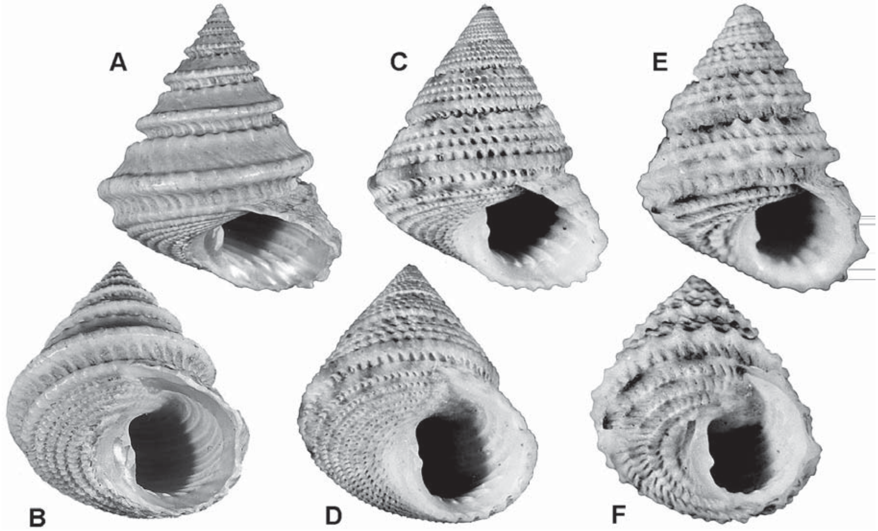

Fig. 71. *Perrinia* species examined for comparison: (A, B) *Turcica chinensis* Sowerby, 1888, syntype, China, length 23.7 mm, diameter 20.1 mm (NHMUK 1889.2.1.5) [one of two original specimens, the other in NMW 1955.158.00996]; *Thalotia maculata* Brazier, 1877, syntype, Darnley Is., Torres Strait, length 12.4 mm, diameter 10.2 mm (AMS–Macleay coll'n) (Ponder & Stanbury 1972); *Calliostoma* (*Perrinia*) *squamocarinatum* Schepman, 1908, syntype, Indonesia, length 6.1 mm, diameter 4.6 mm (ZMAN 3.08.084).

## APPENDIX I

List of ZooBank LSIDs for new genus- and species-group names.

*Ascetostoma* **gen. n.**:
urn:lsid:zoobank.org:act:D0279238-36EB-49AC-B4CD-5086041F3103
*Clypeostoma* **gen. n.**:
urn:lsid:zoobank.org:act:95C03A7B-D895-4D7C-9983-82097380C75A
*Pholidotrope* **gen. n.**:
urn:lsid:zoobank.org:act:87FD552A-37FE-4052-A663-7C33B91B007D
*Clypeostoma reticulatum* **sp. n.**:
urn:lsid:zoobank.org:act:6D8A255D-8E2F-4F03-8226-7676245092A1
*Danilia boucheti* **sp. n.**:
urn:lsid:zoobank.org:act:14A27583-EDBF-4766-9C32-ED12F075681B
*Danilia textilis* **sp. n.**:
urn:lsid:zoobank.org:act:6D182974-6A68-4DB1-BB17-5AAC1D21B465
*Herpetopoma serratocinctum* **sp. n.**:
urn:lsid:zoobank.org:act:17799E7C-23F3-41F1-8E4A-AD77AA34585A
*Herpetopoma stictum* **sp. n.**:
urn:lsid:zoobank.org:act:F0263838-5720-4412-BA93-A789DF67A783
*Pholidotrope gloriosa* **sp. n.**:
urn:lsid:zoobank.org:act:E0B66995-3C24-4266-BDCD-50AF69B92486
*Vaceuchelus cretaceus* **sp. n.**:
urn:lsid:zoobank.org:act:4AA2DB59-7FBA-4D90-9380-20B53F695AD1
*Vaceuchelus jayorum* **sp. n.**:
urn:lsid:zoobank.org:act:6BFF9762-B343-47C4-B0E5-FDD8F530C85A